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THE WILSON ORNITHOLOGICAL SOCIETY
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Named after ALEXANDER WILSON, the first American Ornithologist.

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Plumage classes of Bald Eagles. Both dark and light variations in head plumage of Basic III plumage are illustrated. A known-age Bald Eagle with "pre-definitive" plumage at 7-1/2 and 8-1/2 years of age (bottom right) is also illustrated.
MOLTING SEQUENCE AND AGING OF BALD EAGLES

MARK A. MCCOLLOUGH

Abstract.—Photographs of 135 wintering Bald Eagles (*Haliaeetus leucocephalus*) of known age were examined to document plumage changes. Criteria were established to age ½-year (Juvenile Plumage), 1½-year (Basic I), 2½-year (Basic II), and 3½-year (Basic III) eagles; primarily from head plumage and iris, beak, and cere color. Body plumage varied among individuals and was not a reliable aging characteristic. Definitive plumage was observed on 4 of 17 4½-year (Basic IV) and all 5½-year (Basic V) eagles; however, individuals up to 8½ years-of-age were observed with gray or brown flecking in the head plumage. Photographs of wintering eagles demonstrated that yearly body molt was not complete. Received 24 Apr. 1987, accepted 19 Oct. 1987.

The age at which Bald Eagles attain “adult” plumage (the “definitive plumage” of Palmer 1972) has not been documented clearly. Most authors have described a similar progression of plumage changes that were assumed to be associated with age (Bent 1927; Southern 1964, 1967; Sherrod et al. 1976); however, these descriptions were based on wild birds and study skins of unknown ages. Gerrard et al. (1978), Clark (1983), and Bortolotti (1984) each has named his own general plumage classes of subadult Bald Eagles derived from observations of a small number of known-age wild birds. The purpose of this paper is to document maturation of a large sample of known-age Bald Eagles from Maine and the Canadian Maritime Provinces, describe the characteristics associated with distinct plumages in traditional molt terminology, and provide distinguishing characteristics for aging young eagles in the field.

Methods

From 1976 to 1985, 428 eaglets (>95% of those known produced) were banded in Maine. Known-age banded Bald Eagles from ½ to 8½ years-of-age subsequently were photographed

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while perched on the ground at winter feeding stations in Cobscook and Frenchman Bay during the winters of 1984-85 and 1985-86 (McCollough 1986). The age, identity, and origin of the birds were determined by reading the U.S. Fish and Wildlife Service (FWS) band or supplementary color bands and tags with an 80 x telescope. A series of photographs were taken of each eagle from a blind 20 to 30 m from the eagles using a 600-mm lens. Plumage characteristics and bill, cere, and iris color were recorded from the photographs.

RESULTS

Photographs of 135 known-age eagles were examined. One-hundred-fifteen of the eagles were banded in Maine, 12 in New Brunswick, 5 in Nova Scotia, 3 in Prince Edward Island, and 1 in Ontario. Twenty-three eagles were photographed in both winters.

Six plumages were delineated corresponding to age (terminology after Palmer 1972, Fig. 1). Bald Eagles have one plumage per year, and sexes are similar in feathering. The juvénal plumage is the first covering of true contour feathers acquired in the nest and is succeeded by basic plumages in subsequent years. Basic plumages are acquired by molts that are initiated each spring and completed in the late fall and retained through the following winter (Stalmaster 1987). Two captive Maine eagles initiated molt for basic plumages in April and completed molt in October.

A Bald Eagle in definitive plumage has a white head, tail, and upper and lower tail coverts. Definitive plumage was first observed in eagles 4½ or 5½ years-of-age (Basic IV and V plumage). Flecks of brown or gray were common on the head and tail of birds in definitive plumage. Distinguishing characteristics of plumages are illustrated in the Frontispiece. Characteristics useful in distinguishing age classes are discussed below. Color descriptions are from Palmer (1962:5–6). Sample size following each plumage denotes N_x = total number of birds photographed of the designated age (x) and N_{x+1} = number of these birds photographed again in the following winter.

Juvénal plumage (½ year, N_{0.5} = 36, N_{1.5} = 3).—Juvenal plumage was completed at 11 to 14 weeks of age and was a uniform blackish-brown. By winter, prolonged exposure to the sun had bleached the crown to a buffy-brown contrasting with the blackish-brown auriculars. Buffy-brown to smoke-gray coloration was restricted to the chin of 32 birds but extended down the throat of the other four individuals. A good field characteristic was the uniform blackish-gray beak and cere. The interior of the nares was blackish-gray in 30 birds and light cream in 6 birds. The iris was sepia.

The belly and underparts were generally buffy-brown and variably mottled with dark brown in contrast to the dark brownish-olive breast feathering with faint buffy-brown tips. The basal portions of the nape feathers and contour feathers were whitish (Fig. 2) and gave the appearance of
white mottling in a strong breeze or when the feathers were wet and matted.

All wing coverts were dark brown and sometimes had smoke-gray or buffy-brown margins. Primaries and secondaries were sooty-black. Wing linings and axillars were mottled white. The distal ½ of the rectrices were sooty-black, and the inner vanes were mottled pale gray and sooty-black. This tail pattern resembled that of a juvenile Golden Eagle (*Aquila chrysaetos*); however, the terminal brown band was not as broad and distinct from the sooty-gray proximal ¾ of the rectrices.

The shape of the juvenile contour feathers, wing coverts, nape feathers, and secondaries were noticeably different from the basic plumages (Fig. 2). The juvenile belly and chest feathers and primary, secondary, and middle coverts were longer and had more acute apices. The nape feathers were shorter with a more obtuse apex and became more lanceolate in the basic plumages. Eagles in juvenile plumage had longer secondaries with cuspidate apices that gave a serrated trailing edge to the wing that could be observed in flight.

**Basic I plumage** (1½ year, N
1.5
 = 35, N
2.5
 = 9).—The distinguishing characteristics of this plumage were in the head, beak, cere, and iris. The tan crown was noticeably lighter than in the juvenile plumage and thus sharply contrasted with the blackish-brown auriculurs. The beak was predominantly blackish-gray. Thirty birds had buffy-yellow restricted to the base of the beak next to the cere or at the curve of the beak. All Basic I eagles had a blackish-gray cere with buffy-yellow interior of the nares and the lining of the nares. The iris lightened to buffy-brown in all but one individual which had advanced to light cream typical of 2½-year eagles.
The breast was 70–100% brownish-olive with variable white mottling but was always darker than the belly, giving the appearance of a bib. The belly and underparts were extremely variable and ranged from dark brown to nearly pure white. The extent of brown in the breast and belly depended on the amount of pigmentation of the contour feathers (Fig. 2). A white-mottled inverted triangle was distinct on the mantle of 31 birds. Four birds retained a dark brown mantle.

The middle and greater wing coverts were brownish-olive and variably mottled white. The rectrices were dark-tipped, but somewhat lighter than the juvénal plumage. Primaries, secondaries, and rectrices of Bald Eagles decrease in length with increasing age (Bortolotti 1984). Retention of some of the longer, pointed juvénal secondaries into the Basic I plumage was particularly noticeable in flight and produced an uneven trailing edge to the wing. Also, the outer rectrices of the 1½-year eagles were more rounded instead of blunt-ended as in the juvénal plumage.
Basic II plumage (2½ year, \(N_{2.5} = 29, N_{3.5} = 3\)).—The distinguishing characteristics of this plumage were in the head, beak, cere, and iris. The auriculars retained the appearance of a broad, brown band that extended through the eye but was flecked with light tan or smoke-gray. The crown was a light smoke-gray, and the throat lightened to an extensive white or buffy-white patch that started at the corner of the mouth and extended down the throat to the top of the breast. This coloration gave an “Osprey-like” (*Pandion haliaetus*) appearance to the bird. All 29 birds had a blackish-gray beak variably mottled with buffy-yellow at the base and as a line extending forward from the nares or from the tip of the upper mandible extending backward. The lower mandible was buffy-yellow at the distal end and faded to blackish-gray at the proximal end. The cere was predominantly buffy-yellow mottled with gray. The iris color was light cream, although one bird retained the light buffy-brown typical of 1½-year-old eagles.

At this age, there was a tendency for the belly and chest to be considerably darker, but body plumage varied among individuals. Twenty-seven birds had a predominantly brown belly and chest with little (<30%) white flecking. Three eagles had an entirely brown belly and chest; however, two birds retained a mostly (60%) white belly and white mottled chest. The mantle was darker than Basic I plumage, with a less distinct inverted white triangle. Two birds had a completely brown mantle.

The greater and middle coverts were all brown in 9 eagles, but the others retained some feathers with white mottling from the previous plumage. The distal \(\frac{1}{3}\) of the rectrices was mottled brown and was smoke-gray proximally.

Basic III plumage (3½ year, \(N_{3.5} = 19, N_{4.5} = 3\)).—Molt into Basic III plumage produced a notable change into near-definitive appearance. The head was white with distinct brown flecking on the forehead and crown. Fifteen birds had brown or gray flecking extending posteriorly behind the eye and darker flecking around the eye. The white nape feathers of these birds extended only partially down the neck. Three birds had faint gray flecking through the cheek without an eye stripe and one had a pure white head with faint gray flecking around the eye. Seventeen eagles had a predominantly yellow beak usually with a brown-black line extending forward from the nares and along the crest of the beak. One bird had a pure yellow beak and another retained beak coloration similar to a 2½-year-old eagle. The lower mandible was almost pure yellow. Most Basic III eagles had a yellow cere with some blackish-gray mottling dorsally (15 birds) but the cere was pure yellow in three birds, and one bird’s cere was yellow only at the nares. The iris was pale yellow.

The contour feathers generally were dark brown with buffy margins;
however, five eagles had slight white flecking on the belly and chest and two birds had slight white flecking on the mantle. Wing coverts were dark brown, but three eagles had slight white mottling on the proximal wing coverts. Some white flecking was evident on the wing linings in flight. The rectrices of all birds were mostly white, with brown flecking proximally and heavy brown mottling on the distal margins of the feathers.

**Basic IV plumage (4½ year, \(N_{4,5} = 17, N_{5,5} = 1\)).**—The only consistent field-identification characteristic distinguishing Basic III and IV plumages was the predominantly white rectrices of the Basic IV that lacked a terminal brown stripe. Four birds were in definitive plumage with white heads and tails. The remaining 13 birds had white heads with brown flecking around the eye and on the forehead next to the cere. One eagle had a heavily flecked eye stripe and, apart from the nearly white tail, would easily be confused with a 3½-year eagle. The beak and cere were yellow but usually had light brown at the base that extended forward as a faint line from the nares. The cere was usually all yellow. The iris was pale yellow. The body contour feathering and wing coverts were dark brown with the margins of the feathers tipped with buffy-brown.

**Basic V plumage (5½ year, \(N_{5,6} = 6, N_{6,5} = 1\)).**—All six birds were in definitive feathering and were indistinguishable from the four, 4½-year birds in definitive Basic IV plumage. The beak and cere were generally yellow, but two birds had slight brown mottling at the base of the beak or top of the cere. The head was white with faint gray flecking around the eyes. The iris was pale yellow. The body and wings were dark brown with scalloped buffy feather margins. Rectrices were white with occasional flecks of black or brown.

**Older eagles** (\(N = 13, 4\) photographed in successive plumages).—Twelve birds were in definitive plumage; however, one eagle photographed at 7½ and 8½ years-of-age had extensive gray flecking around the eyes, auriculars, and forehead (see Frontispiece). In 1984, 6½-year eagle was photographed with similar markings, but had molted into a pure white head plumage when photographed in 1985 at 7½ years-of-age.

**DISCUSSION**

In all 24 instances when an individual eagle was photographed in two successive winters, the plumage conformed to the six plumages described. This supports the interpretation that changes in plumage and in color of the beak, cere, and iris are age-related and are not the result of random variation among subadults. In addition, 108 banded eagles were observed, but not photographed, during two to four successive winters at the feeding stations. The observed plumage and color changes of these also followed the sequence described. The key field identification criteria for each plumage are summarized in Table 1.


**Table 1**

A Key to Field Identification of Bald Eagle Plumages.

1. Head and tail white or mottled white. Iris pale yellow. Beak and cere >70% yellow ................................................................. 4  
1. Head brown or tan, beak and cere blackish-gray or <30% yellow. Iris brown or ochre  
2. Beak and cere entirely blackish-gray, iris sepia, no inverted white triangle on mantle ............................................. Juvenal ½-year-old  
2. Beak and cere blackish-gray mottled with buffy-yellow  
3. Iris buffy-brown, buffy-yellow mottling restricted to nares and base of the beak near gape ............................................. Basic I 1½-year-old  
3. Iris pale ochre (light cream), cere and beak mottled buffy-yellow throughout ................................................................. Basic II 2½-year-old  
4. Heavy brown mottling at distal margin of rectrices. Usually extensive gray or brown flecking in auriculurs, forehead, and crown. Often white flecking on wing linings, belly, and chest .................................................... Basic III 3½-year-old  
4. Tail white. Some birds with occasional brown flecks in tail or head ................................................................. Basic IV or Definitive  

(Basic IV: About 75% of birds retain some gray flecking around eye and on forehead next to cere. Remainder are definitive. Definitive: White head and tail, yellow beak and cere. Many birds retain brown flecks on rectrices and nape feathers.)

Southern (1967) described seven plumages of Bald Eagles based on study skins of unknown age birds thought to represent six or seven age classes. Appropriate ages could be assigned to Southern’s seven plumage categories by using Table 1.

Juvenal plumaged eagles (½ year old) closely resembled Southern’s plumages A and B, although there is no evidence of a late-winter molt during the first winter as suggested by Southern. Basic I plumaged eagles matched Southern’s B/C and C plumages. Basic II plumaged eagles corresponded with C/D and D plumages. Near-definitive plumage (Basic III plumage) was equivalent to Southern’s E and possibly F classes. Basic IV plumaged eagles corresponded with much of Southern’s description of plumage F, except for the presence of white on the mantle and up to 60% brown mottling on the tail. Some Basic III specimens examined by Southern were likely included with the Basic IV eagles in plumage F. Adult definitive plumage of Basic V was similar to Southern’s plumage class G.

There has been considerable confusion in field studies attempting to assign Bald Eagles to age classes based on plumage characteristics. Juvenal, Basic I, and Basic II plumages have been particularly difficult to differentiate because of the similarity in body feathering, and, traditionally, they have been combined into one or two plumage classes (e.g., Sherrod
et al. 1976, Bortolotti and Honeyman 1983). The amount of buffy or white mottling on the belly and chest is variable among individuals, and the best field characters for aging young eagles seems to be in the head plumage, and the color of the beak, cere, and iris. Both the 1½- and 2½-year-old eagles have an “osprey-like” head although this characteristic is more distinct in 2½-year-old birds. The lighter cap and throat of 2½-year-old eagles combined with the light cream iris and extent of yellow in the cere and beak allows correct separation of these age groups. The distinct predefinitive plumage of 3½-year-old eagles allowed consistent classification of this age group.

Definitive plumage was observed in 4½- and 5½-year-old birds (Basic IV and V plumages), which would cause difficulty in correct classification of these age groups. In general, 4½-year-old eagles had more brown flecking around the eye and on the forehead and more brown in the cere and beak than 5½-year-old eagles; however, brown or gray flecking on the forehead or cheek was retained by some birds at least 8½ years-old or longer which created further difficulty in correctly aging older birds.

Attainment of definitive plumage is not synonymous with sexual maturity. A 3-year-old Bald Eagle nested successfully in predefinitive plumage in Tennessee (D. A. Hammer, pers. comm.). There is evidence, however, that some birds do not successfully raise young until 6 or 7 years old (Gerrard, unpubl. data).

There are few data available to compare geographic variability in the molt sequence of Bald Eagles. Other known-age eagles from Nova Scotia (N = 11), Prince Edward Island (N = 4), Ontario (N = 2), Saskatchewan (N = 1), Michigan (N = 1), and South Carolina (N = 1) were observed during this study and could be assigned to the appropriate plumage classes using the aforementioned criteria. Descriptions of marked known-age eagles observed in Saskatchewan (Gerrard et al. 1978, Bortolotti and Honeyman 1983) and Chesapeake Bay (Clark 1983) also followed a similar pattern of plumage replacement. Saskatchewan eagles showed a similar molt sequence to that observed in Maine. Clark’s (1983:823) description of molt sequence was similar, but he referred to the “white belly” plumage being “completed the end of the first year of age,” although it seems from his description of plumage that second-year was intended. Confusion in several accounts occurred by interchanging the terms “x year old” and “xth year.” For example, an eagle in its first year has not had its “first birthday” and is still in juvenile plumage. Use of the molt terminology in Fig. 1 should prevent such errors.

Early descriptions of plumage changes in Bald Eagles were from observations of captive eagles. An eagle taken in Michigan (Wilson 1922) exhibited a molt sequence identical to that described in this paper. Near-
definitive appearance was acquired with the completion of molt into the Basic IV plumage at 4 years-old. Injury and nutritional deficiencies in captive birds are known to interrupt normal molt sequences (Payne in Palmer 1972). A captive Bald Eagle in Maine delayed pre-basic molt after a gunshot wound and remained a year behind the appearance of wild birds of the same age. Jollie (1947) noted the same tendency in a captive Golden Eagle and suggested that captive birds may take longer to attain definitive plumage than do wild birds.

Molt in northern Bald Eagles seems to be limited to about 6 months in the late spring, summer, and early fall, but it may be initiated earlier (November or December) in southern birds. There was no evidence of active molt or cast feathers in the winter at any of the feeding sites in Maine. It is likely that yearly body molt is not complete, in that some feathers are retained from one year to the next. Jollie (1947) documented that two molts were needed to renew the body plumage of a captive Golden Eagle. Retention of contour feathers would explain the white mottling in the belly, chest, and mantle in Basic III and IV plumages. Incomplete yearly molt of the nape feathers may explain the retention of brown or gray flecking in the otherwise white head of eagles in Basic IV and V plumages. Gray or brown flecking was observed in the nape feathers, rectrices, and tail coverts of most Bald Eagles in definitive plumage. The pattern of flecking may be consistent in consecutive molts in definitive plumage (Bortolotti and Honeyman 1983).

Primaries and secondaries also may be retained for 2 to 3 years. The closely related White-tailed Sea Eagle (Haliaeetus albicilla) loses 3 or 4 primaries and 6 or 7 secondaries during each annual molt (Forsman 1981). Some greater and lesser wing coverts are not molted yearly and are retained from one plumage to the next. For Bald Eagles, usually all 12 rectrices are molted randomly (Bortolotti and Honeyman 1983), although a few 4½- and 5½-year-old eagles photographed in Maine retained a mottled brown rectrix from the previous plumage. White-tailed Sea Eagles have a tendency for the innermost pair of rectrices to be shed first, followed by the outermost 2 pairs (Love 1983).

Because many of the better distinguishing characteristics for determining most age groups are in the beak, cere, and iris coloration, care should be taken in aging museum specimens. Fading and discoloration of the beak and cere and written descriptions of iris color may be misleading.

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LITERATURE CITED


COLOR PLATE

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CROP MILK AND CLUTCH SIZE IN MOURNING DOVES

DAVID E. BLOCKSTEIN

ABSTRACT.—Doves are unique among birds in producing crop milk and in having a determinate clutch size of 1–2 eggs. In North Dakota, 97.2% of 1203 Mourning Dove (Zenaida macroura) nests had 2 eggs. Clutches of 3 (N = 24) and 4 (N = 4) eggs probably were laid by more than one female per nest. Experimental additions of a second egg to incomplete clutches and removals of the second egg from recently completed clutches verified that Mourning Doves are determinate layers. To examine the role of crop-milk production as a factor that limits clutch size, a third nestling was added to nests of Mourning Doves during (early addition: 3-E) and after (late addition: 3-L) the period of complete dependence on crop milk. All three young fledged at 31% (3-E) and 42% (3-L) of these nests. Growth rates were significantly reduced for 3-E nestlings relative to normal broods of 2; growth rates of 3-L broods were intermediate. Crop-milk production is apparently an important reason why the clutch size of doves (Columbidae) is not more than two eggs. Received 7 Oct. 1987, accepted 19 Aug. 1988.

The most accepted hypothesis for the evolution of clutch size in nidicolous birds states that the modal clutch size corresponds to the maximum number of young that can, on the average, be fed and raised (Lack 1947). An offshoot of this hypothesis may explain the evolution of clutch size in the Columbiformes, a group with little or no intraspecific variation in clutch size. With the exception of Apterygiformes, Columbiformes are the only land birds in which no species has a typical clutch size of more than two eggs. With their rapid growth rates (Vandeputte-Poma 1980), columbids are a conspicuous exception to the usual avian pattern of slow growth with small clutches (Ricklefs 1968). Rapid growth appears to be facilitated by the capacity, unique among birds, to produce crop milk which is the exclusive food of 1–4-day-old nestlings (Mirarchi and Scanlon 1980, Vandeputte-Poma 1980).

Crop milk is produced by both males and females. It consists of desquamated cells sloughed off from the germinal epithelium of the crop (Beams and Meyer 1931, Patel 1936). Crop milk is rich in proteins and lipids and contains an uncharacterized growth-promoting factor (perhaps digestive microflora) (Pace et al. 1952, Hedge 1972).

The two exceptional features of columbid reproductive biology, a clutch size of one or two (depending upon the species) and crop-milk production

probably are related. Lack (1947:310) noted that the Columbidae are an exception to the usual pattern of seasonal variation in clutch size and that crop-milk production would not be expected to vary with daylength. He regarded crop milk as one of “a number of physiological adaptations [that] are associated with raising a family of two” and that have resulted in reduced plasticity of clutch size (Lack 1948:32).

I tested the crop-milk limitation hypothesis in a wild population of Mourning Doves. I created broods of three, both early in the nestling period when the young are dependent on crop milk and later in the period when the young are fed seeds and crop milk. Three predictions follow from the hypothesis: first, few, if any, broods will produce three fledglings. Second, nestlings in broods of three will have reduced growth rates relative to normal broods of two. Finally, broods of three created after the nestlings have passed the period of total dependency on crop milk will have higher survival and growth rates than broods of three created when the nestlings are wholly dependent on crop milk. An alternative hypothesis is that clutch size is limited by the number of eggs that can be incubated. I manipulated clutch size of Mourning Doves to test this hypothesis.

METHODS

I studied Mourning Doves at the J. Clark Salyer National Wildlife Refuge, northern McHenry County, North Dakota, from April through September 1981–83 and in June and July 1984. Two primary study areas were used: a series of three 4.5-ha planted shelterbelts and 20 ha at the refuge headquarters 2 km southeast of the shelterbelts. In 1981, nest searches were also conducted at nearby farm woodlots. Detailed descriptions of the study area are in Blockstein (1986). All trees and shrubs in each shelterbelt were searched weekly for nests. Eggs were aged by candling (Hanson and Kossack 1957). Unless observed, laying and hatching dates were determined by backdating; hatch day was designated day 0. I visited and checked nests every seven days before hatching, within two days after the projected hatch date, and then every three days until fledging.

To test the assumption that Mourning Doves have a determinate clutch size of two, I added a second egg to 23 nests with an incomplete clutch of one fresh egg (<24 h old). The added egg either came from an abandoned nest or was removed temporarily from another active nest. I checked the nest at least 24 h later to determine whether or not the presence of two eggs had inhibited the female from laying a second egg. I removed the “added” egg at this time.

To test whether or not Mourning Doves are able to replace an egg within a clutch, at 30 nests I removed the second egg of the clutch within 10 h after it was laid. These nests were checked again at least 24 h later to see if an additional egg was laid. Most nests were checked again within 7 days. To test the hypothesis that clutch size is limited by the doves’ ability to incubate three eggs, at 33 nests I added a third egg within 48 h of clutch completion. The additional egg was always the same age as one of the original eggs in the nest. I checked these nests shortly after the calculated hatching date to see if all had hatched.

To test the crop-milk limitation hypothesis, I added a third nestling at 68 nests. Each nestling was within one day of age and similar in size to the original nestlings. Whenever possible, I altered the brood so that there were two younger nestlings and one oldernestling.
This minimized the cases where the smaller nestling was at an immediate competitive disadvantage. Sometimes one nestling was removed from the nest and two transfers added to make a brood of three. The transfers were not always younger than the original nestlings. Generally, only one pair of broods was available for transfer on any day, but, if several choices were available, I tried to create the best match among similar-sized nestlings. To minimize the chances of nestlings falling from the nest, I placed the extra nestlings only in large nests or in nests in wire baskets, which were used for nesting by a few pairs. Although Mourning Doves that hatch early in the nesting season may gain weight more slowly than later nestlings (Holcomb and Jaeger 1978), less than 10% of the transfers were made during the first month of the season.

I divided the sample of experimentally enlarged broods according to nestling age: (1) early addition (3-E): all nestlings ≤4 days old (N = 49) and (2) late addition (3-L): at least one nestling 5–8 days old (N = 19). Broods of three created by clutch manipulation or addition of pipping eggs and nests with an unmanipulated clutch size of three were included in the 3-E group for analysis of growth rate. Nests that I found containing three eggs were analyzed separately for nest success. These large clutches probably resulted from laying by more than one female (Weeks 1980, this study).

Every 3 days I measured the nestlings in experimental (both additions and removals) and unmanipulated broods of one, two, or three young. Broods of one created by removal and broods in nests where only one nestling hatched did not differ in growth rates and were combined for comparison with other brood sizes. Nestlings from normal 2-young broods were considered controls. I made 14 exchanges between same-age broods of two young, but discontinued this because there was no evidence that adults distinguished between transfers and their own young.

I weighed nestlings to the nearest 0.5 g using Pesola scales. Total length, natural (unflattened) wing chord, tail length, and length of the sixth primary were measured to the nearest mm. The proportion of seeds and milk in the crop was estimated by external massage. I used plumage development, opening of the eyes, and remission of the egg tooth as aging criteria (Hanson and Kossack 1957). Nestlings were marked on the feet with a colored marking pen and later banded for individual identification. To avoid inducing premature fledging, I usually measured nestlings only through 10 days of age.

I used a jackknife procedure to create Richards growth curves (Richards 1959) as modified by Bradley et al. (1984). This technique combines repeated measurements of individual nestlings with cross-sectional (grouped) data on age-classes to create a composite curve for each brood-size treatment group. Because the nestlings added late in the nesting cycle were not measured separately on days 0–4 when they were in broods of two, measurements from control broods of two on days 0–4 were combined with measurements from 3-L broods, which started at day 5. This data set represented the 3-L group for analysis of growth rates. Growth for each treatment group is expressed as the sum of a smooth growth curve plus its residuals. The curve represents the major trend. The residuals incorporate short-term deviations from this trend. The curve was calculated as:

\[
W = A(1 + (M - 1)e^{-K(T-J)})^{1/(1-M)}
\]  \hspace{1cm} (1)

Where:

- \(T\) = time of measurement (age of the organism)
- \(W\) = size of the organism at time \(T\)
- \(A\) = asymptotic size after growth is completed
- \(K\) = a growth constant (describes the rate of growth)
- \(J\) = time to reach the inflection point in the curve
- \(M\) = a shape constant (describes the shape of the curve)
The parameters A, K, J, and M are used to fit the curve and to calculate summary statistics with 95% confidence intervals for each treatment group (Bradley et al. 1984). The statistics are asymptotic size (A), weighted mean growth rate or slope at inflection (R), percentage of asymptotic size at inflection (P), and time to grow from 10–90% of asymptotic size (G).

Following Bradley et al. (1984), these statistics are calculated as follows:

\[
\begin{align*}
A & = \text{the raw parameter value from the curve} \\
R & = K/M \\
P & = M^{1/(1-M)} \\
G & = \ln((1 - 0.10^{1-M})/(1 - 0.90^{1-M}))/K
\end{align*}
\]

Mourning Doves fledge at about half of adult size (McClure 1943) and growth curves have not leveled off by the time of fledging at day 14, so measurements of known-age fledglings from broods of two were included in the data set (sensu Bradley et al. 1984). These individuals were captured in nests and walk-in funnel traps (Reeves et al. 1968, Blockstein 1986), and most were 20–34 days old when measured. Because there were few recaptures of individuals from broods of one and three (due to small sample sizes), I artificially fixed the asymptotes for these brood sizes at the values determined empirically for broods of two: weight—80 g, total length—175 mm, wing chord—135 mm, tail—100 mm, and sixth primary—73 mm. Thus all curves were forced through the same asymptotes. Because the age at which this value is attained was not fixed, all statistics other than A are valid. This technique is conservative towards differences between groups because it assumes all nestlings will reach the same asymptotic value and compares the time it will take to reach that point.

The confidence intervals for the growth statistics are asymmetrical, and, it is not always possible to compare treatments by looking for means that are outside the 95% confidence interval of the other group. “Borderline” cases may exist, such as when the mean of the group with the larger variance is outside the confidence interval of the group with the smaller variance, but not vice versa. To compare treatment groups for these cases, I used a multiple comparison technique (Gabriel 1978) modified by Hochberg et al. (1982), which is similar to comparing multiple treatment means in an unbalanced one-way ANOVA. I calculated “uncertainty intervals” around the sample means as \pm \frac{1}{4} of the width of the 95% confidence intervals (David Bradley pers. comm.). This allows a graphical examination of the growth statistics and provides an approximate test at \( P = 0.05 \). Any pair of sample means is significantly different if their uncertainty intervals do not overlap (Hochberg et al. 1982). Significance levels for all tests are set at \( P = 0.05 \) unless stated otherwise.

RESULTS

Clutch size and success of supernormal clutches.—Of 1203 nests where clutch size was known, 1169 (97.2%) had 2 eggs. Six (0.5%) 1-egg clutches may have been incomplete or the result of partial predation. Nests that contained 3 eggs (\( N = 24, \) 2.0%) and 4 eggs (\( N = 4, \) 0.3%) probably resulted from more than one female’s laying in a nest (see below; Weeks 1980). Four additional 3-egg nests were found on farm woodlots outside the main study area.

All eggs were laid within 4 days at each of two 4-egg nests. At one of these, all eggs pipped within 4 days, but only three hatched. At the other, three hatched within 2 days, but the fourth was infertile. Two nestlings fledged from each of these nests. At another nest with 4 eggs, there were
2 weeks between two 2-egg "clutches." Two eggs hatched on the same day; another was developing when collected, and the fourth was infertile. At the fourth nest, all 4 eggs were present when the nest was found, but none showed any development 12 days later.

Of 3-egg nests where the laying interval was known (N = 20), all eggs were laid within 3 days at 6 nests (30%), 4–5 days at 6 nests (30%), 6–8 days at 4 nests (20%), and 9–12 days at 4 nests (20%). All three eggs hatched at 9 of 18 nests where at least one egg hatched. Two eggs hatched, and the third was near hatching at three other nests when they failed. Three nests had at least one infertile egg. At two nests, the first two eggs hatched, but the third, which was laid much later, never hatched. At one nest, one egg hatched, one fell out of the nest, and the third developed almost to term, but never hatched.

Three young fledged at only 1 of 9 nests where three eggs hatched, although another had nestlings aged 5, 6, and 7 days when last visited. Two young fledged at two nests where the youngest nestling died. One nest was not checked again. No young fledged from the other five nests because of nestling death and predation.

**Nestling diet.**—Crops of nestlings contained almost no seeds during days 0–3, an increasing proportion of seeds from days 4–8, and almost entirely seeds beginning at day 8.

**Determinate laying.**.—The female laid her own second egg at 19 of 23 nests where a second egg had been added to an incomplete clutch. One nest was abandoned immediately, and at one the female probably did not lay a second egg. Two nests were destroyed by predators.

No replacement eggs were laid at nests where the second egg had been removed. Fifteen pairs continued to incubate the remaining egg although two nests were abandoned after the second nest check. One nest was abandoned immediately and predation occurred at 14 other nests before they were checked.

**Incubation limitation.**.—Eggs hatched at 17 nests where a third egg had been added: all three at 9 nests, two at 5 nests, and one or two at 3 others. Causes of hatching failure included: failure to begin development (3 eggs), embryo death (2 eggs), and death during pipping (1 egg). At least half of the eggs that did not hatch were the eggs that had been transferred. Seven clutches were abandoned and predators destroyed seven others.

**Fledging success.**.—All three young fledged at 31% of the early additions and 42% of the late additions ($\chi^2 = 0.57, P > 0.25$, Table 1). Apart from predation, all the young died at 8 (16%) 3-E nests, including two where the female abandoned, but at no (0%) 3-L nests. One or two nestlings died at 17 (35%) 3-E and at 7 (35%) 3-L nests. Both young fledged at about 60% of the control (two nestling) nests.
Table 1

OUTCOME OF ADDING A THIRD NESTLING TO BROODS OF TWO

<table>
<thead>
<tr>
<th>Outcome</th>
<th>3-E* No. nests (%)</th>
<th>3-L* No. nests (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Three fledged</td>
<td>15 (31)</td>
<td>8 (42)</td>
</tr>
<tr>
<td>Two fledged</td>
<td>11 (22)</td>
<td>3 (16)</td>
</tr>
<tr>
<td>One fledged</td>
<td>4 (8)</td>
<td>3 (16)</td>
</tr>
<tr>
<td>All died in nest</td>
<td>8 (16)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Some died in nest</td>
<td></td>
<td></td>
</tr>
<tr>
<td>before predation</td>
<td>4 (8)</td>
<td>2 (11)</td>
</tr>
<tr>
<td>Predation on all</td>
<td>7 (14)</td>
<td>3 (16)</td>
</tr>
<tr>
<td>Total nests</td>
<td>49</td>
<td>19</td>
</tr>
</tbody>
</table>

* Third nestling added on days 0–4.
* Third nestling added on days 5–8.

Nests where a third nestling was added produced a greater average number of fledglings than did broods of two, both for successful nests ($\bar{x} = 2.36$ and 1.73 for broods of three and two, respectively, $t_{36} = 3.37$, $P = 0.002$) and for all nests ($\bar{x} = 1.71$ and 1.08, $t_{38} = 3.18$, $P = 0.003$). Early and late additions did not differ significantly in the average number of fledglings either for successful nests ($\bar{x} = 2.37$ and 2.36 for 3-E and 3-L, respectively, $t_{13} = 0.04$, $P > 0.50$) or for all nests ($\bar{x} = 1.45$ and 1.74, $t_{15} = 0.83$, $P > 0.40$).

The relative ages of nestlings within the enlarged broods affected the prospects for survival. Where there was one older nestling and two same-age younger nestlings, all three fledged at 13 of 21 nests, but where there were two same-age older nestlings and one nestling a day younger than the others, all three fledged at only 1 of 7 nests ($\chi^2 = 4.76$, $0.025 < P < 0.05$). Individuals that died, either from starvation or falling out of the nest, included 13 that had originally been the youngest or smallest, six that had been the oldest or largest, and nine that were intermediate.

**Nestling weight.** — Nine and 10-day-old nestlings in broods of two ($\bar{x} = 61$ g) were significantly heavier than 3-E nestlings ($\bar{x} = 48$ g) even when the effect of differing amounts of food in the crop was removed by covariance analysis ($F_{1,46} = 11.02$, $P = 0.002$). Nine and 10-day-old nestlings in 3-E and 3-L broods did not differ in weight or in any linear measurement. Seven (17%) 3-E nestlings weighed <35 g and were considered “runts.” Runts occurred in 47% of the 3-E broods that fledged three young ($N = 15$).

**Growth rates.** — Richards growth curves were generally lower for 3-E broods than for broods of one and two, which were very similar (Figs. 1, 2). Broods of 3-L were intermediate, but closer to controls. Curve shape
varied considerably, depending upon the feature measured. Broods of 3-E showed the smallest values of M (shape) and K (growth constant) for all measurements except total length. Broods of 3-L had the smallest values of M and K for total length and had lower values of K than broods of two for all measurements. This represents an "incretion" of the growth curve shape as the shape shifted to lower values with presumably greater stress (Brisbin et al. 1986).

Weighted mean growth rate (R) and growth period (G) were derived from the growth constant in different ways. The percentage of asymptote at inflection (P) depends entirely on the shape of the curve. Each is a measure of growth speed.

One-nestling broods did not differ from broods of two in growth statistics for any linear measurement (Fig. 3), but growth rate for weight was marginally lower (P = 0.05) than for controls (Fig. 3).

For weight, early additions (3-E) differed from controls for growth pe-
Fig. 2. Richards growth curves of weight for broods of different sizes. Curves taken from Figure 1.

period and marginally for percentage of asymptote at inflection ($P = 0.05$), but not for growth rate. In all cases, young in the 3-E broods grew more slowly (Fig. 3). That 3-E broods differed from controls in growth period but not in growth rate may have resulted because growth period is more sensitive to changes in shape. The shape parameter of the controls (0.965) was 40% greater than that of 3-E broods (0.691), an indication that weight of 3-E broods began to level off sooner. Weights of late addition broods (3-L) showed the greatest variance and did not differ from controls in any growth statistic. The only difference in weight between 3-E and 3-L broods was that 3-L had a shorter growth period.

For linear measurements, 3-E broods had slower growth rate and longer growth period than controls for three of four features (all but sixth primary) (Fig. 3). There were no differences in percentage of asymptote at inflection. Broods of 3-L had slower growth rate and longer growth period than controls for two measurements (Fig. 3). Early (3-E) and late (3-L) additions
differed only in growth rate and asymptotic percentage for total length. The 3-L group, although intermediate between the 3-E and controls, was usually more similar to the controls.

In broods of two, position within the brood did not affect growth. Older and younger nestlings differed in only one growth statistic (growth period for wing chord); in this case, the younger nestlings grew faster.

There was considerable variation in growth among the 3-E nestlings. There was a preponderance of "runts," some of which died before reaching fledging age. Other 3-E nestlings grew at rates comparable to controls. The oldest and middle nestlings did not differ in growth rates for weight. Nestlings that were originally the youngest or smallest had a slower growth rate but a higher percentage of asymptote at inflection. The growth period did not differ according to position within the brood (Fig. 4). Thus, the effect of position on growth rates was equivocal for 3-E broods.

**DISCUSSION**

**Determinate laying.**—Clutch manipulations verified that Mourning Doves are determinate layers with a clutch size of two. Addition of an egg did not prevent females from laying a second egg nor did removal of the second egg induce the laying of a third egg. These results coupled with the wide variation in laying dates within supernormal "clutches" support Weeks' (1980) hypothesis that enlarged clutches resulted from more than one female's laying eggs in a nest.

Invariance of clutch size in Mourning Doves and other columbids implies strong selection against a 3-egg clutch. This could result from an inability to incubate three eggs or an inability to feed adequately and fledge three young.

**Incubation limitation.**—I found that Mourning Doves can incubate 3-egg clutches, both manipulated and unmanipulated, although hatching success was reduced. However, hatching success at unmanipulated nests with three eggs is expected to be less than 100% because the third egg often is laid several days after incubation begins. In my experiments, chilling of the transferred eggs may have reduced hatching success. In studies where several 3-egg nests were found (not including nests where no eggs hatched), all three eggs hatched at 25–67% of the nests (range of N = 8–22) (McClure 1943, Quay 1951, Klataske 1966, Olson 1980). Burley (1980) found that Rock Doves (*Columba livia*) nests given a third egg had identical hatching success to 2-egg nests. Westmoreland and Best (1987) manipulated clutch size in Mourning Doves and also concluded that incubation ability is unimportant as an ultimate factor limiting clutch size to two in columbids.
Fledging success. — Three young fledged from only one unmanipulated nest in this study. At least one nestling (usually the youngest) died at 6 nests where three eggs hatched. McClure (1943) reported three fledglings at 8 of 15 nests where three eggs hatched. According to the crop-milk limitation hypothesis, the poor fledging success of supernormal broods is due to the parents' inability to produce adequate crop milk for three nestlings. My experiments tested the predictions of this hypothesis: that fledging success would be very low in broods of three, that growth rates would be reduced in broods of three, and that these effects would be more pronounced in broods of three created when the young are crop-milk dependent (3-E) than in broods of three created when the young are being weaned from crop milk (3-L).

Fledging success of experimental broods, although lower than control broods, was better than expected, with three fledglings at 38% of the
experimental broods. Broods of three produced more fledglings per nest than did broods of two. Although death of all three nestlings occurred only among 3-E broods, 3-E and 3-L broods did not differ in fledging success. Wood Pigeons (Columba palumbus) (Murton et al. 1974) and Rock Doves in an outdoor aviary (Burley 1980), but not Mourning Doves (Westmoreland and Best 1987), also showed reduced fledging success in experimental broods of three compared with controls.

Growth rates.—Survival to fledging may not be a sufficient criterion for evaluating the success of nests with three young. Young fledged at abnormally small size may be less likely to survive to reproductive age. In Wood Pigeons, experimental broods of three fledged at lower weights and had lower fledging success compared with broods of one or two; they also appeared to suffer increased post-fledging mortality (P = 0.10) (Murton et al. 1974). Based on these results, Murton et al. (1974) concluded that pairs could, on the average, leave more progeny by producing two nestlings than three.

Reduced growth rates in crop-milk-dependent young have also been found in artificially enlarged broods of Mourning Doves (Westmoreland and Best 1987), Wood Pigeons (Murton et al. 1974), and Rock Doves (Burley 1980). The mean brood weight at 9 and 10 days was only 18% higher for 3-E broods than for controls as opposed to the 50% increase expected if the adults were able to provide enough food for broods of three. Even if adults could gather extra seeds to feed older nestlings in an expanded brood, they are unlikely to be able to increase their production of crop milk. The first few days of life, during which the young are fed only crop milk and have among the fastest growth rates of any bird (Riddle 1928, Riddle et al. 1932) are apparently critical to reaching normal size (Murton et al. 1974, Burley 1980, Westmoreland and Best 1987). The same conclusion can be drawn from experiments showing that a single parent is unable to raise two nestlings until after the crop-milk stage (Haas 1980).

Crop-milk limitation.—The significantly reduced growth in 3-E broods supports the crop-milk limitation hypothesis. The nonsignificant tendency toward reduced growth in the 3-L group is suggestive that there may also be difficulty in providing food for three nestlings beyond the crop-milk stage (cf. Westmoreland and Best 1987). Thus it is unlikely that parental feedings of seeds can compensate for the stunting caused by crop-milk limitation. All brood-size experiments in columbids show that limits on crop-milk production cause undersize fledglings (Murton et al. 1974, Burley 1980, Westmoreland and Best 1987, this study), which may take longer to fledge and thus have a lengthened exposure to nest predators (West-
moreland and Best 1987), and lower post-fledging survival (Murton et al.
1974). Because these latter attributes are direct results of crop-milk lim-
itation, it is proper to point to crop milk as the key feature that limits 
clutch size in columbids. Westmoreland and Best (1987) in ascribing 
clutch-size limitation in Mourning Doves to an interaction of physiolog-
ical and ecological factors (including crop milk) fail to emphasize that 
crop-milk limitation may be sufficient as an explanation for the small 
clutch size in columbids. Ecological factors help to enforce the impact of 
crop-milk limitation.

The mode of nestling feeding may exacerbate the effects of crop-milk limitation by determining the distribution of food with the brood. Nestling 
doves feed by inserting the bill into the corner of the parent’s mouth and 
swallowing the crop milk or seeds that the adult disgorges. With a normal 
brood of two, the parent often feeds both nestlings simultaneously with 
one on each side. There is no space for a third nestling. If food is limited, 
there would not be enough food for a third nestling to feed after the first 
two have finished. The smallest nestling may consistently lose this com-
petition and become a runt, if it lives at all.

The validity of this mechanism is supported by the distribution of 
mortality within broods of three. The younger nestlings were more likely 
to die and mortality was more common when one nestling was initially 
smaller than the other two. Nestlings that died had grown more slowly 
than those that survived, but growth rates of younger nestlings (as a group) 
were not consistently lower than those of older nestmates. The nestling 
showing reduced growth was often the smallest initially both in Wood 
Pigeons (Murton et al. 1974) and in Mourning Doves (this study). Trans-
ferred nestlings fared no worse than their new nestmates in either species, 
as would be expected if parents rejected unfamiliar nestlings.

The importance of crop milk. — The reproductive strategy of Mourning 
Doves and other columbids features rapid production of multiple broods 
in a nesting season (Blockstein 1986, Westmoreland et al. 1986). Crop 
cycles of adults (Mirarchi and Scanlon 1980, Mirarchi et al. 1982) and 
weaning of fledglings (Hitchcock and Mirarchi 1984, Blockstein 1986) 
appear to be timed for rapid renesting. A key to this strategy is a relatively 
short nesting cycle. This is possible because crop-milk production allows 
rapid growth of one or two nestlings in a brood.

An increased rate of crop-milk production and delivery may be difficult 
to achieve evolutionarily. The fact that none of the nearly 300 species of 
Columbiformes has a clutch size larger than two eggs suggests that there 
is limited plasticity in crop-milk production. If this were not the case we 
would expect to see a variety of clutch sizes and concurrent variation in
crop-milk production ability among Columbiformes. It is apparently more successful to alter features such as the interclutch interval and the number of broods rather than the rate of crop-milk production and clutch size.

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LITERATURE CITED


SONG PATTERNS OF WARBLERS AT DAWN AND DUSK

DOUGLASS H. MORSE

ABSTRACT.—Unaccented Ending Songs or their equivalent occurred nearly exclusively in the dawn and dusk singing of male Northern Parula (Parula americana), Magnolia (Dendroica magnolia), Yellow-rumped (D. coronata), Black-throated Green (D. virens), and Blackburnian (D. fusca) warblers. The proportion of Unaccented Ending Songs at dawn and dusk differed from those given at 06:00, 10:00, and 15:00 when the warblers often sang other songs as well. Total songs/time were low at dawn and dusk, birds were well spaced when singing, and females were not in evidence. I suggest that dawn and dusk songs play an important role in advertising the singer’s presence to potential territorial intruders. Received 17 June 1988; accepted 12 Sept. 1988.

The dawn and dusk choruses of birds have traditionally generated considerable interest among ornithologists. However, most of the resulting literature has dealt with the roles of light or meteorological phenomena in eliciting vocalizations and with the sequence of species in joining or quitting the choruses (see Leopold and Eynon 1961). The detailed characteristics of singing behavior at these times have received much less attention, although Craig’s (1943) pioneering studies on Wood Pewee (Contopus virens) vocalizations clearly indicated that certain song types of that species’ repertoire predominated at twilight.

Largely independently of interest in dawn and dusk choruses, the function of bird song has attracted considerable interest over the past 30 years. A topic central to this discussion has been the roles of different songs within a bird’s repertoire. It is now known that a rather wide range of species with relatively simple song repertoires may sing their different songs in different contexts (e.g., Craig 1943; Smith 1959; Morse 1967a, 1970).

Several species of wood warblers (Parulinae) have two or more types of songs, which are often given in distinctly different contexts (e.g., Ficken and Ficken 1962, Morse 1967a, Lemon et al. 1987). This pattern is well illustrated by the songs of the Black-throated Green Warbler (Dendroica virens) (Morse 1967a, 1970). This species has two distinct songs (Morse 1967a, Lemon et al. 1987). Accented Ending Song (Ficken and Ficken 1962), the song A of some authors, usually occurs when males are unpaired, are in close contact with females, or are foraging below their song

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perches, where their females are nesting and foraging. Unaccented Ending Song, song B, is associated with territorial proclamation or contact with other males. In large populations it is the song given at high frequency during most of the breeding season, and it reaches its highest frequency immediately after overt encounters between adjacent territory holders have declined. It is also the song usually given by stationary males on elevated singing perches (Morse 1970, 1976a). The contexts in which these two songs are given are consistent with them serving as pair-formation/maintenance songs and territorial-aggressive songs, respectively.

Arguing from Smith’s (1965, 1969) message-meaning hypothesis of communication, Lein (1972) proposed a simpler explanation for the function of these songs: that Accented Ending Songs simply occur in the absence of external stimuli that trigger Unaccented Ending Songs. In this scenario, Unaccented Ending Songs could be a response to certain stimuli, and males might sing Accented Ending Songs in the absence of such stimuli, regardless of whether females were present. Although Lein’s hypothesis is attractive in its simplicity, it does not invalidate the hypothesis of the two songs playing separate and distinct roles, so data that help to distinguish between them are needed.

Information on the song types sung at dawn and at dusk may provide useful clues to interpreting these songs, since these are times at which contact with other individuals is likely to be minimal. Only limited attention has been paid to the song types of warblers at such times (Lein 1972, Lemon et al. 1987), or for other species, either, with the exception of Craig’s (1943) work on Wood Pewees. Here I report the dawn and dusk song types of several warblers, including the Black-throated Green Warbler, that nest in the boreal spruce forest. These songs are highly consistent, and are therefore of potential interest.

METHODS

Dawn and dusk songs were identified to type (Fig. 1) and tallied on 11 mornings and 16 evenings between 8 June and 15 July 1975 in a spruce forest on Hockomock Point, Bremen, Lincoln Co., Maine. This area is described in detail elsewhere (Morse 1976b). Five common warblers were selected for this analysis: Northern Parula (Parula americana) and Magnolia (Dendroica magnolia), Yellow-rumped (D. coronata), Black-throated Green (D. virens), and Blackburnian (D. fusca) warblers. Five or more males of each Dendroica species and three or more Parula could be heard clearly from the listening site under calm conditions, to which these observations were confined. A majority of these birds held territories on the study area described in Morse (1976b), and additional birds were located in similar habitats immediately adjacent to that site.

I arrived in the study area to record dawn songs before any warblers had commenced singing. I noted the type of the first song that each species sang, as well as the time at which it first commenced to sing. In addition to tallying the first song of each species, I also recorded
Fig. 1. Sound spectrograms (tracings) of predominant dawn and dusk songs (called Unaccented Ending Songs) and other principal songs (Accented Ending Songs and others). Note that the other song of the Blackburnian Warbler, the highest of any depicted, has an axis of 0–16 kHz. A = Northern Parula, B = Magnolia Warbler, C = Yellow-rumped Warbler, D = Black-throated Green Warbler, E = Blackburnian Warbler.
the song types of other individuals of each species that commenced to sing within two minutes of the first bird of that species. For dusk songs I continuously counted the types and times of songs given by each species after 20:15, a time slightly before the different species ceased to sing. This procedure simultaneously allowed me to determine the last songs given by each individual still singing at this time. I remained until singing had completely ceased.

In analyzing these data I treated each bird-day as an independent observation, since it represented a new experience for each of the birds involved. However, it should be kept in mind that I have gathered these data from a number of individuals that is much smaller than the number of observations reported in Table 1 (see above).

To compare these patterns with songs given at other hours, I used data from song censuses made at various hours in an adjacent spruce forest (Hog Is., Bremen: 8 June–15 July 1966), mostly 06:00–06:30 and 10:00–10:30 h, but with a few censuses at 15:00–15:30 and 19:00–19:30 h. Briefly, I walked a transect of approximately 2 km, recording each song that I heard clearly. This area contained a minimum of eight pairs of Northern Parulas and considerably larger numbers of the other species (also see Morse 1968, 1976b).

For convenience I refer to the predominant song type sung at dawn and dusk as Unaccented Ending Song, which follows its use elsewhere for the Black-throated Green Warbler (Morse 1967a, 1970). Use of similar terminology for the Northern Parula, Magnolia, Yellow-rumped, and Blackburnian warblers is for convenience only and does not make any implications about the function of these songs. The other songs are referred to as Accented Ending Songs, again following its previous usage for the Black-throated Green Warbler. The Unaccented Ending Song is comparable to the serial mode of Lemon and his associates (McNally and Lemon 1985, Lemon et al. 1987), the Accented Ending Song to their repeat mode.

RESULTS

Unaccented Ending Songs were given significantly more often as first dawn songs and last dusk songs by Black-throated Green Warblers. One of the two songs (here called the Unaccented Ending Song) was also given significantly more frequently than the other by each of the remaining species. The only partial exception was the Yellow-rumped Warbler, which in the sample for the first singing of any individual of the species in a day did not differ significantly from random (Table 1). The complete sample of first songs (first songs of all of the individuals of a species) was significant for the Yellow-rumped Warbler, however. In no instance did the first morning singers and last evening singers of a species give Unaccented Ending Songs significantly more or less often than did their conspecifics (Table 1: \( P > 0.05 \) in \( \chi^2 \) tests).

Proportions of dawn and dusk songs did not differ significantly from each other in any of the species (Table 1: \( P > 0.05 \) in Fisher tests). This pattern held, whether the first and last songs from all members of each species were compared, or the first and last songs of each species as a whole on a given day.

The relative frequencies of the different song types given by each species at dusk differed significantly from those given at 06:00 and 10:00 h (Table
TABLE 1
FIRST AND LAST SONGS SUNG BY WARBLERS AT DAWN AND DUSK BETWEEN 8 JUNE AND 15 JULY 1975. SEE TEXT FOR EXPLANATION

<table>
<thead>
<tr>
<th>Species</th>
<th>Dawn</th>
<th>Dusk</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>First birds</td>
<td>All birds</td>
</tr>
<tr>
<td></td>
<td>UES&lt;sup&gt;a&lt;/sup&gt;</td>
<td>AES&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Northern Parula</td>
<td>11 0 &lt;0.001</td>
<td>27 0 &lt;0.001</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>11 0 &lt;0.001</td>
<td>32 1 &lt;0.001</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>7 3 &gt;0.05</td>
<td>19 3 &lt;0.05</td>
</tr>
<tr>
<td>Black-throated Green Warbler</td>
<td>11 0 &lt;0.001</td>
<td>28 0 &lt;0.001</td>
</tr>
<tr>
<td>Blackburnian Warbler</td>
<td>10 0 &lt;0.001</td>
<td>23 0 &lt;0.001</td>
</tr>
</tbody>
</table>

<sup>a</sup> Unaccented Ending Songs or equivalent.
<sup>b</sup> Accented Ending Songs or equivalent.
<sup>c</sup> Two-tailed binomial tests.
2) \( P < 0.001 \) in \( \chi^2 \) tests on the original data). Although comparable quantitative data were not taken on dawn songs, the results in Table 1 strongly suggest that the relationship between dawn songs and those sung later in the morning closely follows the pattern for the dusk songs reported in Table 2.

The dawn and dusk results are profitably compared further with the proportions of different song types given at other times of the day (Table 2). The minimum proportion of Unaccented Ending Songs occurred at 06:00 h. The proportion of Unaccented Ending Songs increased by 10:00, but did not approach the dusk (or dawn) results. This pattern occurred in each species over the three times of day for which I have large samples of data (06:00, 10:00, dusk), and is highly significant \( (X_1^2 = 10.00, \text{df} = 2, P < 0.01 \) in a Friedman two-way analysis of variance). Conclusions do not change if one incorporates the sparser data from 15:00 and 19:00 into the analysis \( (X_1^2 = 18.09, \text{df} = 4, P < 0.01) \). Proportions of Unaccented Ending Songs are still lowest at 06:00, mid-day proportions (10:00 and 15:00 h) are higher than the early morning proportions and similar to each other, and evening (19:00) results are intermediate between mid-day and the nearly absolute dominance of Unaccented Ending Songs at dusk. Thus, proportions of song types change through the day, with the greatest diversion from the dawn and dusk pattern occurring soon after dusk (06:00). However, at no period during the day does the dominance of Unaccented Ending Songs to reach that observed at dawn and dusk.

**DISCUSSION**

The Unaccented Ending Songs given by Black-throated Green and Blackburnian warblers at dawn and dusk were the same songs that these birds used when countersinging with conspecific males, as well as preceding and following hostile encounters with other males (Morse 1967a, 1970; Lein 1972). This pattern was also observed in Northern Parulas (Morse 1967b). While giving twilight songs the males were well-spaced from each other and stationary. I never observed any evidence of female activity at these times: females usually remain much lower in the vegetation than the elevated perches used by males in stationary singing (Morse 1967a) and probably were on their nests at this time. Since the densities of warblers at Hockomock Point and Hog Island are similar (Morse 1976b), total numbers of songs should also be similar; although they were recorded from more birds in the Hog Island sample, because that census was run on a transect and the Hockomock Point census at a single point. However, the numbers of Northern Parula, Black-throated Green, and Blackburnian warbler songs given at dusk at Hockomock Point are lower than those
### Table 2

**Percentages of Unaccented Ending Songs or Equivalents (UES) Sung by Warblers during 30 Min Census on Hog Island. See Text for Explanation**

<table>
<thead>
<tr>
<th>Species</th>
<th>06:00 (17 censuses)</th>
<th>10:00 (17 censuses)</th>
<th>15:00 (3 censuses)</th>
<th>19:00 (2 censuses)</th>
<th>Dusk (16 censuses)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>UES</td>
<td>N⁶</td>
<td>UES</td>
<td>N⁶</td>
<td>UES</td>
</tr>
<tr>
<td>Northern Parula</td>
<td>38.3</td>
<td>962</td>
<td>54.1</td>
<td>885</td>
<td>80.0</td>
</tr>
<tr>
<td>Magnolia Warbler</td>
<td>71.4</td>
<td>1016</td>
<td>78.3</td>
<td>769</td>
<td>58.6</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>46.9</td>
<td>484</td>
<td>75.6</td>
<td>400</td>
<td>75.0</td>
</tr>
<tr>
<td>Black-throated Green Warbler</td>
<td>63.3</td>
<td>3638</td>
<td>87.6</td>
<td>3831</td>
<td>82.3</td>
</tr>
<tr>
<td>Blackburnian Warbler</td>
<td>32.4</td>
<td>1470</td>
<td>70.7</td>
<td>1581</td>
<td>73.8</td>
</tr>
</tbody>
</table>

⁶ Total of all songs.

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Note: The above table provides a summary of the percentages of unaccented ending songs or equivalents (UES) sung by various warbler species during a 30-minute census on Hog Island. The data are divided into time slots and include UES and the total number of songs (N) for each species at different times of day. The table shows fluctuations in the percentages of UES, which may indicate changes in vocal behavior or activity levels across the day.
run at 06:00 and 10:00 on Hog Island. This difference is striking for the commonest species, the Black-throated Green and Blackburnian warblers. Thus, the high proportion of Unaccented Ending Songs given by these species at dawn and dusk is not a consequence of abundant conspecific song—if controlled on the basis of the number of songs given, Accented Ending Songs should predominate at these times. The results thus suggest that dawn and dusk songs are associated with territorial maintenance, even if they do not involve close or intense contact with contenders.

Since the warblers sing their twilight songs when vocalizations are not being given in large numbers, other environmental disturbances (wind, turbulence, etc.) are apt to be low, and atmospheric conditions ideal for sound transmission (Wiley and Richards 1978, Henwood and Fabrick 1979), they may be useful in territorial proclamation far out of proportion to their number. I do not have adequate data on the contexts of Magnolia and Yellow-rumped warbler songs at other times of the day to comment substantively on their patterns; however, the great preponderance of a single song type at dawn and dusk invites an explanation similar to that offered for the other three species.

The nearly exclusive use of Unaccented Ending Songs at dawn and dusk, times of minimal vocal and physical interference, does not cleanly fit Lein’s hypothesis of song function (1972, 1978), which proposes that Unaccented Ending Songs are given in response to strong external stimuli, such as the presence of a conspecific male, the song of a conspecific, or location on the edge of a territory. According to this hypothesis, in the absence of conflicting external stimuli, including lack of interaction with other males as well as association with females, Accented Ending Songs should occur. Unless one imposes special conditions for the dawn and dusk song patterns, this hypothesis thus does not predict Unaccented Ending Song at dawn or dusk, given the scenario I have described; rather, it would predict Accented Ending Song. Lein (1972) included low light intensity as a strong external stimulus eliciting Unaccented Ending Songs, but did not explain the relation of this special condition to the others that generate Unaccented Ending Songs.

Since a territory holder’s song may function in advertising his presence and thereby discourage entry by would-be intruders (Göransson et al. 1974, Krebs 1977, Krebs et al. 1978), clear communication at such times might assume considerable importance. Consistent with this interpretation, Mace (1986) found that male Great Tits (Parus major) continued their dawn singing bout longer when their females were held in their nest boxes than if they were free to leave. This result is consistent with a basically male-male function for dawn song in that species at least, a pattern eventually broken by the appearance of the females. It is also
consistent with the relatively high number of Accented Ending Songs by the warblers in the early morning (06:00) song censuses (Table 2).

The dawn and dusk warbler songs may thus be of particular importance in maintaining territorial integrity, although observations on isolated birds (Morse 1970) and experiments are needed to test their role further. These results do not support the notion that song types (or silence) can be predicted in any simple way solely on the basis of the external stimuli acting on them at the moment.

ACKNOWLEDGMENTS

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LITERATURE CITED


Morse • SONG PATTERNS OF WARBLERS


WILSON SOCIETY ANNUAL MEETINGS

The 1989 annual meeting of the Wilson Ornithological Society will be held 25–28 May, at St. Mary’s College, Notre Dame, Indiana. Doris J. Watt will chair the Committee on Arrangements. Richard C. Banks will chair the Scientific Program Committee. A special feature of this meeting will be a round table discussion of “How to get a paper accepted” for publication in the ornithological literature. Several editors and ex-editors will participate in the discussion.
THE SINGING BEHAVIOR OF GOLDEN-WINGED WARBLERS

R. Tod Highsmith

ABSTRACT.—Golden-winged Warbler (Vermivora chrysoptera) males show distinct daily, seasonal, and social patterns in their use of two stereotyped song types. Type II song is used in an extended early morning bout, is sung at a rapid rate, and may be interspersed with flight song displays. Soon after sunrise, males switch to type I song, which is sung at a lower rate, often intermittently, throughout the morning. During actual or simulated agonistic encounters, long type I, short type I, and type II songs are used as a graded series. The amount of long type I singing, but not of short type I or type II singing, decreases upon attraction of a mate, and males were observed to sing only type I songs when consorting with females. These patterns of use support the view that song types in this species have special intrasexual (type II) and intersexual (type I) functions. The association of song types with specific singing behaviors suggests an organization of vocal behavior similar to that of parulines with much larger, more complex repertoires. Received 19 May 1988, accepted 15 Oct. 1988.

Unlike those songbirds that appear to use a variety of songs interchangeably, many wood warblers (Parulinae) have a repertoire of song types that are used in different ways in different contexts. In some warblers, the contexts in which songs are used suggest that song types are functionally distinct and carry predominantly intersexual (mate attraction) or intrasexual (territorial) messages (Chestnut-sided Warbler [Dendroica pensylvanica], Yellow Warbler [D. petechia], and American Redstart [Setophaga ruticilla], Ficken and Ficken 1965; Golden-winged Warbler [Vermivora chrysoptera] and Blue-winged Warbler [V. pinus], Ficken and Ficken 1967, Kroodsma 1981; Black-throated Green Warbler [D. virens], Morse 1970; and Grace’s Warbler [D. gracieae], Staicer 1982). In addition, observations of some species reveal that certain song types, or groups of song types, may be associated with distinct singing behaviors characterized by, for example, differences in rate of delivery or in sequential variety (Grace’s Warbler, Staicer 1982; American Redstart, Lemon et al. 1985).

Golden-winged and Blue-winged warblers have a simple song system in which each male has a repertoire of two stereotyped songs, type I and type II (Lanyon and Gill 1964). An extensive literature, often with an emphasis on the role of vocalizations, documents within- and between-species behavioral interactions in this frequently hybridizing species pair (Gill and Lanyon 1964; Baird 1967; Ficken and Ficken 1967, 1968a, b.

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METHODS

I studied Golden-winged Warblers in the Itasca State Park area, Hubbard and Clearwater Counties, of north-central Minnesota during May and June 1984–1986. Although Blue-winged Warblers nest only 300 km to the southeast, only one Blue-winged Warbler and one female hybrid have been reported from the area, both in 1986 (Highsmith 1987). Except for these individuals, the Itasca population appears phenotypically pure and shows no signs of genetic introgression with Blue-winged Warblers (Gill 1987). I performed all observations and experiments on active Golden-winged Warbler territories between 04:30 and 13:00 h CDT, with the help of several field assistants.

Song description.—Type I song (Fig. 1a) normally consists of a high frequency buzzy phrase followed by one to six buzzy phrases of lower frequency. Type I song length is referred to by the number of times each phrase type occurs in a song; a song with a single high frequency phrase followed by three lower frequency phases, for example, is a 1-3. Based on observations of song use by undisturbed males, I consider type I songs with four or more total phrases to be long type I songs, and songs with three or fewer total phrases to be short type I songs (see Results). Type II song (Fig. 1b) contains three to five syllable types and ends with a terminal buzzy phrase.

Observations of singing behavior.—Although the singing behavior of over 15 different males was observed, I here report data from the six color-banded males that were observed most intensively. Because previous accounts of Golden-winged Warbler singing behavior did not cover the early morning period, my assistants and I usually arrived on territories between 04:30 and 05:00 h to begin our observations before males started their singing activity each day. Males A, B, and C (1986), D and E (1985), and F (1984) were monitored continuously from the beginning of song activity to well after sunrise, and at various times later in the day. We used binoculars, stop watches, and data sheets, marked in minutes and seconds, to record the following: song type; song length; whether songs were loud or muted;
the male's position on the territory; and the behavioral context of a male's singing, including any interactions with conspecifics.

The data from males A, B, and D that were used to compare singing behavior during the pair formation period were limited to those that were collected between the start of singing activity and 06:30 over the birds' first nineteen days on territory. I determined singing rate by counting the number of songs in each bout of continuous singing and dividing by the number of minutes of continuous song. I express the amount of type II song activity as the duration in minutes of the essentially continuous early morning type II bout, measured from the first type II song of the day to the last type II song given before the switch to pure type I singing. Because type I songs are sung more intermittently, the amount of type I song activity is best expressed as songs per minute of observation. Multiple linear regression analysis of male A's singing behavior was done using the Interactive Data Analysis Package (Wiedmann and Hosmer 1983).

*Song playback experiments.*—We noted responses to simulated territorial intrusions during the course of song playback experiments on species discrimination with over 250 different males. Pairs of song stimuli were played at a natural singing rate from two speakers placed on a male's territory. Each playback experiment consisted of five periods: 5 min of pre-playback observation, 5 min of stimulus presentation, a 3 min silent intermission, 5 min of stimulus presentation, and 5 min of post-playback observation. Males were scored on the basis of whether they sang any type I or type II songs during each period, and on the length of type I songs sung. If an individual sang both song types during a particular period, it was scored for both.

We used Uher 4200 or 4400 Report Monitor tape recorders and Olympus SP5 speakers (modified by Mineroff Electronics) to broadcast songs. Type II song stimuli (total of 8 different experimental tapes) consisted of natural Golden-winged and Blue-winged warbler type II songs. Type I song stimuli (total of 25 different experimental tapes) included various...
TABLE 1
MEAN SINGING RATES OF TYPE I AND TYPE II SONGS (IN SONGS·MIN⁻¹)

<table>
<thead>
<tr>
<th>Male</th>
<th>Type I</th>
<th>Type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3.9 ± 1.4 (10)ᵃ</td>
<td>6.5 ± 1.4 (7)ᵃ</td>
</tr>
<tr>
<td>B</td>
<td>3.7 ± 0.5 (6)</td>
<td>6.5 ± 1.9 (7)</td>
</tr>
<tr>
<td>D</td>
<td>4.3 ± 1.4 (5)</td>
<td>10.4 ± 1.6 (6)</td>
</tr>
<tr>
<td>E</td>
<td>4.5 ± 0.6 (6)</td>
<td>10.0 ± 1.9 (2)</td>
</tr>
<tr>
<td>F</td>
<td>3.2 ± 0.3 (6)</td>
<td>10.8 ± 2.6 (6)</td>
</tr>
</tbody>
</table>

ᵃ Mean ± SD (number of song bouts used to calculate mean).

combinations of natural Golden-winged Warbler type I, natural Blue-winged Warbler type I, and artificial type I songs composed of elements from both species. Some males also heard several type I songs during pre-playback or intermission from a separate tape used to attract males to the playback area. A small number of males received both a type I and a type II playback, but otherwise a male was used only once. Vocal responses of males to playbacks containing only natural or only artificial type I songs did not appear to differ, so all type I playbacks were lumped for analysis. Results from type I and type II playback experiments were analyzed separately. Statistical comparisons of changes in singing behavior between experimental periods were made using McNemar's test for significance of difference between two correlated proportions (two-tailed, Ferguson 1976).

RESULTS

Daily Patterns of Singing Behavior

Undisturbed, mated Golden-winged Warbler males exhibited two distinct modes of singing behavior that were characterized by differences in song type and time of day.

Type II singing behavior.—Except for very early in the season, males began each day's singing activity with an extended and rapidly paced bout of type II songs. Many males began the bout from the same perch each day and sang continuously for 30–40 min, stopping around sunrise. Typically a male sat mid-level or high in a shrub or tree, often at an edge of his territory closest to conspecific neighbors with whom he counter-sang. Males frequently made short-distance perch changes.

Although most males began the bout with complete songs, others sang only the first two or three syllable types of their normal type II song for several minutes, and only gradually lengthened these songs to include the terminal buzz. Chip notes, similar in structure to the initial type II syllables, were used frequently between songs. Songs were delivered at a rapid rate throughout the bout, although the rate differed greatly both among males (mean = 8.8 ± 2.2 [SD] songs-min⁻¹, N = 5 males) and within individuals (Table 1). Male E, for example, was once observed
singing at the unusually high rate of 18–20 songs·min⁻¹ for a two-minute period.

Interruptions of the type II bout were not uncommon, but their causes were difficult to observe because of low light levels and thick vegetation. Males sometimes paused to chase intruding males or to accompany females. In both cases, males and females uttered a low, buzzy "zzt," either singly or repeated in slow chatter-like strings. Following such disturbances, males typically returned to the same or a different perch and resumed type II singing.

Flight song displays can be given at any point in the type II bout, but five of the eleven males in which I observed it used it frequently as one of their very first songs of the morning. To perform the display a male flew up in an arching path, flapped his wings stiffly, gave the song at the peak of his ascent, and flapped or glided down to the same or a different perch (similar to description for other parulines in Ficken and Ficken 1962). The song itself was a modified version of the male’s type II song, differing in the addition of two or three syllable types to the beginning of the song (Fig. 1C). I was able to obtain good recordings from only two males, but the structure of the syllables peculiar to the flight songs was similar in each individual. I frequently observed one to three flight song displays during a male’s early morning type II bout, but on some days I heard none at all. The most I observed during a single bout was a total of nine given by male A in a 30-min period on 23 May 1986. Flight song displays were noted as early in the season as 17 May and as late as 20 June.

A male’s early morning type II bout ended with a minute of intermingled type I and II songs, an abrupt switch to type I songs, or a cessation of singing activity. Type II songs were often used later in the morning, but with several notable differences. Rather than forming a distinct bout, strings of type II songs were likely to be mixed with strings of type I, usually preceding or following an interaction with another male. Although song rate remained high and some males sang incomplete songs, flight song displays were not used, chipping between songs was less frequent (although the "zzt" note was sometimes used), and males often sang at reduced volume.

**Type I singing behavior.** —Whether a male’s first type I songs of the day were continuous with the end of his type II bout, or whether he stopped and began later in the morning, type I singing was characterized by a lower mean song rate (3.9 ± 0.6 [SD] songs·min⁻¹, N = 5 males), lack of chip notes between songs, and absence of flight song displays. Relatively little variation existed in type I song delivery rates among males (Table 1); even during counter-singing the highest type I rate I observed was 8 songs·min⁻¹, again from male E.
There was variation among males in the length of type I songs included in their individual repertoires. Individuals generally had a “preferred” type I rendition that was their most common song in bouts of undisturbed singing. This song was usually the longest or next longest type I song in a male’s repertoire and contrasted with the shorter songs that a male sang during territorial disputes (see below). The “preferred” song for most males was a 1-3 (Fig. 1A), but I encountered a small number of males who sang predominantly 1-2’s and another who sang predominantly 1-4’s. Male A is typical of 1-3 singers; 57% of all songs observed over two seasons were 1-3’s and less than 1% were 1-4’s or longer. All of the six males that I intensively observed “preferred” 1-3’s, except for male D, who sang mostly 1-2’s (85% were 1-2’s, only 3% were 1-3’s).

There was no distinct type I bout, analogous to the type II bout, that was predictable in time and place. Although an unmated male sometimes sang type I for hours from a single exposed perch, mated males were more likely to sing intermittently from a succession of perches around the perimeter of their territory, or not to sing at all for long periods. I have observed undisturbed males singing type I while preening or foraging, and from perches in thick vegetation where they were mostly obscured from view. Type II singing, at least during the pre-dawn bout, appeared to preclude preening or foraging, perhaps because of low light levels.

Seasonal Patterns of Singing Behavior

Type II singing behavior.—Analysis of samples from four males over the first nineteen days after their arrival on territory showed that the duration of the early morning type II bout tended to increase throughout this period (Fig. 2). Males did not begin singing these type II bouts until two to four days after arrival, and bouts were likely to be quite short (less than 15 min) for the first ten days or so. Some bouts eventually increased to 45 min in length as males began singing earlier before sunrise.

Type I singing behavior.—Type I singing activity decreased over the course of the breeding season. Following an abrupt drop from almost constant type I singing before males were paired in May, type I singing decreased more gradually until, by mid- to late June, songs were quite sporadic. Early in the season, before type II bouts were established, some males began their daily singing before sunrise with type I songs. In these instances, singing rate and behavior were the same as in typical later morning type I singing.

Social Patterns of Singing Behaviors

Singing behavior during song playback experiments.—Males used both their type I and type II singing behaviors during simulated territorial intrusions provided by song playback experiments. The most striking
Fig. 2. Duration of early morning type II song bouts for four Golden-winged Warbler males over their first nineteen days on territory. Only those days on which data were taken are numbered on the abcissa. Date of arrival on territory (day one) for males A, B, and C is 10 May 1986; for male F, 17 May 1984. Spearman rank correlations (two-tailed): male A, \( r_s = 0.91, P < 0.001, N = 11 \); male B, \( r_s = 0.54, 0.05 < P < 0.1, N = 11 \); male C, \( r_s = 0.87, P < 0.001, N = 10 \); male F, \( r_s = 0.90, P = 0.05, N = 5 \).

change in song type use occurred during the first stimulus presentation period, regardless of whether the experimental songs were type I or type II (Fig. 3). Although the number of males singing type I songs decreased slightly from the pre-playback to the first stimulus period, the number singing type II songs increased significantly. The same general pattern was evident over all five experimental periods: the number of males singing type II increased during periods of stimulus presentation and decreased during periods of silence, while the number of males singing type I decreased during stimulus periods and increased when the stimulus was withdrawn. These results agree with other playback experiments and observations of males in actual territorial encounters (Ficken and Ficken 1967, 1968b, 1969, 1973; pers. obs.). Responses to the playback experiments also showed that there was an overall increase in singing activity, in that more males were vocalizing after the experiments than before.

A pattern was also evident in the length of type I songs used by males during playback experiments (Fig. 4). Although the numbers of males singing short and long type I songs was approximately equal just before both type I and type II experiments, the number of males singing short songs increased significantly, and those singing long songs decreased sig-
Fig. 3. Changes in song type use by male Golden-winged Warblers during song playback experiments. Graphs show the percentage of males that sang type I and type II songs in each of five experimental periods. Change in type II use between the pre-playback and first playback periods was statistically significant \((P < 0.01)\) for both categories of stimuli. Change in type I use between the same periods was not significant \((P > 0.05)\) for either type of stimuli. a. type I playback stimulus (median date 6 June, range 14 May–29 June). b. type II playback stimulus (median date 19 June, range 24 May–26 June).

Significantly, during the first stimulus period. Singers of short songs outnumbered singers of long songs throughout all but the pre-playback period.

**Singing behavior during mate attraction and pair formation.**—My assistants and I were able to follow three Golden-winged Warbler males through the process of mate attraction and pair formation. All three males engaged in a variety of visual courtship displays, which are well documented elsewhere (Baird 1967, Ficken and Ficken 1968a). Two of the males, B and D, successfully attracted and paired with single females. Male A, on
the other hand, provided a natural mate-loss experiment. Male A's first potential mate, a female Blue-winged Warbler, remained on his territory for only three days, during which time she was closely attended by male A and appeared to prospect for nest sites. After her disappearance, male A remained unpaired for five to seven days until he finally attracted a Golden-winged Warbler female. Although male A's circumstances were unusual in this study population, I believe his behavior may be considered representative of a normal Golden-winged Warbler male. Interspecific
pairing of Golden-winged and Blue-winged Warblers is not uncommon in areas of more extensive sympatry and, except for song morphology, courtship displays of the two species are essentially identical (Ficken and Ficken 1968a). Also, male A’s behavior with the two females did not differ in any notable way, nor did it differ from that of the other two males under observation.

The presence of a female on a male’s territory had no consistent effect on the type II singing behavior of the three males during pair formation. Male A sang progressively longer type II bouts throughout this period (Fig. 2). Analysis by multiple linear regression showed that the number of days since he arrived on territory contributed significantly to explaining variation in the amount of his type II singing (t = 6.89, P = 0.0001), but female presence did not (t = 0.86, P = 0.41); female presence and days together: F = 25.3, df = 2.7, R² = 0.88, P = 0.0006). Male B (Fig. 2) showed a smaller increase in type II bout length before and after female arrival, and male D’s bouts decreased in length the first two days on which he was closely attending his female. Males appeared to cut short or abandon their type II bouts in order to closely attend the females on some days, but I never observed males to sing type II while in close association with females.

All three males showed a dramatic change in long type I singing activity with the arrival of the female. In general, males sang extended, uninterrupted bouts of long type I songs before attracting a female, but sang very few long type I’s once a female was present. For male A (Fig. 5), long type I activity decreased with the arrival of the Blue-winged Warbler female, rose when she disappeared, and fell off again with the arrival of the Golden-winged Warbler female. Regression showed that female presence contributed significantly (t = -4.09, P = 0.003) to explaining variation in the amount of his long type I singing, but number of days on territory did not (t = -0.217, P = 0.83; female presence and days together: F = 7.43, df = 2.7, R² = 0.68, P = 0.018). Males B and D (Fig. 5) also showed a sharp drop in the amount of their long type I activity immediately after attracting females.

Males showed no corresponding variation in the amount of their short type I singing, although they did use sporadic, usually muted, short type I songs when close to a female. The amount of short type I activity varied little before and after female arrival for male A (Fig. 5; female presence: t = 0.136, P = 0.89; number of days on territory: t = -0.590, P = 0.57; female presence and days together: F = 0.177, df = 2.7, R² = 0.04, P = 0.84) and for male D (Fig. 5). Male B’s short type I singing did increase on the first day of his female’s presence, but returned to previous levels the following three days (Fig. 5).
Days on territory

Male A

Male B

Male D

DISCUSSION

My results generally support the descriptions of Golden-winged Warbler singing behavior made by Ficken and Ficken (1967) but provide a more complete picture of the ways in which males use their two song types.
Although previously considered an infrequently used song, type II song constitutes a substantial part of a male's vocal behavior and is not limited to use during conflicts between males. Except at the very beginning of the season, type II makes up a distinct and lengthy bout of songs, performed daily at the same time and place, that initiates a male's daily singing activity. Especially late in the season, when most mated males are singing type I only sporadically, the early morning type II bout may be the only predictable element of a male's singing behavior on a particular day.

Singing in flight has been noted in a number of *Vermivora* (Bent 1953, pp. 42, 84; Pitelka 1939; Ficken and Ficken 1962; Gilbert 1983), but modification of both the song and pattern of flight has been previously reported only in the Nashville Warbler (*V. ruficapilla*, Bowles and Bowles 1906, Chapman 1907). Golden-winged Warblers occasionally sing normal type II songs in flight, especially during song playback experiments, but their flight song display is distinctly different. The range of dates and time of day of my observations do not strongly support the suggestion that these displays are primarily given late in the day and late in the season (Ficken and Ficken 1962). I observed all but one of more than 30 displays during the early morning type II bout, and the other one around 07:00 h. Although I have not made extensive observations in the evening, others have noted flight song displays during a brief type II bout at that time (T. Will pers. comm.).

Both observational and experimental data show that a male's song repertoire exists as a graded series. A male sings long type I songs when he is relatively undisturbed, and shortens these when presented with either a real or simulated male intruder (Fig. 4), or when closely accompanying a female. If an interaction with another male escalates, males switch to type II songs, although I never observed males to use type II songs when in close contact with females. Responses to song playback show that males often switch songs in stepwise fashion, up or down the series (e.g., 1-3 to 1-1 to type II), but they may also switch directly from long type I to type II or vice versa. Ficken and Ficken (1967) obtained similar results for Golden-winged Warblers from a population sympatric with Blue-winged Warblers in New York.

This pattern of song use resembles the “motivational continuum” Lein (1972) has proposed to explain the use of song types by Black-throated Green Warblers. Territorial Black-throated Green Warbler males, Lein suggests, spontaneously produce type B songs when undisturbed, but switch to type A in the presence of a variety of external stimuli including other males, low light levels, or proximity to the territory boundary (but see Morse 1970). Similarly, Chestnut-sided Warblers (Lein 1978) switch up or down within a series of accented and unaccented ending song types depending on the singer’s “mood,” location on his territory, and the
likelihood of a dispute with a neighbor. Lein argued that song in these and other warbler species functions primarily in territorial establishment and defense. While he notes that the message a song type carries may well have different meanings for male and female conspecifics, he concludes that any intersexual function of song is supplementary to the intrasexual (Lein 1978). Although song use by Golden-winged Warblers appears consistent with Lein's "motivational continuum," observations of the contexts in which songs are used do not support his functional explanation. There appears to be a major functional distinction between the two extremes of the graded series, type II songs and long type I songs.

Patterns of song use by Golden-winged Warblers early in the season suggest that long type I songs, but not short type I or type II, are particularly important in mate attraction. The early morning type II bout is absent, or of short duration, during this period (Fig. 2), although type II is used during encounters with other males at that time. The presence of a female on a male's territory had no consistent effect on the amount of short type I (Fig. 5) or type II singing. In contrast, female presence correlated strongly with a sharp drop in long type I singing activity, and one male who lost his first mate reverted to a high level of long type I activity until he attracted another (Fig. 5). Further, although both song types are used in agonistic situations, songs from the middle of the graded series (short type I) are used with conspecifics of either sex; daytime type II songs appear to be reserved for use during interactions with other males.

The data thus support the general view that type I and type II songs carry inter- and intrasexual messages, respectively (Ficken and Ficken 1967, Kroodsma 1981), but with two important qualifications. First, the mate attraction function appears limited to a male's long type I song. Second, each song type has a specific, but not a solitary, message: despite type I song's special mate attraction function, it is also used by males in territorial disputes, and despite type II's special territorial function, it may also carry information about species or individual identity that is available to listening females.

Differences between type I and II songs are further underlined by the distinctive behaviors associated with the delivery of each song type. Type I and type II singing behaviors differ in song rate, use of chip notes between songs, use during flight displays, and use during well defined, ritualized song bouts. It is likely that Blue-winged Warblers share many of the patterns of behavior, if not specific behaviors, that I have described for Golden-winged Warblers. Blue-winged Warbler males sing an early morning type II bout and singing rates of type I and type II songs differ in ways parallel to those of Golden-winged Warblers (mean rate of type I songs

\[ 4.6 \pm 0.8 \text{ [SD]} \text{ songs.min}^{-1}, \text{ mean rate of type II songs} = 11.9 \pm 1.7 \]
[SD] songs·min\(^{-1}\), N=5; Massachusetts Blue-winged Wargler males). There is also evidence that modified type II songs are used in a flight display (pers. obs.; Kroodsma, unpubl. data).

This correlation of particular behaviors and particular song types is also seen in some parulines with much larger, more complex repertoires. Species may sing specific song types, or groups of song types, with consistent differences in rate or pattern of delivery. Male American Redstarts (mean repertoire size = 4.4 songs per adult male), for example, consistently repeat one of their song types over and over (repeat mode) but sing the others with high immediate variety (serial mode) (Lemon et al. 1985). For Grace’s Warblers, which typically have repertoire sizes of six or more song types per male (Staicer 1982), similarities with Golden-winged Warblers are pronounced both in how the songs are sung and in what contexts they are used. Group A songs, used prior to pairing and in the presence of females, are sung with low or no sequential variety and at a slow rate. Group B songs, used primarily during an early morning bout and in interactions with other males, are sung with immediate variety and at a high rate (Staicer 1982).

These comparisons among warbler species suggest that the complexity of singing behavior may depend as much on how the repertoire is used as it does on repertoire size. Despite the limitation of two stereotyped song types per male, the flexibility of Golden-winged Warbler singing behavior serves to create a larger effective repertoire. Golden-winged Warbler males use songs as a continuous series and as discrete song types. Distinctions between mate attraction and agonistic functions are apparent both between the two song types and within a single song type (type I).

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LITERATURE CITED


BREEDING BIOLOGY OF PROTHONOTARY WARBLERS IN RIVERINE HABITAT IN TENNESSEE

LISA J. PETIT

ABSTRACT.—The breeding biology of Prothonotary Warblers (Protonotaria citrea) was studied in the center of their summer range along the Tennessee River in west central Tennessee in 1985 and 1987. Data were collected on clutch and brood sizes, numbers of young fledged, fledging weights, incidences of predation, cowbird parasitism, and nest abandonment for birds nesting in nest boxes. Warblers in this study had relatively high reproductive success compared to populations studied by Walkinshaw (1941) in Tennessee and Michigan. Prothonotary Warbler clutch sizes, brood sizes, and numbers fledged were significantly smaller in the second half of the season than in the first half. However, fledging success (number fledged/number eggs laid) was similar in both early and late nests. Prothonotary Warblers suffered 7.1% (of 831 eggs) hatching failure due to egg infertility or embryo death. Nestling mortality not due to predation or abandonment was low (2.6% of 700 nestlings), occurring mostly in broods where hatching was asynchronous. Frequency of predation was relatively low (20.9% of 191 nests) compared to Walkinshaw’s (1938) results. However, although no cowbird parasitism was observed in 1987, parasitism in 1985 was much higher (20.3% of 128 nests) than that reported by Walkinshaw (1938). Received 10 May 1988, accepted 11 Oct. 1988.

Little has been published on breeding biology of Prothonotary Warblers (Protonotaria citrea) in the past 40 years. Walkinshaw (1938, 1939, 1941, 1953) intermittently collected data on nest initiation dates, clutch sizes, and life histories in southern Michigan. The population he studied was fairly small (11–14 pairs), perhaps because it was near the edge of the breeding range for the species. Walkinshaw (1941) also compared data gathered on Prothonotary Warblers in Michigan to data from a population in northwestern Tennessee. Some differences in nesting behavior were found between the two populations, although relatively fewer data on ecology of the warblers in Tennessee were obtained. Only two other studies of Prothonotary Warbler breeding biology, other than anecdotal reports, have been published during this century. Meyer and Nevius (1943) studied only four nests, and Kleen (1973) considered only territory sizes and return rates of the warblers.

It is important to gather more quantitative data on breeding biology of this species for two reasons: (1) the Prothonotary Warbler is unique because it is one of only two cavity-nesting wood-warblers (Parulinae). Data

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on Prothonotary Warblers can be compared with data from other, more intensely studied cavity nesters from different families and at different latitudes (e.g., Pied Flycatchers [Ficedula hypoleuca], parids [Parus spp.], bluebirds [Sialia spp.], and various wrens). (2) Prothonotary Warblers require swampy or riparian habitat for nesting and populations may be declining in northern states due to loss of suitable swampy habitats (Grabber et al. 1983; but see Robbins et al. 1986). This species breeds in relatively large numbers in southern states, but even in those areas, wetland and bottomland hardwood habitats are disappearing at an alarming rate (less than 25% of the original bottomland forest in the southeastern United States exists today; Harris et al. 1984).

Here I present quantitative information on the breeding ecology of Prothonotary Warblers nesting in riverine habitat within the center of their breeding range.

**STUDY AREA AND METHODS**

Field work was conducted from 5 April to 17 July 1985 and from 4 April to 20 July 1987, along the Tennessee River in Benton County, Tennessee. The study area extended approximately 25 km along an impounded section of the river (Kentucky Lake). In this area the width of the river ranges from approximately 1 to 3 km. During summer months the river level is raised, due to damming, flooding vegetation along the shores and creating 1-5-ha islands. The river is bordered by hilly, oak-hickory forests. Riparian habitat occurs in narrow strips (usually less than 50 m in width) along the shores and is dominated by willows (Salix spp.), buttonbush (Cephalanthus occidentalis), sweetgum (Liquidambar styraciflua), red maple (Acer rubrum), hackberry (Celtis occidentalis), river birch (Betula nigra), and American elm (Ulmus americana).

In 1985 and 1987, I placed a total of 426 milk carton nest boxes (Fleming and Petit 1986) on trees along shores and on islands (1985 only) within the river at heights of 1.5-2.0 m. Because Prothonotary Warblers usually require standing water in the breeding habitat (Petit et al., unpubl. data), nest boxes were arranged in a linear fashion parallel to the river and were placed over water approximately 5-15 m inland from the outer edge of the vegetation. Boxes were erected in late March to early April before the return of the warblers to their breeding grounds.

Territories of color-banded males were mapped intensively only in 1985 and were based on observations of locations of singing posts and aggression between males over a period of 30-40 days. In some cases, a male’s response to a playback of song was used in determining boundaries. Nest boxes were checked once every 7-10 days for the presence of nests. Once nests were found, they were checked an average of 2-3 times per week. For each nest, I recorded clutch size, brood size, and number of young fledged. Clutch size was number of eggs incubated by the female, and brood size was number of young that hatched, if known, or number of nestlings present in the nest. Adult Prothonotary Warblers usually do not remove unhatched eggs from the nest (pers. obs.). This aided in determining how many young had hatched successfully and, in many cases, the cause of hatch failure (e.g., embryo death, egg infertility). Lengths and widths of eggs were measured to the nearest 0.1 mm with dial calipers. Number of young successfully fledged was the number of young present in the nest at 9 or 10 days after hatching. I weighed nestlings at 9 days, when possible, to avoid causing premature fledging. Weights were obtained to the nearest 0.1 g using a 50-g Pesola
scale. Analyses of nest success included only nests in nest boxes which I monitored from incubation through termination. Nests in natural cavities and nests of birds in polygynous matings (unpubl. data) also were not included in analyses. Because there were no statistical differences in clutch and brood sizes and numbers of young fledged between years (Mann-Whitney U-tests, $P > 0.10$), data from both years were pooled for analyses. For analyses of nest success over time, nesting attempts were categorized as early or late according to distributions of nest initiation dates in each year.

Incidence of predation, nest abandonment, and Brown-headed Cowbird ($Molothrus ater$) parasitism were also noted. Predation was assumed to have occurred if nest contents were prematurely absent. The type of predator was determined according to whether the nest was disturbed (mammalian) or not (snake) (Best 1978).

**RESULTS**

**Dates of arrival and territory establishment.**—In both 1985 and 1987, male Prothonotary Warblers were first seen on study sites between 8 and 11 April, and females were seen about a week later. Within the first several days after their arrival, males explored nest boxes and natural cavities, usually without singing. Males established territories around one or several nest boxes/cavities and increased singing rates usually to 4–6 songs per minute, although this rate varied with time of day (unpubl. data). Small amounts of moss usually were placed by the male into each nest box within his territory. Occasionally, males placed up to 7.5 cm of moss within one box, fashioning a nest depression by sitting down in the moss much like an incubating female. Territorial behavior included vigorous displays toward and attacks on neighboring males, which often involved long chases and some actual contact between birds. Territory sizes in 1985 ranged from 0.1 ha to 1.2 ha ($x = 0.48 \pm 0.23$ [SD] ha; $N = 80$).

Upon their arrival, females inspected cavities or nest boxes, and once a cavity was chosen, they filled that cavity nearly to the entrance hole with moss. Then they constructed a nest lining from rootlets, bark strips, and grape ($Vitis$ spp.) vine. Colored fishing line also was used in construction of nearly all nests.

**Nest initiation and clutch sizes.**—Data were collected from 265 Prothonotary Warbler nests, including 27 nests in natural cavities. Most of the latter were in abandoned Downy Woodpecker ($Picoides pubescens$) cavities; one was in an abandoned Red-winged Blackbird ($Agelaius phoenicus$) nest (Petit and Petit 1988). The first nest was initiated (first egg laid) on 23 April and 1 May in 1985 and 1987, respectively. Mean initiation date for early nests (initiated prior to 22 May and 30 May in 1985 and 1987, respectively) was significantly later in 1987 ($x = 10$ May) than in 1985 ($x = 3$ May; Mann-Whitney $U$-test, $Z = 5.02$, $P < 0.0001$). In both years, most females laid two clutches, resulting in bimodal distributions of clutch initiation dates (Fig. 1). Of the 66 females which were known to make at least two nesting attempts, 51 (77%) at-
Fig. 1. Distributions of Prothonotary Warbler clutch initiations (first egg laid) per week in west central Tennessee during 1985 and 1987.

tempted a second clutch after a successful nesting attempt (at least one young fledged), and 36 (55%) were successful in both nesting attempts. No female was observed to attempt a third nest after two successes. Mean initiation dates for late nests (initiated after 22 May 1985 or 30 May 1987) were 7 June in 1985 and 13 June in 1987 (Mann-Whitney $U$-test; $Z = 2.26$, $P = 0.024$). An overall average of $4.73 \pm 0.65$ [SD] eggs ($N = 123$ nests) were laid per nest, and incubation lasted approximately 12 days
Fig. 2. Distributions of Prothonotary Warbler clutch sizes in early (initiated on or before 22 May 1985 or 30 May 1987) and late (initiated after 22 May 1985 or 30 May 1987) nests. Early clutches were significantly larger than late clutches.

and began when the penultimate egg was laid. Prothonotary Warbler eggs had a mean length of 17.68 ± 0.64 [SD] mm and a mean width of 14.30 ± 0.51 mm (N = 512). In both early and late nests, the most common clutch size was 5 (Fig. 2).

Comparisons of early and late nests. — Comparisons between early and late nests included only nests for which data were complete (i.e., all parameters were known) and which did not suffer predation, cowbird parasitism, or abandonment. Clutch sizes, brood sizes, and numbers of young
TABLE 1
PROTHONOTARY WARBLER CLUTCH SIZES, BROOD SIZES, NUMBERS OF YOUNG FLEDGED, AND FLEDGING WEIGHTS IN EARLY AND LATE* NESTS

<table>
<thead>
<tr>
<th></th>
<th>Early</th>
<th></th>
<th>Late</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>(x) (SD)</td>
<td>N</td>
<td>(x) (SD)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clutch size</td>
<td>65</td>
<td>4.95 (0.54)</td>
<td>55</td>
<td>4.56 (0.56)</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td>Brood size</td>
<td>65</td>
<td>4.47 (1.01)</td>
<td>55</td>
<td>4.16 (0.82)</td>
<td>0.04</td>
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<tr>
<td>Number fledged</td>
<td>65</td>
<td>4.43 (1.03)</td>
<td>55</td>
<td>3.98 (0.97)</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Fledging weight (g)</td>
<td>120</td>
<td>11.71 (0.71)</td>
<td>79</td>
<td>11.51 (0.93)</td>
<td>0.14</td>
<td></td>
</tr>
</tbody>
</table>

* Early nests = initiated on or before 22 May 1985 or 30 May 1987. Late nests = initiated after 22 May 1985 or 30 May 1987. Nest suffering predation, cowbird parasitism, or abandonment were excluded from these analyses. Data were combined for 1985 and 1987.

fledged were significantly greater in early nests (N = 65) than in late nests (N = 55; Table 1). However, mean fledging success (number fledged/number eggs laid) was similar for both early (89%) and late (87%) nests (Mann-Whitney U-test; \(Z = 0.77, P = 0.44\)).

Overall hatching and fledging success.—Of 831 eggs laid, 700 (84.2%) hatched and 620 (74.6%) young fledged. Fifteen (1.8%) eggs were known to have suffered embryo death, and 11 (1.3%) were infertile. Twenty-four (2.9%) other eggs failed to hatch for one of these two reasons, but actual causes of failure were not determined. The remainder were lost to predation or abandonment.

Two Prothonotary Warbler young apparently died in the process of hatching. Sixteen (2.3%) nestlings died either from starvation or apparent trampling by larger nestmates. Five of those nestlings were in broods where hatching was asynchronous and in which the last egg hatched 12 to 24 hours after the penultimate egg hatched. The remaining nesting mortality was due to predation or nest abandonment.

Predation, cowbird parasitism, and nest abandonment.—Predation occurred in 20.9% of all Prothonotary Warbler nests (Table 2) and occurred more often on nestlings than on eggs. Although overall predation rates were significantly different in 1985 and 1987 (16.9% vs 29.5%; \(G = 3.82, P = 0.051\)), when nests were separated into early and late, predation rates were not different between years (Table 2). Nests were apparently depredated by snakes and mammals (mostly raccoons [Procyon lotor], whose prints have been visible on and around depredated nest boxes). Frequency of predation did not differ between early and late nests (1985 and 1987 combined; Table 2). In 1985, predation occurred in similar proportions on island (11 of 78 nests) and mainland (11 of 82 nests) plots (\(G = 0.01, P > 0.50\)).
TABLE 2
Frequencies of Predation, Cowbird Parasitism, and Nest Abandonment in Early and Late Prothonotary Warbler Nests in 1985 and 1987

<table>
<thead>
<tr>
<th>Number of nests</th>
<th>1985</th>
<th>1987</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Late</td>
</tr>
<tr>
<td>Total</td>
<td>77</td>
<td>53</td>
</tr>
<tr>
<td>Depredated (%)</td>
<td>14 (18.2)</td>
<td>8 (15.1)</td>
</tr>
<tr>
<td>Parasitized (%)</td>
<td>19 (24.7)</td>
<td>7 (13.2)</td>
</tr>
<tr>
<td>Abandoned (%)</td>
<td>6 (7.8)</td>
<td>2 (3.8)</td>
</tr>
</tbody>
</table>

* Early nests = initiated on or before 22 May 1985 or 30 May 1987; Late nests = initiated after 22 May 1985 or 30 May 1987.
* Significant difference between overall (early and late) predation rates in 1985 and 1987; $G = 3.82, P = 0.051$.
* Significant difference between overall (early and late) parasitism rates in 1985 (N = 128) and 1987 (N = 59); $G = 21.60, P < 0.0001$.
* Significant difference between parasitism rates in early nests in 1985 (N = 75) and 1987 (N = 35); $G = 16.35, P < 0.0001$.
* Significant difference between parasitism rates in late nests in 1985 and 1987; $G = 5.54, P = 0.02$.

Twenty-six (20.3%) Prothonotary Warbler nests were brood parasitized by Brown-headed Cowbirds in 1985, and although early nests were parasitized more frequently than late nests, the difference was not statistically significant ($G = 2.94, P = 0.09$; Table 2). No brood parasitism occurred in nests in 1987. Data on effects of cowbird parasitism on warbler reproductive success will be published elsewhere.

Female Prothonotary Warblers abandoned 10 (5.2%) of 191 nests, and abandonment rates did not differ between years ($G = 0.75, P = 0.39$) or between early and late nests (Table 2). Two (20%) of the 10 nests were abandoned after young had hatched. Based on timing of abandonments, none was attributable to observer disturbance.

**Fledging weights.**—Prothonotary Warbler young fledged 10–11 days after hatching, and overall mean weights at 9 days were $11.71 \pm 0.71$ g and $11.51 \pm 0.93$ g from early and late nests, respectively. Weights of fledglings from early nests in 1985 were nearly significantly greater than those from early nests in 1987 ($Z = 0.732, P = 0.058$). However, weights did not differ between years for fledglings from late nests. Whether years were analyzed separately or together, mean fledging weights did not differ significantly between early and late nests (Table 1).

**DISCUSSION**

Dates of arrival and territory sizes.—Because most of the information on Prothonotary Warblers comes from Walkinshaw’s (1938, 1939, 1941, 1953) studies, I compare my data primarily with those from his Michigan and Tennessee populations. The time of arrival for male Prothonotary
Warblers on my study area falls approximately one month earlier than in Walkinshaw's (1938) Michigan study and 1–2 weeks later than for males on Walkinshaw's (1941) Tennessee study site (based on date of first egg laid). The reason for the discrepancy between arrival dates in this study and in Walkinshaw's Tennessee study is not clear, but it simply may reflect normal yearly variation.

Mean territory size for 13 Prothonotary Warbler pairs in Michigan (Walkinshaw 1953) was 1.48 ha, nearly three times larger than the mean territory size in my study. Manipulation of nest-box density (Petit 1986) in my study may account for this difference. (Results of those manipulations will be published elsewhere.) However, even on plots where no nest boxes were present, territory size averaged only 0.64 ± 0.10 ha (SD) (N = 10). On the other hand, Kleen (1973) found that the average size of 10 Prothonotary Warbler territories in southern Illinois was approximately 0.50 ha, similar to the average territory size in this study. All of the birds in Kleen's (1973) study defended territories around natural cavities. Differences in territory size may also be due to differences in habitat quality in the different studies. Walkinshaw (1953) studied Prothonotary Warblers nesting in bottomland habitat bordering a fairly small river (Battle Creek River, Michigan). Kleen (1973) and this study dealt with warblers nesting in flooded habitat where there probably were more nest cavities (dead snags) available and where nearly all nests were situated over standing water.

Variation in clutch sizes and reproductive success.—Average clutch size and incubation time in this study were similar to those for Walkinshaw's (1941) Tennessee population, and as in Walkinshaw's study, clutch size decreased during the season. In both Walkinshaw's Tennessee population and this study, mean clutch sizes were smaller than those of Michigan warblers, particularly early in the season. Egg measurements in the present study were similar to those for Walkinshaw's (1941) Tennessee population \((\bar{x} = 17.88 \times 14.29 \text{ mm}, \ \text{N} = 98)\) and were smaller than warbler eggs in Michigan \((\bar{x} = 18.53 \times 14.70 \text{ mm}, \ \text{N} = 196; \ \text{Walkinshaw} 1941)\). Although warblers in Michigan (Walkinshaw 1941) often attempted a second nesting after the first was successful (at least one young fledged), none of the breeding pairs had two successful nests. In Tennessee, Walkinshaw (1941) found that two broods often were raised in one season, although he did not document exact percentages. More than three-quarters of the females in this study made at least two nesting attempts during the season, and a large percentage of those were successful in both nesting attempts. Differences in clutch sizes and tendency to double-brood in the different areas may be a consequence of differences in lengths of breeding seasons at the different latitudes (Lack 1947, 1948). For instance, Walkinshaw
(1941) reported the average breeding season (from date of first egg laid to date of termination of last nest) of Prothonotary Warblers in Michigan was 53 days compared with 108 days of nesting in Tennessee.

Hatching and fledging success.—Prothonotary Warblers in this study had high hatching success (84.2%) and low nestling mortality (11.4%), including losses due to predation and nest abandonment. Walkinshaw (1941) found hatching success of 38% of 413 eggs laid in Michigan, and 61% of 163 eggs laid in Tennessee. Nestling mortality was 33% in Michigan, but no nestling mortality occurred at his Tennessee area. Walkinshaw (1941) attributed the lower nesting success in Michigan to competition from and nest destruction by House Wrens (Troglodytes aedon) which were not present in either Tennessee site. Similarly, preliminary data from an Ohio population of Prothonotary Warblers (K. E. Petit 1988, Petit et al., unpubl. data) suggest that House Wrens may have an adverse effect on warbler nesting success there.

Much of the nestling mortality not due to predation or abandonment occurred in nests where hatching was asynchronous. In those nests, the nestlings that hatched last were apparently at a disadvantage compared with their older, larger nestmates, and, at least in some cases, the youngest nestling was the one to die.

Predation, cowbird parasitism, and nest abandonment.—Although predation increased in frequency from 1985 to 1987, the percentage of nests depredated in this study was lower than in Walkinshaw's (1941) study, where at least 41% of 27 Prothonotary Warbler nests suffered predation. By placing their nests over water, Prothonotary Warblers may be better protected from mammalian predators. In Ohio, Prothonotary Warblers nesting over fairly deep (30–50 cm) water within a marsh suffered no predation, whereas House Wrens nesting over land in the same marsh and the same nest box type suffered 20% predation by mammals (K. E. Petit 1988). As might be expected, most of the predation in the present study was on nestlings rather than on eggs, perhaps due to increased activity around the nest site (e.g., Best 1978). Predation frequency did not vary with time of the season, and nests on island plots were not safe from predation. This last result perhaps is not surprising because the majority of nests apparently were destroyed by snakes. Raccoons also were present on some island plots.

In Walkinshaw's (1938) study, cowbirds parasitized only 3 (10.7%) of 28 Prothonotary Warbler nests in Michigan. Warblers in this study suffered more than twice as much brood parasitism in 1985, but none in 1987. Differences in parasitism rates in Walkinshaw's and my study simply may reflect annual variation in regional or local densities of cowbirds.

Fledging weights.—Fledging age for Prothonotary Warblers in this study
was similar to those in Walkinshaw's (1941) Michigan (11 days) and Tennessee (10.75 days) populations. Walkinshaw did not report fledging weights for his Tennessee birds, and in Michigan mean weight of 10 birds at 9 days was 12.41 g (Walkinshaw 1938, 1939). Meyer and Nevius (1943) reported mean 9-day weight of 11.82 g (N = 12) for Prothonotary Warbler young in eastern Tennessee. Whether those differences between studies are real, and reflective of geographic variation in weights, or the result of sampling error is not known. However, because Michigan birds laid larger eggs than Tennessee birds (Walkinshaw 1941, this study), it is probable that nestlings were also larger (and consequently weighed more) in that northern population. A positive correlation between egg size and nesting size has been found for some other passerine species (e.g., Howe 1976, Richter 1984).

Prothonotary Warblers in this study had relatively high nesting success, certainly higher than that reported for a population in Michigan (Walkinshaw 1941). Although predation had the greatest effect on warbler reproductive success, relatively fewer nests were lost to predation in this study than in Walkinshaw's Michigan population. The high reproductive success in this study is probably due to a longer nesting period, compared to that in Michigan, and a lack of competition for nest-sites with other, more aggressive species (i.e., House Wrens).

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LITERATURE CITED

Petit • PROTHONOTARY WARBLER BREEDING BIOLOGY

OBSERVATIONS ON THE BREEDING BIOLOGY OF PASSERINES IN A SEASONALLY FLOODED SAVANNA IN VENEZUELA

ALEXANDER CRUZ AND ROBERT W. ANDREWS

ABSTRACT.—The breeding biology of passerines was studied in a seasonally inundated savanna in the llanos of western Venezuela. A total of 412 nests of 36 species were located, and other evidence of breeding activity was observed for 13 additional species. Most species bred principally in the early half of the wet season, sometimes starting very late in the dry season. Other species bred throughout the wet season, although generally with a gradual decline in the latter half. A few species bred primarily or entirely in the latter half of the wet season. Ground-nesting species bred principally, and often exclusively, at the beginning and end of the wet season, avoiding the main part of the rains. The Shiny Cowbird (Molothrus bonariensis) was a brood parasite on four species, with two important host species, the Pied Water-Tyrant (Fluvicola pica) and the White-headed Marsh-Tyrant (Arundinicola leucocephala). The first known nest of the River Tyrannulet (Serophaga hypoleuca) and the first known breeding north of the Amazon River for the transequatorial migrant Yellow-browed Tyrant (Sattrapa icterophrys) are described. Natural history information is presented for the little-known White-naped Xenopsarí (Xenopsarí albinucha), and for the Yellow-browed Sparrow (Ammodramus aurifrons) and the Grassland Sparrow (A. humeralis) in one of the few known areas of sympatry. Received 20 May 1988, accepted 15 Sept. 1988.

The savannas (llanos) in Colombia and Venezuela cover an area of approximately half a million km², constituting the largest uninterrupted surface of neotropical savanna north of the equator (Sarmiento 1984). The llanos constitute approximately a third of the surface of Venezuela, and dominate the landscape in the plains that surround the Orinoco River. The Venezuelan llanos have two dominant types: Trachypogon savannas (which are nearly treeless in the east and semi-wooded in the central llanos and the Andean Piedmont), and the seasonally flooded savannas in the west (Fig. 1) (Ramia 1967).

The passerine avifauna of the llanos, especially of the flooded savannas, is imperfectly known. Basic distribution and ecological information is included in Meyer de Schauensee (1964) and Hilty and Brown (1986) for Colombia, and in Phelps and Phelps (1958, 1963) and Meyer de Schauensee and Phelps (1978) for Venezuela. Species lists, with varying amounts of additional information, have been provided for the Colombian llanos by Olivares (1974), Barreto (1981), and Furniss (unpubl. data), and for the eastern and central Venezuelan llanos by Berlepsch and Hartert (1902),

Cherrie (1916), Friedmann and Smith (1950, 1955), Smith (1952), and Thomas (1979). The only detailed passerine data for the flooded savannas of the western Venezuelan llanos are in de Visscher (1983), who examined avian community structure, principally in the isolated woodlands, and Ramo and Busto (1981, 1984), who studied breeding biology, based on 164 nests of 35 species.

In this paper, we present information on the breeding biology of 45 species, including data on 412 nests of 36 species and for the sake of completeness we also summarize the records of Ramo and Busto (1984), for a total of 54 species, and 576 nests of 48 species. We report the first known nest of Serpophaga hypoleuca, and the first known nest of Satrapa icterophrys in northern South America.

STUDY SITE

We made observations at Hato El Frío (the same site used by Ramo and Busto 1981, 1984), a cattle ranch located at 7°35′–7°55′N, 68°45′–69°00′W, in northern Apure state.
Venezuela (Fig. 1). It covers 78,000 ha at an elevation of 65–75 m. The land is flat with an east-west slope of 0.02%, and the climate is characterized by slight annual temperature variations and by well-defined rainy and dry seasons. The median annual temperature is 27°C, with a daily mean variation of 9.5°C. Temperatures vary little annually, with March the hottest month and July the coolest. At Mantecal (approx. 40 km southwest of Hato El Frío), annual precipitation varied from 1314–2080 mm, with an average of 1645 mm. About 90 percent of the rain falls in the May–October rainy season. The start of the rainy season is variable; it may be as early as late March or as late as June (Thomas 1985) or even July (pers. obs.). The December–March dry season is virtually or entirely rainless; April and November are transitional months.

Hato El Frío is situated in a flooded savanna. Most of the ranch is covered by savannas and water bodies; only about 20% is wooded. Ramia (1972) and Castroviejo and López (1980) recognized the following vegetational types on El Frío. Matas are isolated groves of trees 20–25 m high, with a dense shrub understory, found on sites slightly above maximum water level within an open landscape. Gallery forests occur along major watercourses and are subject to wet season flooding. They have a single stratum of trees 10–12 m tall. Esteros are alluvial bottom savannas found in depressions up to 2 m deep. They are flooded throughout the wet season and retain water into the dry season. Caños are riverine overflow channels which also retain water into the dry season. Bajíos are floodplain savannas that are shallowly flooded (up to 5 cm) only in the wet season. Their vegetation is dominated by low grasses and sedges (<15 cm). Spiny shrubs (mostly <3 m) occur sporadically, either singly or clumped. Bancos are riverbanks of active or former watercourses. Never flooded, they are covered by tall grass with some shrubs in different associations on the lower and higher parts. Many introduced shrubs and trees occur around buildings and on the dikes constructed for water control and/or roads.

All data were collected within a circle (diameter 4 km, area 12.6 km²) centered on the Estación Biológica de El Frío, located beside the main complex of ranch buildings. The circle composition is approximately as follows: banco (mostly with human-induced disturbance communities) 25%, estero/caño 25%, bajíos 40%, and matas 10%. Gallery forest was only marginally represented. Approximately 6 km of dikes were in the area.

METHODS

Data were collected from 12 August–28 November 1982, 5 June–2 November 1983, and 28 June–7 July 1984. Nests were located by daily searches through the study area. The amount of effort in major habitat types was approximately as follows: banco 45%, estero/caño 45%, bajíos 10%. The nests that we located were visited regularly until no longer active. We tried to visit nests every 2–4 days, but some were checked less often. We tried to minimize the time spent at the nest and of disturbance to the surrounding vegetation. We also noted the presence or absence of eggs and nestlings of Shiny Cowbirds.

RESULTS

A total of 412 nests of 36 species were found, and behavioral evidence of breeding activity was found for an additional 13 species (Table 1). Clutch size and egg measurements are recorded in Table 2. The following species accounts amplify previous natural history observations. Detailed information is generally not included unless it is new information or augments published information.

River Tyrannulet (Serpophaga hypoleuca). This scarce and local species
<table>
<thead>
<tr>
<th>Species</th>
<th>Apr</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scardafella squamnata*</td>
<td>7(^b)</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Columbina minuta*</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>11</td>
<td></td>
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</tr>
<tr>
<td>Synallaxis albescens</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Certhiaxis cinnamomea</td>
<td>11 (1)(^c)</td>
<td>5</td>
<td>11</td>
<td>3 (1)</td>
<td>2 (2)</td>
<td>32 (4)</td>
<td></td>
<td></td>
<td></td>
</tr>
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*a* Non-passerines.
*b* Nests recorded in this study.
*c* Nests recorded by Ramo and Busto (1984) in parentheses.
*d* C—nest under construction; N—food being carried to nestlings; F—dependent fledglings.
*e* Number of parasitized nests; not included in numbers of total nests.
*f* Passerines only.
### Table 2

**CLUTCH SIZES AND EGG MEASUREMENTS**

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### Table 2
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**Note:** For some common species, egg measurements were not obtained from all clutches.

a Total number of clutches.
b Total number of eggs.
is little known, and the nest was undescribed. On 27 July 1983, a family
group was observed within a Mimosa thicket along a dike. One member
was a fledgling otherwise identical to the adults in plumage. It infrequently
foraged, but usually followed the adults through the thicket, constantly
begging. On 13 October 1983 at 08:40 h, we found a nest with 2 eggs.
The nest was a delicate, tightly constructed cup made of fine grass with
spider web woven in, especially at the points of attachment to the sup-
porting plant. It was lined with large white feathers. The nest measured
3.5 cm from the bottom to the rim top, and 4.5 cm across the outer edges
of the rim top. The cavity measured 2.7 cm deep and 3.2 cm wide. The
nest was placed 55 cm above the ground in a fork between the main stem
and a major side branch of an 88-cm tall Paltea trinervis (Malvaceae), a
semi-woody herb. The plant was in the middle of a 180-m wide dry bajío
pasture, bordered on 3 sides by dense, 2-m high thickets of Cassia and
several scattered 7-8-m-tall trees. The 2 eggs were unmarked dull white
with a very slight buffy-cream tinge (Table 2).

Pied Water-Tyrant (Fluvicola pica). Water-tyrants breed throughout the
wet season, beginning soon after the rains start, which may be as early as
late March or as late as July. In June and July 1983, 86.5% (64/74) of
nests were placed adjacent to caños or lagunas, in trees, shrubs or Mimosa
piagra thickets. As the season progressed and stiff emergent vegetation
grew, nests were more often placed within such vegetation in esteros
(84.4% in September and October).

White-headed Marsh-Tyrant (Arundinicola leucocephala). The species
breeds throughout the wet season, with a peak in the latter half of the
season (15 of 19 nests in August–October). As with F. pica, early (June–
July) nests were near caños and lagunas (100%, N = 4), while late (Sep-
tember–October) nests were in esteros (100%, N = 15).

Yellow-browed Tyrant (Satrapa icterophys). It was uncommon in semi-
open bancos, mostly near water. This species breeds during October–
December from northeastern and central Brazil and northern Bolivia to
Northern Argentina and migrates north across the equator to spend the
austral winter in Venezuela (Meyer de Schauensee 1966, Meyer de
Schauensee and Phelps 1978). We recorded 2 cases of confirmed breeding
at Hato El Frío. On 17 August 1982, a pair was observed constructing a
nest. On 21 August, it appeared complete but it had no lining when we
examined it. The nest was a shallow cup of fine twigs and rootlets with
some untidy strands of material hanging below. The nest was placed 2 m
above ground in a distal fork of a branch of a 20–25-m-tall Ceiba pen-
tandra. The nest subsequently disappeared, perhaps due to the activity
of a pair of Phacellodomus rufifrons, which constructed a nest at the precise
spot where the tyrant nest had been.
At 08:00 h on 21 September 1983, two recently fledged dependent juveniles were observed in a thicket bordering a small laguna. They perched together low in the shrubbery, only occasionally attempting short, clumsy flights. They did not move about or follow the adults, and their begging was generally restrained. The young birds were about ¾ adult size, with very short bills and stubby tails. All four birds were seen at the same spot on 26 September, but not thereafter.

White-naped Xenopsaris (Xenopsaris albinucha). Uncommon in bancos, with scattered trees, shrubs, and tall herbaceous vegetation. Nests were found through most of the wet season (June–September). All were cups placed in forks between branches 10–15 m high in trees 15–20 m tall. Sitting birds were seen on these nests on 23 and 28 August.

Saffron Finch (Sicalis flaveola). Nest were placed in nests of Certhiaxis cinnamomea (8), Phacellodomus rufifrons (7), Icterus nigrogularis (5), 1 each in nests of Fluvicola pica, Pitangus sulphuratus and Cacius cela, and 1 in a hole in a wooden fence-post. Man-made structures such as buildings, stone walls, and hollow pipes have also been used (Friedmann and Smith 1950, C. Casler pers. comm.).

Yellow-browed Sparrow (Ammodramus aurifrons) and Grassland Sparrow (A. humeralis). The distribution of these species is generally allopatric; aurifrons occurs mainly in the Amazon basin (especially the western half), and humeralis is found widely both north and south of the Amazon basin (Short 1975). At El Frío, both species were found, aurifrons much more commonly. Their distribution overlapped widely but only humeralis was found in bajios (except at the borders between bajios and bancos, where both species were found). In general aurifrons was found in areas with more shrubs and scattered trees, while humeralis preferred more open areas such as bajios and grassy bancos. Most aurifrons nests were found in grassy-herbaceous sites on bancos, while most humeralis nests were in bajios (either wet or dry), but they were generally widely separated. In other areas of sympatry either the two species showed complete habitat segregation or only one of the two species was present locally.

Yellow-hooded Blackbird (Agelaius icterocephalus). Two solitary nests recorded at El Frío were unusual for this normally highly social species. At Hato Masaguaral, Wiley and Wiley (1980) recorded nesting only in a 6-week period from mid-October to late November; however, they do not nest there every year (B. T. Thomas pers. comm.). At Masaguaral, blackbirds nested only in stands of Thalia, a tall, stiff emergent, aquatic plant. Prior to October, the plants were not large enough to support nests, and by late November, the wet areas were dry or rapidly drying, and the plants were decaying. The July nest at El Frío was in the grass Paspalum fasciculatum in an estero, and the October nest was in a small (60 m²)
stand of Thalia in an estero. The absence of Thalia stands or similar dense, robust emergent vegetation in the study area probably accounts for the rarity of this species.

Shiny Cowbird (Molothrus bonariensis). This widespread species is a brood parasite, with records of parasitism on 201 species (Friedmann and Kiff 1985). Seven passerine species were found to be parasitized at Hato El Frío (4 in this study, and 6 by Ramo and Busto 1980, 1981); four species were important hosts. The 7 species were: 1. Cranioleuca vulpina. Ramo and Busto found 1 parasitized nest, and 1 parasitized nest had been observed previously (in Venezuela) by Cherrie (1916). 2. Fluvicola pica. Ramo and Busto recorded an 11% rate of parasitism (3 of 27), whereas 54 of 102 (54%) nests that we found were parasitized. 3. Arundinicola leucocephala. Rates of parasitism at Hato El Frío were very high: 80% (4 of 5 nests) by Ramo and Busto and 92% (12 of 13 nests) in this study. 4. Campylorhynchus griseus. One parasitized nest was found by Ramo and Busto, and 1 case was recorded at Masaguaraal (Thomas in Friedmann and Kiff 1985). 5. Agelaius icterocephalus. Three nests have been found at El Frío: 1 unparasitized nest by Ramo and Busto, and 1 unparasitized and 1 parasitized nest by us. 6. Sturnella militaris. Ramo and Busto found that 71% (10 of 14) of the nests were parasitized, all early in the breeding season (May–June). 7. Quiscalus lugubris. Ramo and Busto found 30% (6 of 20) of nests parasitized. All four nests we found had been parasitized; all had been abandoned when found.

**DISCUSSION**

Savannas appear to be one of the most marked examples of seasonal tropical ecosystems with rainfall concentrated in 4–6 months, and a dry season of no less than 4 months with little or no rain. The contrast between the periods of rain and drought is marked. The landscape at Hato El Frío changes accordingly; in the wet season much of the land is flooded, at least shallowly, with only small and widely scattered (and mostly man-made) areas remaining above water, while in the dry season it has an arid appearance, with the little remaining water highly concentrated in a few watercourses, esteros, and man-made stock ponds. The annual cycles of plants and animals are consequently highly seasonal.

In seasonal areas of the tropics, passerines are primarily wet season breeders (Skutch 1950, Snow and Snow 1964, Fry 1983). At Hato Masaguaraal, only 3 of 54 species of breeding passerines are known to nest exclusively in the dry season (Thomas 1979), although an additional 8 species started breeding in the late dry season and continued into the wet season. Even within the wet season, breeding activity is not evenly distributed. Breeding activity at El Frío showed a peak in the first half of
the wet season, then dropped to a lower level in the second half before virtually ending in November (Fig. 2). Both our data and those of Ramo and Busto (1984) show the same pattern.

Although the avifauna as a whole bred throughout the wet season, individual species showed different peak breeding periods within the wet season. We have grouped 42 species according to peak breeding times in the llanos. These periods are based principally on data from Hato El Frío (Ramo and Busto 1984, this study) and Hato Masaguaral, 170 km to the northeast in an area of semiwooded *Trachypogon* savanna (Thomas 1979, pers. comm.). The El Frío data were collected from April to mid-December in 3 years, and presented as number of nests by month (Table 1). The records from Masaguaral, collected in all months over a period of 6 years, give the months when a species was found breeding, but not the number of nests. The breeding season patterns observed were as follows:

Group 1. Through most of the wet season, with a decrease in the late wet season (Fig. 2): *Synallaxis albescens*, *Certhiaxis cinnamomea*, *Tolmomyias flaviventris*, *Fluvicola pica*, *Xenopsaris albinucha*, *Troglodytes aedon*, *Coereba flaveola*, *Paroaria gularis*, *Sporophila intermedia*, Mol-
othrus bonariensis, and Icterus icterus—(11 species, 26.2%). A brief decrease apparently occurs in the middle of the wet season for at least some species (Synallaxis albescens, Fluvicola pica).

Group 2. Mainly in first half of the wet season (June peak), with many or most beginning to breed very late in the dry season (March or April) and some breeding in small numbers in the second half (Fig. 2): Crani-oleuca vulpina, Todirostrum cinereum, Machetornis rixosus, Pitangus sulphuratus, Myiozetetes cayanensis, M. similis, Conopias inornata, Tyrannus melancholicus, T. dominicensis, Campylohychnus griseus, Thraupis episcopus, Sicalis flaveola, Quiscalus lugubris, Icterus nigrolagus, Gymnomyctax mexicanus, and Cacicus cela—(16 species, 38.1%).

Group 3. Second half of the wet season (August–October), sometimes with sporadic or much lower levels of activity in the first half (Fig. 2): Phacellodomus rufigrions, Arundinica leucocephala, Satrapa icterophyrs, Pitangus lictor, Tyrannus savana, Pachyramphus polychropterus, Volatinia jacarina, and Agelaius icteropehalus—(8 species, 19.0%).

Group 4. Bimodal, breeding at the start (May–June) and end (August–October) of the wet season, sometimes with limited numbers during the middle of the wet season (Fig. 2): Pyrocephalus rubinus, Anthus lutescens, Ammodramus aurifrons, A. humeralis, Sturnella militaris, Sicalis lateola, and Emberizoides herbicola—(7 species, 16.7%). With the exception of P. rubinus, these species breed on or near the ground in or near bajios, and they nest either before the bajios become flooded or after they have begun to dry out.

Data from Hato Masaguaraal (Thomas 1979) and Carimagua, in Meta, Colombia (Furniss, unpubl. data) indicate that Mimus gilvus and Sicalis colombiana breed in late dry to early wet season (February–June) and that Campostoma obsoletum and Tachycineta albiventer breed in the dry season (December–February).

Since the optimal period for reproduction is that when food is most abundant, it is not surprising that most of the birds in the llanos and other seasonal areas of the tropics breed in the wet season, when they exploit the seasonal flush of vegetation, insects, and other food then available (Immelmann 1971, Fry 1983). Seasonal fluctuations in tropical insect populations have been documented in a number of studies, including the llanos (Wolda 1978, Travieso et al. 1977). Insect biomass increases with plant productivity and standing crop biomass. The lower insect biomass values are found during the dry season, whereas peak values are reached during the wet season.

ACKNOWLEDGMENTS

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LITERATURE CITED


RESPONSE OF PASSERINES TO ABRUPT FOREST-RIVER AND FOREST-POWERLINE EDGES IN MAINE

MARY F. SMALL AND MALCOLM L. HUNTER, JR. 1

ABSTRACT.—The effects of abrupt edges upon passerine richness and density in avian communities were investigated by censusing birds along transects perpendicular to two forest-estuarine river edges and two forest-powerline edges. Density and species richness were not consistently greater near the edges than in the forest interior. Richness within 30 m of powerlines was greater than richness from 60 to 90 m of them, perhaps because there were four species that used both forest and powerline habitats. Received 25 Jan. 1988, accepted 1 July 1988.

Forest edges often have greater density and diversity of birds than does adjoining forest (Lay 1938, Johnston 1947), a phenomenon known as the edge effect. The cause of edge effect has been variously explained. Species needing two adjacent ecosystems may join with inhabitants of each ecosystem, resulting in greater density and diversity than occurs in either system alone (Odum 1971). High primary productivity or a large variety of insects at the edge (Hansson 1983) or dense multi-layered foliage or high light intensity (Strelke and Dickson 1980) may be special attributes of edges that attract birds. Edges may act as boundaries of territories and concentrate birds (Anderson et al. 1977). To determine whether the edge effect at forest-water and forest-open land interfaces are similar, and to isolate some of the characteristics of an edge associated with edge effect, we compared patterns of passerine density and species richness at the edges of four oak-pine forest sites in south coastal Maine. Two of the sites were beside powerlines, two beside estuarine rivers. The forests beside estuaries had no riparian vegetation; that is, the upland forest extended to the high-tide level and there was no zone of intermediate vegetation. The terrestrial edges were also abrupt, with a very narrow or no ecotone or zone of intergradation. Thus, the special vegetation of an ecotone would probably not influence bird distribution at these areas.

Study areas.—The areas bordering powerlines, Deer Meadow and Newcastle Ridge, were in Lincoln County, and two areas beside estuarine rivers, Robinhood Cove and Holt Forest, were in Sagadahoc County. Robinhood Cove and Newcastle Ridge were 28.8 ha in size. Deer Meadow had an area of 11.5 ha, and the part of the Holt Forest that was studied

extended for 14.4 ha. The periphery of each area was at least 200 m from any other edge. Vegetation at all areas was composed primarily of red oak (*Quercus rubra*) and white pine (*Pinus strobus*). Hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamia*), and white birch (*Betula papyrifera*) were common. All study areas except Holt Forest contained parts of a red maple (*Acer rubrum*) swamp. Several juniper patches were located from about 180 to 300 m from the edge at Robinhood Cove. The Robinhood Cove study area on Georgetown Island ended abruptly at a rocky shoreline. The Holt Forest was on Arrowsic Island; most of the shore was rocky, but part of it was a tidal flat with some salt marsh vegetation. Newcastle Ridge and Deer Meadow were along a powerline established between 1965 and 1966. The powerline corridor was 60-m wide and was dominated by grasses and low shrubs such as raspberry (*Rubus* spp.) and blueberry (*Vaccinium angustifolium*). The right-of-way is maintained with a 4-year periodic application of herbicides. The most recent application was in 1985. Newcastle Ridge is south of the powerline; Deer Meadow is about 1 km east of Newcastle Ridge, on the north side of the powerline. Selective cutting had been done in past years at both sites, and damage from gypsy moths was also apparent.

**METHODS**

Parallel transects were established from the powerline or river edge to 360 m into the forest interior, with flagging dividing it into 30 m segments. There were eight transects each at Newcastle Ridge and Robinhood Cove and four each at Deer Meadow and Holt Forest. Transects were 100 m apart and at least 240 m from any other edge; at Deer Meadow, transects were only 80 m apart. Bird densities were censused by line transect sampling (Anderson et al. 1976, Mikol 1980). Six censuses were conducted at each study area in 1984 and again in 1985. Study areas were censused sequentially from 28 May through 4 July in 1984 and from 26 May to 5 July in 1985. We began censusing within a half hour of sunrise and ended before 0945 hours. We alternately began each census at the first or last transect of a study area. Censuses were not conducted during rain, strong wind, or moderate to dense fog. During each census, we recorded species, sex, perpendicular distance from the transect, and the 30-m segment for each bird that was observed. Pairs and flocks of birds were recorded as a unit or group, although the number of individuals was recorded and later used to correct estimates of density (Burnham et al. 1981). Densities for passerines were estimated using a modification of Emlen’s technique (Ramsey and Scott 1979).

Several passerine species were grouped as “edge” or “interior” birds. A species was included in the edge group if more than 60% of its sightings were within 60 m of one study area’s edge during both years of the study. For species with few observations, this trend also had to occur within another study area for a year. If fewer than 5% of the sightings for a species were within 60 m of an edge at one study area for both years, it was classified as an “interior bird.”

Multiple linear regressions (Dixon 1983) were used to determine whether passerine density or passerine richness was related to the distance from the edge. Ramsey and Scott’s (1979)
modification of Emlen's technique was used to determine the density of passerines at various intervals from each edge. These intervals were 30-m long at the two larger study areas, but 60-m segments were used at Deer Meadow and Holt Forest to increase sample size. The density of passerines in the interval nearest the edge was compared to the density of the rest of the study area according to Chebyshev's theorem (Lapin 1980). Richness from 0 to 30 m from an edge was combined for each edge type and compared to richness at 60 to 90 m by a t-test.

RESULTS

The study areas beside powerlines had more passerine species within 30 m of the powerline than within 60 to 90 m of it ($P < 0.05$), but study areas beside rivers did not show this abrupt change in richness ($P > 0.05$) (Fig. 1). Overall, multiple regressions indicated a decline in species richness as distance from edge increased for three of eight surveys in 1985: Holt Forest ($P = 0.0049$), Robinhood Cove ($P = 0.0357$), and Deer Meadow ($P = 0.0414$).
Density of passerines showed no consistent relation to distance from an edge (Fig. 2) and passerine density near an edge was different from the average density of all other segments only at Holt Forest in 1985 \((P < 0.05)\) (Table 1). Multiple linear regressions indicated that density decreased with increasing distance from the edge at Holt Forest in 1985 \((P = 0.0425)\) and at Deer Meadow in 1985 \((P = 0.0003)\).

Chestnut-sided Warbler \((Dendroica pensylvanica)\), Magnolia Warbler \((D. magnolia)\), Common Yellowthroat \((Geothlypis trichas)\), Indigo Bunting \((Passerina cyanea)\), Rufous-sided Towhee \((Pipilo erythrophthalmus)\), Song Sparrow \((Melospiza melodia)\), and Great Crested Flycatcher \((Myiarchus crinitus)\) were classified as edge birds. Interior birds were comprised of Canada Warbler \((Wilsonia canadensis)\), Northern Parula \((Parula americana)\), Wood Thrush \((Hylocichla mustelina)\), and Eastern Wood-Pewee \((Contopus virens)\). Thirty-seven species could not be classified as either edge or interior species. Of the edge species, Chestnut-sided Warbler, Magnolia Warbler, and Indigo Bunting occurred only in the forests bordered by a powerline; Song Sparrows occurred only beside the river edges. Great Crested Flycatchers and Rufous-sided Towhees occupied both pow-
erline and estuarine forests. The flycatchers acted as edge birds only beside one river, and towhees, only beside powerlines.

**DISCUSSION**

Passerines showed no consistent edge effect: richness and total density were not always greater near the edge than in the forest interior. Richness within 30 m of powerlines was greater than richness from 60 to 90 m of them, but this pattern did not occur beside rivers. Also, this trend did not extend farther into the forest: richness declined as distance from the edge increased in only 3 of 8 surveys, two at river sites and one at a powerline site. Different edge species occurred at the powerline and river edges; only the Common Yellowthroat was found at both edge types. Because forest vegetation was similar among study areas, the difference in bird species composition was likely due either to microclimate differences or to the presence of a brushy ecosystem beside one edge type and not the other. The Indigo Bunting (Conner et al. 1983), Chestnut-sided Warbler (Collins 1983), Magnolia Warbler (Collins 1983), and Rufous-sided Towhee (Bent 1968) all need shrubs or brush, and all were found near the powerline edges but not near the river. These species were probably using both the powerline and forest as habitat.

Several studies of abrupt edges have shown that greater densities of birds (McElveen 1979, Strelke and Dickson 1980, Hansson 1983) may occur at the edge than in forest interior. In contrast, Kroodsma (1982) found that in two of three surveys, density was no greater at an abrupt

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**Table 1**

<table>
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<tr>
<th>Study area</th>
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<th>Mean density* interior</th>
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* Densities are per 10 ha. Holt Forest and Deer Meadow have 60-m segments; Newcastle Ridge and Robinhood Cove have 30-m segments.

P (SD). Probability of no difference as tested by Chebyshev's inequality.
powerline edge than in the forest interior. Our findings concur with his results. The study areas where an edge effect occurred (McElveen 1979, Strelke and Dickson 1980. Hansson 1983) were all beside clearcuts, and the edges were unmaintained and younger than the powerline edges; such edges would change with time (Ranney et al. 1981). In contrast, the powerline edges in both studies were maintained every four years, and the river edges were essentially permanent. Balda (1975) suggested that permanent ecotones may not support as diverse a bird species community as temporary ecotones and perhaps density is also not enhanced in permanent edges.

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LITERATURE CITED


Female-female aggression in polygynously nesting Yellow Warblers.—Ford (1983) described the Yellow Warbler (*Dendroica petechia*) as primarily monogamous but facultatively polygynous. This classification has been supported recently by reports of polygyny in two populations (DellaSala 1986, Reid and Sealy 1986). Since male Yellow Warblers provide substantial parental care when mated monogamously (Biermann and Sealy 1982, Sutherland 1987), polygyny may threaten a female's reproductive success and promote female-female aggression (see Yasukawa and Searcy 1982). Both Reid and Sealy (1986) and DellaSala (1986) described the behavior of polygynous male Yellow Warblers but the behavior of females in this mating relationship has not been reported. Here we document another case of polygyny in this species and describe associated female-female interactions.

Study area and methods.—During 1986 and 1987, observations were made of Yellow Warblers nesting in a stand of sandbar willow (*Salix interior*) on the forested dune ridge, Delta Marsh, Manitoba (see Goossen and Sealy 1982, MacKenzie 1982). Four pairs nested on the 25 *×* 100-m site in 1986, and one of two males that settled on the site in 1987 was polygynous. The polygynous male (M1), banded as an adult in 1986, was at least two years old. The primary female's (F1) age was not known; the secondary female (F2) was at least three years old, i.e., banded as an adult in 1985. F2 nested on the site in 1986 and, together with a 2-year-old male, fledged 5 young.

Observations were made for 1–2 h per observation day between 0630 h and 1030 h CDT. We observed individuals at 10–25 m, either from the ground or from a 2-m stepladder. The stage of the nesting cycle for each pair was determined by checking the contents of each nest daily. The males' territories were mapped based on the positions where they sang and where border disputes occurred. Areas of territories were later calculated by superimposing territory maps on a vegetation survey grid and counting squares. Nestlings were weighed daily to the nearest 0.1 g until 6 days old using a digital scale.

Nesting chronologies.—F1 began nestbuilding on 18 May, laid her first egg on 23 May, but after her third egg was laid on 25 May the nest and eggs were preyed upon. F1 started another nest on 27 May and the clutch of 4 eggs was initiated on 30 May. All 4 young hatched and fledged by 22 June. F2 settled on the site on 26 May just after F1's first nest was destroyed. Two successful copulations with M1 were observed on 29 May when nest-building began 7.5 m from F1's nest. F2 initiated a 4-egg clutch on 1 June but only 2 young hatched. They fledged by 24 June. The 2 unhatched eggs were removed on 18 June and were infertile.

Parental feedings and nestling growth.—After mating with F2, M1 appeared to direct his efforts to F1's second breeding attempt. From 3–11 June, M1 fed F1 during incubation at a rate of 3.4 ± 2.6 [SE] trips/h (N = 5 h), within the range of values reported by Sutherland (1987) for older males in this population. However, M1 did not feed F2 while she incubated (N = 10 h). M1 averaged 2.3 ± 0.7 trips/nestling/h (N = 8 h) when feeding F1's nestlings. He first fed F2's nestlings 4 days after they hatched and averaged 0.8 ± 0.5 trips/nestling/h (N = 10 h) until they fledged. M1's feeding rates were within and below the range observed for older males in the population for the nestlings of F1 and F2, respectively (Biermann and Sealy 1982, Sutherland 1987). M1 continued to feed fledglings at least until 5 July but we could not identify them to nest.

Although we did not quantify such departures, during incubation F2 appeared to leave her nest to forage more frequently than F1. F2 also fed nestlings more frequently (4.5 ± 1.0 trips/nestling/h, N = 8 h) than did F1 (0.4 ± 0.3 trips/nestling/h, N = 10 h; *t* = 3.93, df = 8, *P* < 0.01), and this rate was considerably higher than the population average for older

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females (Sutherland 1987). No difference was found in the growth rates of nestlings in the primary and secondary nests (mean mass at 6 days of nestlings in F1’s brood was 8.4 ± 1.3 g, N = 4; F2’s brood, 9.2 ± 0.2 g, N = 2).

Female-female interactions.—During 16 h of observation from 27 May to 10 June, we recorded 29 aggressive interactions between F1 and F2. Only 13 interactions were observed between neighboring females of the 5 monogamously paired Yellow Warblers that nested on this site in both years of the study (N = 127 h of observation). No aggressive interactions between F1 and F2 were observed after 10 June when F1’s brood hatched. Most interactions were initiated by F1 (N = 20; χ² = 9.0, df = 1, P < 0.005) and, of these, 17 were displacements and 3 were contacts. F2 initiated 5 displacements and in 4 interactions the initiator was not identified. Although F1 initiated most interactions during incubation breaks, twice she left her nest while incubating to attack F2. Within M1’s 474-m² territory, 2 female territories were apparent. These were exclusively used areas that were defended aggressively (see Searcy 1986). F1’s territory was approximately twice the size of F2’s but their commonly defended boundary was about half-way between their nests.

Discussion.—Females are expected to mate polygynously when the benefits of male or territory quality exceed the costs of reduced male parental care (Searcy 1982). Age and nesting feeding are two measures of male quality. Sutherland (1987) found that older (>1 yr) males more successfully raised young that returned to the study site than did yearling males. F2 may have chosen M1 because he was older (but see Reid and Sealy 1986) although M1 did not provide more parental care in the form of higher nesting feeding rates than other males in the population. M1’s territory was located on the south side of the forested dune ridge, an area usually settled first by arriving Yellow Warbler males (Sutherland 1987). However, M1’s territory was close to the average size for the site (x = 429 m², N = 6) and the vegetation density and composition was similar to territories held by monogamous males (Hobson 1988).

DellaSala (1986) suggested that polygyny in Yellow Warblers may be promoted by persistent disturbances by the brood-parasitic Brown-headed Cowbird (Molothrus ater) at the nest site causing a female to desert a male’s territory in order to take a chance with an already-mated male. On our study site the incidence of cowbird parasitism is typically about 21% and may have been a proximate factor causing polygyny in this case. As well, the failure of F1’s first nest may have contributed to the polygynous behavior of M1. Hence, M1 may have paired with F2 as “insurance” after F1’s nest failed. When F1 renested, M1 appeared to resume interest in F1 and largely abandoned F2. Although male Yellow Warblers may benefit from polygynous matings, instead of being a male or female strategy per se, polygyny in this species may often be the result of chance nest failure (see DellaSala 1986).

Within territorial passerines, mated females may respond aggressively toward intruding conspecific females in order to defend territorial resources (Morton et al. 1978, Power and Doner 1980, Gowaty 1981) or the parental investment of their mates (see Yasukawa and Searcy 1982). In our population of Yellow Warblers, both males and females foraged primarily on their territories (Hobson 1988). This may have promoted female territoriality in the polygynous trio. Smith et al. (1982) found little evidence for female territoriality within polygynously nesting Song Sparrows (Melospiza melodia), but there females foraged away from their territories. While M1 fed primarily F1’s young (see also Smith et al. 1982, Petit et al. 1988), the care he directed to this female was threatened by F2’s presence. That most aggressive interactions were initiated by F1 toward F2 supports the hypothesis that primary females attempt to prevent polygyny in order to ensure their mates’ parental care. This aggression may fail to exclude secondary females due to differential female quality or time constraints on females, such as egg laying and incubation (Wittenberger 1979, Yasukawa and Searcy 1982).
Acknowledgments.—This work was funded by a Natural Sciences and Engineering Research Council of Canada grant (A9556) to SGS and post-graduate scholarships from NSERC and the University of Manitoba to KAH. The officers of the Portage Country Club permitted us to conduct this work on their property. N. Ford and W. Searcy made useful comments on an earlier draft of this manuscript. This publication is contribution number 163 of the University of Manitoba Field Station (Delta Marsh).

LITERATURE CITED


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**Wintering population of Greater Sandhill Cranes in the Okefenokee Swamp, Georgia.—** Use of the Okefenokee Swamp by eastern Greater Sandhill Cranes (*Grus canadensis tabida*) as a migration stopover or wintering area was first reported by Walkinshaw (1949) and later by Cypert (1957). Patterson (1978) reviewed the migration of sandhill cranes through Georgia and the history of sightings in or near the Okefenokee Swamp. Recent estimates of the number of cranes that winter in the swamp range from 600 (Melvin 1977) to 1000 (J. Eadie in Patterson 1978:44). From 1985 to 1988 we conducted a population study of Greater Sandhill Cranes in the Okefenokee Swamp, Georgia, to determine: the number and distribution of cranes, the duration of winter residence by individual cranes, and their fidelity to the swamp as a wintering area during successive years.

The Okefenokee Swamp (the swamp) is a deep peat swamp-marsh complex of 1890 km$^2$ in southeastern Georgia. Water chemistry and biology are influenced by low pH (range = 3.8 to 4.2). The swamp is composed of a mosaic of freshwater wetland types including emergent marshes, shrub swamps, swamp forests, and lakes (Hamilton 1977). Water levels, fire, and underlying stratigraphy determine the spatial distribution of plant communities and pathways of succession (Rykiel 1977). Marshes, which are locally called prairies, occur as scattered openings in the swamp forest and cover 220 km$^2$ (15%) of the swamp (Cohen 1973).

The swamp exhibits a long hydroperiod, frequently extending over several years, with a normal annual amplitude of 80 cm (Rykiel 1977). Water levels are normally highest in February and reach a low point in June (Rykiel 1977).

Marshes larger than 1 km$^2$ were surveyed for cranes on or near the first and 15th day of each month from 1 October to 15 April (1985–88). Accessible marshes were surveyed by boat and inaccessible marshes were surveyed by helicopter or fixed-wing aircraft. Both ground and aerial surveys were systematic and designed to cover all marsh habitat. Surveys were conducted between 0800–1100 h while cranes were feeding or loafing. To minimize counting pairs or families of Florida Sandhill Cranes (*G. c. pratensis*) that are nonsocial (Bennett and Bennett, in press), we recorded only groups of $\geq$ 5 birds.

In 1985 and 1986, 66 cranes were captured by rocket netting (Wheeler and Lewis 1972) and individually color marked with plastic neckbands, leg bands, or both (Drewien and Bizeau 1978). Eight of these cranes were also equipped with radio transmitters (Melvin et al. 1983). Cranes were aged by examining their wing molt pattern (Nesbitt 1987) and classified as juveniles (<1 year), subadults (1–3 years), or adults (>3 years). Greater Sandhill Cranes were distinguished from Florida Sandhill Cranes on the basis of morphological measurements (Walkinshaw 1973), behavior (Bennett and Bennett, in press), and plumage coloration. Capture and tagging was conducted between 15 November and 15 December each year. Data were also collected on cranes that were color marked or radio tagged by other researchers on the breeding grounds and in Florida. Radio-tagged cranes were monitored from boats, using directional 4- and 8-element Yagi antennae. Tracking from the air was accomplished using two, 2-element “H” style directional antennae clamped to each wing strut of an airplane. Locations were obtained on radio-tagged cranes a minimum of 3 days/week. Observations of color-marked cranes were obtained from boats using 20–45× spotting scopes. Monitoring for color-marked and radio-tagged cranes began on 1 October and continued until the last cranes migrated north in early March.

**Population and distribution.—** Greater Sandhill Cranes normally began arriving in the swamp during October. The earliest date that cranes were sighted on the ground was 27 September 1986. However, most early migrants overflow the swamp and the largest survey
count on 1 November was 31 birds. After mid-November the number of cranes steadily increased and reached a peak in early January (Fig. 1). The population remained relatively constant throughout January but slowly declined during February. Major northward migration occurred during the first week in March and by 15 March less than 50 cranes remained. A small number of cranes, primarily juveniles, remained throughout March and the latest known departure date was 11 April. In northern Florida, cranes begin their northward migration during the final week in February (Williams and Phillips 1972). The largest number of cranes sighted in the swamp was 810 on 1 January 1986. Between years, the magnitude of population peaks was relatively similar, $\bar{x} = 715$, range = 641–810. The greatest variation between years occurred during November and December. This variation probably reflected the timing of fall migration, which is often controlled by weather conditions on northern breeding and staging areas.

Greater Sandhill Cranes also wintered near Banks Lake, which is a state and federally owned swamp-marsh complex 60 km west of the swamp. The number of cranes at Banks Lake was small (60 birds), except during 1987–88 when 270 birds were present. Increased use during this season might have been in response to a managed drawdown of the lake. The distribution of cranes in the swamp was not uniform (Fig. 2). Chesser Prairie and Grand Prairie, although only 10% of the marsh habitat, accounted for 75% of the population. No cranes were observed in the 9 other prairies that comprised 44% of the available marsh. This general pattern of distribution was consistent between years. Water levels seemed to have a moderate influence on distribution. During high water conditions, cranes exhibited a greater tendency to concentrate, especially in Grand Prairie. Low water levels resulted in a wider distribution.

Habitat quality for Florida Sandhill Cranes varies widely between individual marshes in the swamp (Bennett, in press) and seemed to influence the distribution of cranes. Unlike other marshes, Grand Prairie contains extensive stands of red root (*Lacnanthes caroliniana*) which is a major food item in the winter diet of cranes (Walkinshaw 1973). Marshes that lacked red root received little or no use by cranes.
Fig. 2. Distribution of Greater Sandhill Cranes wintering in the Okefenokee Swamp, 1985-1986.

Melvin (1977) and J. Eadie (in Patterson 1978) suggested that the crane population in the swamp was larger than they estimated. Because cranes concentrate in several southeastern marshes that are readily accessible by boat, the birds give a misleading impression of their overall abundance in the swamp. The size of the eastern Greater Sandhill Crane population was estimated at 22,300 birds in fall 1987 (L. Schuman pers. comm.). Based on that estimate, the swamp supports approximately 3.5% of the population and is of relatively minor significance as a wintering area.
Fig. 3. Arrival and departure dates, and length of winter residence by 11 radio-tagged Greater Sandhill Cranes in the Okefenokee Swamp, 1986–1988.

Duration of winter use.—The mean length of time that 11 radio-tagged cranes remained in the swamp from the date of their arrival was 38 days, range = 10–106 days (Fig. 3). Of these cranes, 3 (27%) remained in the swamp from November until spring migration in late February. Of 47 cranes that were color-tagged by 15 December 1985, only 18 (38%) were sighted in the swamp after 1 February 1986.

We made no effort to locate cranes that left the Okefenokee Swamp and moved to wintering areas in Florida or elsewhere. However, observations were received from cooperators in Florida. A crane tagged 4 December 1985 in the swamp was sighted on 14 January 1986 near Gainesville, Florida, by S. Nesbitt. A radio-tagged crane that arrived in the swamp on 1 December 1986 and remained for 30 days was located near Orange Lake, Florida, on 4 January 1987 by R. Urbanek, and a second crane that arrived in the swamp on 25 December 1987 and remained for 17 days was located in central Florida on 13 January.

The tendency for cranes to remain in the swamp did not appear to be related to their arrival date. Cranes arriving in late December were just as likely to continue their migration southward as those arriving in early November. However, of 42 color-tagged cranes that were in the swamp after 14 January, 34 (81%) stayed for the remainder of the winter.

Movement between marshes was common for cranes that wintered in the swamp. Intra-swamp movements by tagged cranes were most common in mid-winter and were normally southward toward Grand Prairie. However, dispersal out of Grand Prairie was uncommon,
which resulted in a growing concentration of cranes in this prairie throughout the winter. Of 47 cranes tagged in Grand Prairie, 43 (91%) remained in Grand Prairie until they eventually left the swamp.

Analysis of our data indicates the crane population that winters in the swamp has a high rate of turnover. Many cranes that arrive in November and December continue their migration southward after spending 1 to 6 weeks in the swamp. Cranes that leave are often replaced by later migrants from the breeding grounds or from wintering areas in Georgia and Florida. Because of this exchange, the winter population in the swamp remains relatively constant. The high population turnover in the swamp during November and December might be due to its position in the migration corridor. Most cranes destined for Florida pass over or near the swamp, and many use it as a stopover area. This northernmost wintering area for cranes commonly experiences sub-freezing temperatures. A possible weather-induced migration was observed in January, 1985 when −10°C overnight temperatures kept the marshes frozen for 3 days. Some cranes abandoned the swamp in December 1986 following heavy rainfall. Feeding and roosting habitat availability in the swamp is influenced by water levels (Bennett, in press). Under high water levels, competition for feeding sites intensifies.

**Wintering site fidelity.**—Return rates for radio-tagged and color-marked birds were combined because many of the radio transmitters failed while cranes were on the breeding grounds. Greater Sandhill Cranes sighted in the swamp at least once were considered returnees even if they later traveled to wintering areas in Florida. Eleven of 32 (34%) color-tagged cranes that wintered in the swamp during 1986–87 returned in 1987–88. However, approximately 130 cranes (16% of the population) wintered in marshes with limited accessibility and not all of these cranes could be examined for leg bands. Assuming that the ratio of tagged to untagged cranes was similar in this group, the actual return rate may have been 41%. The tendency for cranes to return to the swamp did not seem to be related to their known length of stay during the previous winter. Return rates for cranes that spent all of the previous winter in the swamp and those that spent ≤30 days did not differ significantly ($P > 0.05$, $N = 10$). Conversely, several radio-tagged cranes that spent ≤30 days in the swamp during 1986–87 before continuing south returned and spent the entire winter in 1987–88. Cranes that did not return the following winter were sighted in Florida at locations 130–360 km south of the swamp.

Age had a major influence on winter site fidelity. The return rate for adult cranes was 2.4 × greater than that of subadults. Among subadults, those banded as juveniles the year before exhibited the lowest return rate. Only 1 of 14 (7%) juveniles returned to winter in the swamp the following year. Subadults comprised 53% of our tagged sample, and this might have reduced the overall return rate. In 1986–87 and 1987–88, R. Urbanek (pers. comm.) observed an 84% return rate of adult cranes wintering at specific sites in Florida and Georgia.

Although the number of cranes that wintered in the swamp was relatively constant between years, the low return rate suggests that this is not a discrete wintering population. Less than 50% of the population exhibited loyalty to the swamp as a wintering area. Many migratory bird species return in subsequent winters to the area in which they spent their initial winter (Crissay 1965, Nichols et al. 1983). Ralph and Mewaldt (1975) discussed the possible benefits associated with returning to the same wintering area each year, such as familiarity with the distribution of food resources and roost sites. However, Lensink (1964) and Bellrose and Crompton (1970) contended that waterfowl may winter in different areas depending on such factors as weather conditions and food availability. In Florida, Wenner and Nesbitt (1987) found that Greater Sandhill Cranes moved between wintering areas in response to habitat conditions. The swamp might be less attractive to cranes than sites in Florida that offer
greater access to upland agricultural croplands and pasture. In addition, high water levels in the swamp often limit the availability of marsh habitat to cranes in winter (Bennett, in press).

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LITERATURE CITED


Nest habitat and nesting success of Lesser Golden-Plovers.—Many birds, especially ground-nesters with no aggressive nest defense, use camouflage for nest protection (e.g., Lack, Ecological adaptations for breeding in birds. Methuen, London, 1968). At Churchill, Manitoba, I found Lesser Golden-Plovers (Pluvialis dominica) frequently nesting on lichen heath. Their nests appeared far more difficult to see on the variegated lichen substrate than on nesting habitat covered by other vegetation (Fig. 1). At Churchill, scattered trees on the tundra may be used as lookout posts by avian predators and provide cover for surprise-attacking ground predators (Stroud et al., Wader Study Group Bull. 46:25–28, 1986). I examined whether habitat and distance to nearest tree affected nest survival and nest-site selection.

I studied plovers in a 3.75 km² area about 24 km east of Churchill town. I found 23 golden-plover nests. Two nests were excluded from calculations, one because it contained 8 eggs (probably laid by two females) and thus was highly conspicuous even with an incubating bird (the eggs in this nest were eventually depredated, one by one), and another that was deserted for an unknown reason. Twenty of the nests were found during the three first days of the field work (starting 24 June). Four of the nests were found during egg laying, the other ones immediately after laying of the last egg as judged from water flotation.

Nests were visited at 1–4 day intervals during incubation, some of them more than once daily during hatching. On average, hatching took 77 h from pipping until the chick was dry (±30 h [SD]; N = 32 eggs, 10 nests). Eggs that disappeared between two nest visits were therefore counted as robbed. After predation, one (female) or both birds disappeared from their territory (10 of the birds were individually color banded).

At each nest the 3–4 most dominant plants (from % coverage) within a radius of 1 m were recorded and habitat was classified according to the most dominant component (usually covering >60%). The distance from each nest to the nearest tree (>1 m tall; most trees were 2–4 m tall) was measured. Occurrence of the various habitats in the study area was established from parallel transects across the area, 150 m apart. At each 150th pace I classified vegetation by the same procedure as I used at nest sites and measured distance to the nearest tree. Habitat availability is based on 96 point samples throughout the study area. Distances
Fig. 1. Lesser Golden-Plover nests at Churchill, Manitoba, on (A) lichen heath and (B) a non-lichen habitat (dominated by Dryas).
### Table 1

**Habitat Use and Nest Predation of Lesser Golden-Plovers at Churchill, Manitoba, 1986**

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Percent occurrence</th>
<th>Percent use as nest habitat</th>
<th>Depredated &amp; 33.3 nests</th>
<th>Surviving &amp; 71.4 nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lichens</td>
<td>33.3</td>
<td>71.4</td>
<td>2</td>
<td>13</td>
</tr>
<tr>
<td>Sedges</td>
<td>27.1</td>
<td>9.5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Moss</td>
<td>10.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dryas integrifolia</em></td>
<td>9.4</td>
<td>9.5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Tall shrub</td>
<td>13.5</td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Dwarf shrub</td>
<td>3.4</td>
<td>9.5</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Gravel pit; &lt;10%</td>
<td>3.1</td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>vegetative cover</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>96</td>
<td>21</td>
<td>6</td>
<td>15</td>
</tr>
</tbody>
</table>

* Dominating vegetation (from percent coverage within a radius of 1 m).
* On 96 points 150 m apart on parallel transects across the study area.
* Salix spp. (8.3% of the points) or *Betula glandulosa* (5.2%), about 0.2–1 m tall.
* *Rhododendron lapponicum* (2.1% of the points), and *Empetrum nigrum* (1.0%), usually <0.2 m tall.

between nests and trees were compared with 21 points selected randomly from the 96 point samples.

Six of 21 nests (28.6%) were depredated. The predation was total in 5 of the nests, whereas one nest was deserted after 3 of the 4 eggs had been robbed. The predators were never identified, but eggshell remains near one nest had holes indicating avian predation. Nest predation was significantly lower in lichen habitat than in non-lichen habitat (Fisher’s Test, *P* = 0.0307, one-tailed), and lichen habitat was clearly preferred for nesting (*χ²* = 5.60, *P* < 0.02; Table 1).

The six depredated nests were a median distance of 18.5 m from trees and surviving nests a median distance of 19.5 m. The distribution was not statistically significant between depredated and surviving nests (Wilcoxon’s Sum of Ranks test, *R* = 62, *z* = 0.31, *P* > 0.1). The 21 random points from the habitat transects were situated a median distance of 26.5 m from trees, whereas golden-plover nests were a median distance of 19.5 m from trees. These distributions were not significantly different from each other (Wilcoxon’s Sum of Ranks test, *R* = 431.5, *z* = 0.50, *P* > 0.1).

The study shows that the golden-plover nests survived better on the variegated lichen substrate than on a more uniform background of more or less green plants, and that the plovers preferred lichen habitat for nest substrate. Thus, nest predation is a likely factor influencing habitat choice in this species. However, lichen habitats could have been chosen by the plovers for a number of reasons: (1) they are the first to become snowfree and available to the plovers, (2) they are better drained than most of the other habitats, notably the boggy sedge and willow shrub habitats (Skeel, Can. J. Zool. 61:218–225, 1983), and (3) the “porous” lichens may provide better insulating substrate for the eggs. However, *Dryas, Empetrum*, and *Rhododendron* vegetation occurs on the more elevated ground, and should be equally attractive as lichen heath as far as (1) and (2) are concerned. With regard to (3) above in all habitats some lichen would be readily available to line and insulate nests. Camouflage remains the most likely factor making golden-plovers prefer lichen heath as nest substrate.

**Acknowledgments.**—I thank S. Melvin and J. Walters for comments on this note. I am
very grateful to Churchill Northern Studies Centre for their hospitality. The field work was financially supported by a grant from L. Meltzers Hoyskolefond.


Piracy by Ring-billed Gulls on Dunlin.—On 16 December 1987, I observed Ring-billed Gulls (Larus delawarensis) and Black-bellied Plovers (Pluvialis squatarola) pirating Dunlin (Calidris alpina) during a heavy rain at Bolinas Lagoon, California. Dunlin normally feed at the water’s edge preying on polychaetes, amphipods, insects, and small bivalves (Page, pers. obs.); they rarely eat fish. However, during my observations, the Dunlin appeared to be searching specifically for arrow gobies (Clevelandia los). Fish being captured and eaten were generally equal to or less than the length of the Dunlin’s culmen (mean culmen = 37.9 ± 2.7 mm [SD], N = 35; Warnock, unpubl. data). Often Dunlin had difficulty swallowing the fish, and this facilitated kleptoparasitism. Dunlin lost 16 (44%) of the 36 fish they captured during 26 attempts by the kleptoparasites. Twenty-three kleptoparasitic attempts were made by Ring-billed Gulls with a success rate of 65%. Black-bellied Plovers were successful once during two attempts, and once a Dunlin stole a fish from another. Kleptoparasitic attempts were initiated by Ring-billed Gulls standing within 5 m of the feeding Dunlin. Gulls did not chase Dunlin for more than 50 m, and if unsuccessful, the gull landed immediately and resumed watching the feeding Dunlin. Black-bellied Plovers used different attack methods. Both times the plovers were feeding within 1 m of the Dunlin at the moment the latter caught a fish. The plover then ran toward the Dunlin and attempted to snatch the fish from its bill. The unsuccessful plover immediately resumed feeding after the attempt at kleptoparasitism.

The rash of piracy directed toward the Dunlin represents instances of opportunistic kleptoparasitism by visually oriented feeders. During normal feeding, Dunlin prey items are usually not visible when being consumed. This may make them less susceptible to piracy by gulls (Payne and Howe 1976) and plovers. The heavy rainfall may have resulted in a decrease in invertebrate activity (Pienkowski 1981) causing Dunlin to exploit food sources not normally used. In a review of Dunlin stomach contents, Burton (1974) mentioned only one instance of a fish being consumed. On the Bolinas Lagoon in northern California, fish were not found in 30 samples of stomach-pumped Dunlin (Page and Stenzel, unpubl. data), although I have occasionally (<10 times in over three years of extensive observations) seen Dunlin take small fish at this location.

Gulls frequently steal food from shorebirds at Bolinas Lagoon (pers. obs.) and other locations (Brockmann and Barnard 1979, Barnard and Thompson 1985). Interspecific kleptoparasitism in shorebirds is rarer. When it does occur, the aggressor tends to be a visual feeder rather than a tactual one and the contested prey tends to be large rather than small. Many species of shorebirds are tactile feeders. One would predict that shorebirds, when tactile feeding on larger, more visible prey items, will more likely be kleptoparasitized by birds which are visual feeders. Observations of kleptoparasitic behavior by gulls and shorebirds on the Bolinas Lagoon support the above prediction. Shorebirds which switch from small, easily swallowed prey items to larger, more visible, harder to handle prey items must balance the benefits of an energy rich meal to the costs of increased kleptoparasitism.

Acknowledgments.—I wish to thank G. Page, L. Spear, and three anonymous reviewers for their extensive comments on earlier drafts of this note. Additional suggestions by R.
Bowman, S. Griffin, and P. Pyle facilitated my writing. Work at the Bolinas Lagoon was greatly helped by M. Greene’s logistical support. This is contribution number 399 of the Point Reyes Bird Observatory.

LITERATURE CITED


Food and winter territories of Northern Mockingbirds.—In the northeastern United States, the Northern Mockingbird (Mimus polyglottos) may be the only species that maintains a territory throughout the winter. Mockingbirds localize their activities within small territories centered on fruit resources that are defended against conspecifics and often against other frugivorous species (Moore 1978). The fruit resources decline through the winter due to consumption and fruit drop. Despite the food decline, the birds generally are able to remain on a single site throughout the winter. This suggests that the birds have been selected for an ability to compensate for the decline. Two possible proximate mechanisms to achieve this are: (1) assessment of the fruit supply in the fall with establishment of a territory large enough to contain sufficient resources for the winter, or (2) continual adjustment of territories during the winter as the fruit supply declines. This study was designed to test whether mockingbird behavior was consistent with the first mechanism and to document the pattern of food decline through the winter. The primary winter food resource for mockingbirds in the northeast is multiflora rose fruit (Rosa multiflora) (Stiles 1982).

To test the hypothesis that mockingbirds establish initial territories with sufficient food resources to survive the winter, we: (1) determined the multiflora rose berry supply on several territories, (2) monitored the changing availability of this resource, and (3) determined the territory size periodically through the winter. If the hypothesis was correct, we should find that each territory, regardless of size, encompasses at least some threshold minimum in the amount of food resources and, that the density of food resources is inversely proportional to territory size. Furthermore, there should be little change in territory size through the winter, and any changes in territory size should have no relationship to the pattern of declining food resources.

Methods.—We studied seven mockingbirds on the Purchase College campus of the State
University of New York in southeastern New York State. Much of the area is abandoned pasture containing abundant multiflora rose. Five birds were color banded in November and two in January. Each of these birds occupied a separate area; none was paired. Birds' movements were recorded on maps during 68 h of observation during 8 December 1976–5 March 1977. Additional casual field observations were made through the fall and winter. Each bird was observed sequentially during morning, midday, and late afternoon in each of four observation "periods." An observation period was a calendar interval within which each bird was observed for a minimum of three, one-hour periods; one during morning, one at midday, and one in late afternoon. The four observation periods were: 8 Dec.–20 Dec., 6 Jan.–18 Jan., 19 Jan.–2 Feb., 22 Feb.–5 March. Territory boundaries were drawn around all typical defended habitat within the outermost observed sites of each bird. When drawing these lines we excluded undefended areas such as roads and woodlands which intruded into the polygon formed by connecting outermost points. Territory size was measured from these maps using a planimeter. We termed the areas which mockingbirds initially established and defended from late November through December "original territories." We use this term to differentiate areas defended early in the season, the time when territory defense and singing are most vigorous (Breitwisch et al. 1986), from those used later in the winter, when territoriality waned and there was some shifting of the areas occupied.

To monitor the change in relative abundance of the available berries through the winter, we counted berries on sample branches biweekly. On each territory ten multiflora rose bushes were randomly selected and one branch on each bush was marked with an aluminum tag. Tags were hidden to minimize the possibility that mockingbirds or potential competitors were affected by them. The berries on each of these tagged branches were counted once every two weeks.

In early February we estimated food supplies on each territory by belt transect sampling of multiflora rose and Japanese barberry bushes across the length and width of each bird's original territory. Within the transects, height and width of bushes were measured. Berries were sampled at heights of 30, 50, 90, and 120 cm on randomly chosen portions of each bush. At these sampling sites, a 15 × 15-cm square was placed vertically against the bush.
surface, and all berries extending horizontally inward from the square toward the center of the bush were counted. The total number of berries on each bush could be estimated by determining surface area based on height and width (assuming the bushes were roughly cylindrical) and extrapolated from the number of berries sampled in a known area of bush. This February food supply estimate was used in conjunction with our relative abundance index from tagged branches to yield estimates of fruit abundance on each territory from the time of territory establishment until the termination of field work. We ended the study in March when warm weather caused the emergence of insects on which the mockingbirds began to feed heavily. Initial territory size was determined for the five mockingbirds which we color banded in November. We did not measure the other two territories during territory establishment.

Results.—Territorial defense (chasing to the territory boundary) was directed only at other mockingbirds, American Robins (Turdus migratorius), and European Starlings (Sturnus vulgaris). These were the only birds seen foraging on the same fruits.

The five original territories ranged from 0.35 to 1.65 ha (mean ± SE = 0.76 ± 0.56, Table 1). Three of the five birds had similar, small territories, while the other two birds had distinctly larger territories, thus providing a range of variation for analysis.

The original sizes of mockingbird territories (N = 5) appeared unrelated to the number of fruit-bearing bushes (Spearman Correlation \( r = -0.20 \)), the amount of ground covered by these bushes \( (r = 0.10) \), or surface area of the bushes themselves \( (r = -0.30) \). However, inverse correlations suggesting relationships between territory size and food resources were found between the sizes of original territories and the number of berries present \( (r = -0.70) \), the percent of territory area covered by the bushes \( (r = -0.70) \), and the density of bushes \( (r = -0.70) \). Although food supply parameters were not constant among the territories (Table 1), a minimal threshold of fruit-bearing bushes in each territory is suggested. Despite their size disparity, territories 1–3 had similar numbers of bushes (68–80), area covered by fruit bushes (460–495 m²), and fruit bush surface area (1100–1600 m²).

Over the winter, food supply declined rapidly on four of the five original territories (Fig. 1). Most berries disappeared in December and early January, coincident with the first winter snow storms. By mid-January the rates of decline on 6 of the 7 territories were quite low, but they had already lost over 50% of their early December food resources. The size of
utilized territories changed during the winter, but there was no consistent pattern of increase or decrease in size.

Discussion. — Mockingbirds’ multiflora rose food patches represent nonrenewing resources that are most abundant during the initiation of territorial behavior in the fall and decline dramatically through the winter when energy demands are the greatest. At least two alternative strategies for compensation of such a decline are possible: (1) establish as large a territory as is economically possible as long as it contains more than the minimum amount of food resources necessary for winter survival, or (2) adjust the territory throughout the winter as the food supply declines. If mockingbirds assess the food resources in the fall and establish territories containing sufficient food resources to assure survival through the winter, territory size should show an inverse relationship to food density. Such a pattern has been shown previously with other species in the breeding season (e.g., Stenger 1958, Simon 1975) and the nonbreeding season (Gibb 1956, Gill and Wolf 1975, Lederer 1977, Salomonson and Balda 1977). One would thus expect a threshold of minimum food resources as a requisite for territory establishment. That birds can predict long-term suitability of an area has been suggested (Wiens 1973; Stenger 1958). In our study, many berries remained on each territory at the end of the season despite the fact that the winter of 1977 was unusually harsh.

Two systems comparable to the mockingbird’s have been studied. The Townsend’s Solitaire (Myadestes townsendi) (Lederer 1977, Salomonson and Balda 1977) and the European Nuthatch (Sitta europea) (Enoksson and Nilsson 1983) are both territorial during the non-breeding season and subsist on non-renewing food resources that can be assessed in the fall. These studies all found an inverse relationship between food availability and territory size. Supplemental feeding of the nuthatches reduced territory size, suggesting that the nuthatches established territories based on assessment of food resources. Our data for mockingbirds suggest that they may assess the suitability of an area based on a threshold of food resources. Some territories, including the largest ones, contained a similar minimum amount of food resources while others, including the smallest, seemed to contain an excess beyond this minimum.

F. C. Laskey (1933) and A. R. Laskey (1935) found fluctuating winter territory size in mockingbirds. We confirm this finding, and as we predicted, territory size fluctuations later in the season appear unrelated to food. Most birds modified the sizes of the area they used during two-week periods through the winter. Since the supply of berries constantly was declining, it seems unlikely that these expansions and contractions were directly related to the food supply. Logan (1987) found that changes in mockingbird winter territory sizes were related to weather. This further supports our prediction that changes in territory size should be unrelated to food supply decline.

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The correct name for the Olivaceous Cormorant, “Maiague” of Piso (1658).—Nearly 350 years ago, George Marcgraf (also spelled Marcgrave) and Willem Pies (Latinized as Piso), led by Johan Maurits of Nassau-Siegen, conducted natural history explorations in northeastern Brazil (see Whitehead 1979a). Many forms of plants and animals were described for the first time and documented by Piso and Marcgrave (1648) and Piso (1658), with over 500 illustrations based on watercolor and oil paintings (Whitehead 1976). Although specimens were collected on the expedition, no animal specimens are known to be extant (Whitehead 1979a). Some of the descriptions and illustrations from this early expedition were the basis for names introduced by Linnaeus, Gmelin, and others; several of these names have given rise to considerable controversy. Among these is Procellaria brasiliana (Gmelin 1789, p. 564), in the description of which Gmelin cited five references, all of which derive from the bird that Piso (1658, p. 83) called “Maiague” (sometimes rendered “Majaque”).

Gmelin (1789) placed the “Maiague” as the species brasiliana in the genus Procellaria (=order Procellariiformes), but he never saw the original paintings (Whitehead 1979a). In one of the works cited by Gmelin, Willughby (1678, p. 334) stated that Piso’s bird “seems to resemble” Corvus aquaticus, a name then in use for the Cormorant, now Phalacrocorax carbo, of the Old World. Latham (1785, p. 398), also cited by Gmelin, expressed doubt that Piso’s “Maiague” was a petrel. Latham may have consulted the original paintings (Figs. 1 and 2), whereas Gmelin (1789) and the other authors Gmelin cited referred only to Piso’s (1658) published woodcut (Fig. 3) (fide Whitehead, in litt.).

Lichtenstein (1817, p. 175) examined the original oil painting (Fig. 1) and water color (Fig. 2) of the “Maiague” that probably were the basis for the rather crude woodcut (Fig.
3) in Piso (1658). He concluded that the watercolor represented an adult male Anhinga (*Anhinga anhinga*), but later (Lichtenstein 1823, p. 86) reconsidered and used *brasilianus* for the Olivaceous Cormorant.

The name *brasilianus* remained in common usage for over sixty years. Following Brisson's interpretation of Piso (1658) that the feathers of the lower neck are yellow, Ridgway (1889, p. 138) stated that "it is almost incomprehensible" how Piso's "Maiague" could be identified with any known species of cormorant. Ridgway used *vigua* Vieillot (1817) for the name of the Olivaceous Cormorant in which he was followed by Ogilvie-Grant (1898) and the American Ornithologists' Union (1910). Richmond (1926), however, pointed out that *vigua* was based on an older name, *Pelecanus olivaceus* proposed by Humboldt (*in* Humboldt and Bonpland 1805), the name then adopted by the A.O.U. (1931).

Schneider (1938) examined the watercolor (Fig. 2) of the "Maiague" and identified it and the description with the Olivaceous Cormorant. Hellmayr and Conover (1948), on the basis of Piso's (1658) description and Schneider's (1938) identification, used the name *Phalacrocorax brasilianus* for this species. Nonetheless, the A.O.U. Check-list of North American birds (A.O.U. 1957, 1983) and Dorst and Mougin (1979) considered *Procellaria brasili ana* Gmelin to be indeterminate and used *Phalacrocorax olivaceus* (Humboldt and Bonpland 1805), for the species. However, other recent authors (e.g., Gyldenstolpe 1951; Voous 1957; Pinto 1964, 1978; Oberholser 1974) have used the earlier name, *brasilianus*, for the Olivaceous Cormorant, and a review of its validity is warranted.
Marcgraf's natural history notes were in code, apparently to prevent Piso from having access to his records, with only Johan Maurits being entrusted with the code. Following Marcgraf's death in Angola in 1643 (Whitehead 1979a), the natural history accounts in Piso and Marcgrave (1648) were assembled from these coded notes and edited by Johan de Laet. Piso (1658) edited and condensed Marcgraf's natural history section, introducing many errors. He also added some new material (see Whitehead 1979b), including the account of the "Maiague" that may have been from memory.

Piso (1658) described the "Maiague" as having "colli tantum parte anteriori flavis plumis decorata" which Hellmayr and Conover (1948) concluded must refer to the yellow gular skin, not yellow feathers. Other characters given by Piso (1658) leave no doubt that the "Maiague" is a cormorant. These include Piso's statement that the bird is black, the size and shape of a duck, and that it resembles "Corvum aquaticum" (=Phalacrocorax carbo). He added that the "Maiague" has a hooked beak and curved neck like that of a swan, lives at sea and river mouths, and eats fish. Specimens of the Olivaceous Cormorant from South America have dull straw-colored or brownish gulars, and, in first prebasic plumage, the feathers bordering the gular are a pale buff color (Siegel-Causey, in litt.). That Piso's (1658) description and accompanying woodcut (Fig. 3) could apply to a bird in eastern Brazil other than the Olivaceous Cormorant is hardly conceivable.

The published woodcuts (see also Piso [1957] for a reproduction of the description, in

Fig. 2. Watercolor from the Libri picturati labeled "Magua."
Maiague.

Fig. 3. Illustration of the "Maiague" from a woodcut in Piso (1658).

Portuguese, and woodcut illustration) apparently were based on paintings by artists employed by Johan Maurits during his time as Governor-General of Dutch-occupied Brazil, 1637–1644 (Whitehead 1976). The principal painters were Frans Post and Albert Eckhout (Whitehead 1976), the latter possibly visiting Chile during the time of the expedition (Joppien 1979).

The watercolors and oil paintings eventually were deposited in the Preussiche Staatsbibliothek in Berlin and catalogued as Libri picturati A (two volumes of watercolors and four volumes of oil paintings). These were the originals examined by Lichtenstein (1817, 1823) and by Schneider (1938). In 1941, the paintings were evacuated to Silesia and were not seen or heard of until rediscovered in Poland in 1977 (Whitehead 1979b, 1982). They are now in the Jagiellon Library in Cracow, Poland. As noted by Schneider (1938), Piso's “Maiague” is an oil painting (Fig. 1) in the Libri picturati A 33 (p. 13, labeled “Maguajuba” and “Majaja”) and is represented as a watercolor (Fig. 2) in the same collection as A 36 (p. 224, labeled “Migua”). I believe that both represent the Olivaceous Cormorant and that the watercolor is the basis for Piso's (1658) woodcut (Fig. 3).

Geography also serves as evidence that the “Maiague” is the Olivaceous Cormorant. Maurits' expedition and Marcgraf's activities were confined to northeastern Brazil. Previously published itineraries (Hantsch 1896, Gudger 1912) of Marcgraf are fabricated (Whitehead 1979b), but according to Marcgraf's astronomical notes (Whitehead 1979b) he visited northeastern Brazil from Salvador to Rio Grande do Norte, and almost certainly this applies also to Piso. This is a smaller area of Brazil than assumed by Hellmayr (1929). The only species of Phalacrocorax found there, or anywhere in Brazil, is the Olivaceous Cormorant (Dorst and Mougin 1979). That the “Maiague” of Piso could have been an immature
Phalacrocorax magellanicus in an all black plumage (see Rasmussen 1987), and based on Eckhout’s possible trip to Chile (Joppien 1979) is improbable, since immatures of that species have blackish facial skin (Humphrey et al. 1970). The only species of cormorant in Chile having a yellowish gular region is the Olivaceous Cormorant.

Thus, as shown by Piso’s (1658) description, the accompanying illustration, the original paintings, and by geographical probability, the “Maiague” unquestionably refers to the Olivaceous Cormorant. Procellaria brasiliana Gmelin, 1789, clearly has priority over Phalacrocorax olivaceus Humboldt, 1805, for this species, and Phalacrocorax brasiliensis (Gmelin, 1789) should be reinstated as the correct name for the Olivaceous Cormorant, with the type locality as eastern Brazil.

Acknowledgments.—I thank Janusz Podlecki for photographing the two original paintings from the Libri picturati, and extend my appreciation to M. Zwiercan of the Jagiellon Library for making the photographs available. The U.S. Library of Congress provided the photograph of the illustration from Piso (1658). I also thank P. Whitehead for his encouragement and help. He, with R. Banks, G. Graves, S. Olson, K. Parkes, and D. Siegel-Causey, read the manuscript and offered many useful suggestions.

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Pebbles in nests of Double-crested Cormorants.—While censusing Double-crested Cormorants (Phalacrocorax auritus) breeding on Lake Winnipegosis, Manitoba, in 1987 and 1988 (see McLeod and Bondar 1953 for a description of colonies), I discovered several nests that contained pebbles. Because birds nested on flat or gently sloping substrates and built nests with rims well above the ground, these pebbles could not have gotten into the nests accidentally. Instead, they were probably placed into nests by cormorants. Incorporating foreign objects within clutches or creating “artificial clutches” occurs rarely (geese: Hanson and Eberhardt 1971; Knight and Erickson 1977; penguins, gulls and murres: D. G. Ainley pers. comm.) and has not been reported in the Phalacrocoracidae.

From 4 August to 6 September 1987, I visited 37 colonies containing 35,191 cormorant nests. In 10 colonies, 47 of 12,784 nests contained only small pebbles. Pebbles averaged approximately 4 cm in diameter (range 0.5–10 cm) and “clutches” contained 4.7 ± 4.5 [SD] pebbles. Nests with pebbles were found in colonies both at the egg and chick stages and were observed on earlier visits to colonies by R. W. Knapton (pers. comm.). From 14 to 21 June 1988, 35 of these colonies were revisited. In 9 colonies 74 of 11,286 nests contained pebbles. Four of these colonies had nests with pebbles in 1987. However, unlike the previous year, 18 nests with pebbles also contained at least one egg (x = 1.1 ± 1.3 eggs/nest, range 0–4 eggs), and 6 contained one small chick. Nests with pebbles made up 0.1 to 2.5% and 0.1 to 6.2% of all nests at each colony in 1987 and 1988, respectively. In both years, all three of the nests containing pebbles were located on the periphery (i.e., within two nests of the outer edge) of subcolonies. Colonies were visited briefly to reduce disturbance, and so the age or breeding status of birds that constructed or attended these nests is not known.

Although pebble clutches occurred infrequently, the phenomenon may have been limited, in part, by the availability of suitable pebbles at colonies. Several empty nests occurred throughout the season but the substrates of these consisted typically of fine gravels; sand or compacted guano and small pebbles were seen rarely. The only colony with a pebble substrate recorded the highest frequency of nest with pebbles in 1988. It is possible that some of the smaller pebbles found in nests had been regurgitated (see Siegel-Causey 1986). Regurgitated boi were occasionally found in nests after birds had been disturbed from colonies. Since nests with pebbles were typically located on the periphery of colonies, and contained few if any eggs or young, they may have been attended by young or inexperienced birds (Siegel-Causey and Hunt 1986, Kharitonov and Siegel-Causey 1988). Construction of mock or ephemeral nests by subadult and adult cormorants has been reported (Van Tets 1959; Siegel-Causey and Hunt 1986). In younger birds, this behavior may contribute to the development of nesting skills, and the creation and attendance of pebble clutches may be an extension of this behavior.

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LITERATURE CITED

Cranial pneumatization in the Phalacrocoracidae.—In certain regions of the cranium in birds, air spaces separate inner and outer layers of dense, ossified bone. In many cases, these pneumatic areas (“ossified bone” [sic] of earlier studies—see Serventy et al. 1967) are contiguous with cranial air sacs, but precise functions are still being debated (Harrison 1957, Warneke and Stork 1977, Winkler 1979). Pneumatization occurs late in development and has been used to assess cranial maturation (Winkler 1979); its relationship with age, however, is not well understood, and its reliability as an age index is uncertain (cf. Serventy et al. 1967, McNeil and Burton 1972, Sugimori et al. 1985).

The relationship of the bursa of Fabricius with age has been well-documented, and its size is used regularly to assess chronological age (see Gower 1939, Linduska 1943, Kirkpatrick 1944). Davis (1947) and McNeil and Burton (1972) consequently examined the relationship between cranial ossification and bursa size, but found differing results. Davis qualitatively assessed bursa size and cranial ossification in 110 species in 31 families, and although he found widely varying results, he felt that degree of cranial ossification was directly correlated with age. McNeil and Burton found no such relationship among ossification, pneumatization, and age in 21 species of shorebirds, but determined that bursa size tracked chronological age as it did in other birds.

During the course of a phylogenetic study of the Phalacrocoracidae (Siegel-Causey 1988), I was able to obtain data on cranial pneumatization patterns in 15 taxa in the family. Where possible, I measured bursa size, extent of pneumatization, and various skull dimensions. I examine here the phylogenetic patterns of cranial pneumatization in the Phalacrocoracidae and the relationship between the extent of cranial pneumatization, bursa size (age), and body size.

Methods.—All skeletal measurements were done on museum specimens obtained from various collections. Species of Phalacrocoracidae used in this study and sample sizes are: Reed Cormorant (*Phalacrocorax africanus*, 15), Little Pied Cormorant (*P. melanoleucus*, 21), Brandt’s Cormorant (*P. penicillatus*, 4), Black-faced Cormorant (*P. fuscescens*, 2), Olivaceous Cormorant (*P. olivaceus*, 50), Double-crested Cormorant (*P. auritus*, 57), Little
Fig. 1. Pneumatization patterns of phalacrocoracid skulls. A) Cormorants (Phalacrocoracinae); B) Shags (Leucocarboninae). Shaded area represents pneumatic bone.


Skulls were measured by dial calipers to a 95% replicated accuracy of ±0.1 mm. Length and width of bursa of Fabricius were measured in the field to nearest mm by dial calipers with indeterminate accuracy. I visualized the extent of pneumatized bone by back illumination: nonpneumatic bone in the Phalacrocoracidae is translucent, while pneumatized bone is opaque (see Serventy et al. 1967, Fig. 1 in Stork 1970). Multivariate analyses were performed using BMDP statistical programs (Dixon 1985). Cases with missing data for the variables under analysis were excluded.

**Results.**—Among all phalacrocoracids examined, I observed only two qualitative patterns of pneumatization. In the Reed, Little Pied, Brandt’s, Black-faced, Olivaceous, Double-crested, Pied, Little Black, and Great cormorants, all members of the Phalacrocoracinae (Siegel-Causey 1988), the major centers of cranial pneumatization were the mastoid, the dorsal cranial strut, and the posterior half of the frontal (Fig. 1A). Pneumatic bone in the anterior half of the frontal was restricted to a lateral triangular region on both sides and to three narrow strips. Two of them were located laterally along each edge and one medially at the juncture of the optic septum and the frontal. The lateral extent of pneumatized bone within the frontal was correlated with cranium length in Double-crested (DCC) and Olivaceous (OC) cormorants (DCC: \( r = 0.71, P < 0.001 \); OC: \( r = 0.51, P < 0.001 \), and with
the width of the frontal (DCC: \( r = 0.675, P < 0.001 \); OC: \( r = 0.55, P < 0.001 \)). Sample sizes of other cormorants were insufficient for analysis.

In Socotra, Cape, Imperial (IS), Rock (RS), Pelagic, and Red-legged shags (RLS), all members of the Leucocarboninae (Siegel-Causey 1988), the centers of cranial pneumatization were the same as in the first group of species except for the frontal (Fig. 1B). Pneumatized frontal bone was restricted in these species to a narrow lateral strip on each side (IS: \( \bar{x} = 1.43 \pm 0.54 \) [SD] mm; RS: \( \bar{x} = 1.56 \pm 0.81 \) mm; RLS: \( \bar{x} = 0.91 \pm 0.75 \) mm). The width of the lateral strip was correlated with cranium length (\( r = 0.52, P < 0.001 \)) and frontal width (\( r = 0.61, P < 0.001 \)) only in the Imperial Shag. Frontal pneumatization was not correlated with cranium length nor frontal width in Rock, Pelagic, or Red-legged shags; sample sizes of other shags were insufficient for analysis.

In all cases where I could measure bursa size, the extent of pneumatized frontal bone was uncorrelated with bursa area when the log-linear effects of size (frontal width) were removed (OC: \( r = 0.44 \). IS: \( r = 0.01 \), RLS: \( r = 0.11 \), RS: \( r = -0.09 \), RLS: \( r = 0.11 \)).

**Discussion.**—In his survey of cranial pneumatization in birds, Winkler (1979) placed cormorants implicitly into the group B pattern, which included ardeids, gruiforms, falconiforms, galliforms, and lariids. In this group pneumatized bone is restricted somewhat to the lateral and ventral parts of the cranium, with dorsal areas corresponding to the cerebellar prominences of the brain remaining pneumatic. The only study to examine pneumatization in cormorants explicitly was by Harrison (1957), who, judging by the appearance of the illustration (Fig. 6 in Harrison 1957), unfortunately used a juvenile specimen of *P. carbo*.

Pneumatization of the cranium in adult phalacrocoracids proceeds from three centers: the mastoid (see Fig. 6 in Harrison 1957), dorsal cranial strut (see Fig. 4 in Winkler 1979), and frontal. These pneumatized areas are similar in other Pelecaniformes (Harrison 1957, Winkler 1979), but only the first two centers have been examined previously. The frontal pneumatization pattern is the only one that varies phylogenetically in the Phalacrocoracidae, and it seems to be directly related to the shape of the nasal gland depression on the dorsal surface of the frontal. In cormorants (Phalacrocoracinae), the glands are bilobed and small relative to the size of the frontal: in shags (Leucocarboninae), the glands are single-lobed and large (Siegel-Causey, unpubl. data). In all other pelecaniformes, gland shape is small and bilobed; the pneumatization patterns are more complex but generally follow that seen in the Phalacrocoracinae (Harrison 1957). Therefore, the pneumatization pattern in the Leucocarboninae is a derived condition, and supports the previous findings that shags are the most derived members of the family (Siegel-Causey 1988).

Pneumatized frontal bone occurs only in areas not occupied by the gland depression, and its extent is correlated directly with cranial size, but not age (as measured by bursa size). Either cranial pneumatization in cormorants is not age-related, as previous studies have demonstrated for other birds (McNeil and Burton 1972, Winkler 1979), or bursa size does not correlate with age in phalacrocoracids. At present, neither alternative can be disproved.

Various functions have been hypothesized for cranial pneumatization: strength (Chapin 1949, McNeil and Burton 1972), flight speed (Harrison 1964), “mode of life” (Harrison 1957, 1964), thermoregulation (Warneke and Stork 1977), and structural accommodation (Winkler 1979). Full reviews of these and other hypothesized functions can be found in Harrison (1964) and Winkler (1979). The first three hypotheses are not completely separable and many exceptions can be found. For example, heavily pneumatized crania are a feature of birds which hammer their beaks into substrate when feeding (e.g., Picidae), but high-diving waterbirds (e.g., Pelecaniformes) that experience high impact stress have relatively lesser pneumatized skulls, and many passerines which experience neither (e.g., *Parus, Hirundo, Sitta*) have completely pneumatic crania.

Harrison (1964) predicted that slow-flying species would have the greatest amount of
pneumatization, but McNeil and Burton (1972) documented many cases in the Charadrii where the opposite was true. "Mode of life" is harder to define, and thus difficult to test as a hypothesis, but Harrison (1957, 1964) concluded that diving birds had the least amount of cranial pneumatization, presumably as a means to minimize cranial buoyancy and internal air spaces. Until more rigorous criteria for this hypothesis can be developed, its status remains indeterminate.

Warneke and Stork (1977) hypothesized that increased cranial pneumatization assisted in thermoregulation. They observed a proportionate increase in feather-ruffling during cold weather in juvenile passerines compared to adults, and associated it with lessened cranial pneumatization in younger birds. Such an explanation is ad hoc and proximate, and furthermore no such pattern is seen in waterbirds which will incur much greater heat loss while in water. Other explanations relating to diving depth, swimming or flight speed, flight acceleration, foraging technique, etc. suffer similar fates.

Winkler (1979) surveyed pneumatization patterns in 287 species, and hypothesized that simultaneous structural accommodation of internal (i.e., brain, eyes, glands, etc.) and external (muscle attachment, cranial shape) features was the ultimate explanation for the presence of pneumatized bone. Thus, rugose projections for attachment of muscle or aponeuroses (e.g., the crotophyte or temporal crests of phalacrocoracids) can be maintained without undue weight or cranial deformation of internal cavities. The absence of pneumatized bone within the frontal gland depression allows the nasal gland to fit within the orbit which is otherwise occupied by the eyes. The external (ventral) surface of the frontal thus remains streamlined, which is an important consideration in pursuit divers such as cormorants and shags.

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**Historical status of Harlequin Ducks wintering in eastern North America—a reappraisal.**—Vickery (1988) concluded that “Harlequin Ducks (*Histrionicus histrionicus*) in eastern North America are now and have historically been quite rare and of local distribution.” While there is no doubt that this adequately describes the present situation, there is evidence to suggest that formerly this sea duck was more common there. Phillips (1925), Palmer (1949, 1976), and Todd (1963) clearly stated that numbers of Harlequin Ducks had declined over the periods they considered. Phillips (1925) supported his contention that Harlequin Ducks had declined considerably up to the early parts of the present century in Atlantic Canada by quoting Langille (1884) and Dresser (1871-81), who made reference to hundreds in specific areas of the maritime provinces. Downs (1888) considered them rather common in winter in Nova Scotia. References to New Brunswick may be interpreted as unclear; however, Herrick (1873) considered Harlequin Ducks common in winter in the late 1800s in the Grand Manan archipelago. Peters and Burleigh (1951) noted that the Harlequin Duck in Newfoundland had “... become much reduced in numbers during recent years. It has now become so rare that it should receive protection for all times.” Peterson and Fisher (1955) observed “... hundreds of Harlequin Ducks ...” at one site on Cape St. Mary’s, an area that anecdotal information indicates to have supported thousands in winter.

Christmas Bird Counts (CBC) from 1979-80 to 1987-88 disclosed a pattern of decline for Cape St. Mary’s, Newfoundland ($r = -0.701; P < 0.02$), and for Nova Scotia, where sightings have declined significantly since the mid 1970s ($r = -0.575; P < 0.02$) when those counts first incorporated sites such as Port Hebert, which consistently supported small numbers of wintering Harlequin Ducks.

The present scarcity of sightings of Harlequin Ducks in the Gulf of St. Lawrence may not be indicative of former numbers as Comeau (1909) noted rapid declines in numbers wintering near Pointe des Monts. Rowdon (1969), quoted in McNeil et al. (1973), believed that Harlequin Ducks were once fairly common on the Magdalen Islands. Significant winter concentrations (hundreds) were reported for Anticosti Island (Brewster 1884) for the 19th
1884) for the 19th century. Confusion exists because Ouellet (1969) quoted Schmitt (1904), who referred to the rarity of this species there in summer.

Harlequin Ducks had been more numerous in the coastal Maine area before the turn of the present century (Norton 1896; Knight 1897, 1908; Forbush 1912; Palmer 1949, 1976). Vickery (1988) speculated on a possible increase in Harlequin Ducks in the Maine area since Knight's (1908) report, yet it is doubtful that Knight's figures included Isle aux Haut, which represented 80% of Vickery's estimate of the current wintering population there. Longer term CBC data for Maine at areas frequented by Harlequin Ducks are limited to the York County site, and there is no significant trend there (r = 0.207, P > 0.25; for 1970–1985).

In recent years, observations of wintering Harlequin Ducks have been limited to a handful of sites in eastern North America, i.e., very inaccessible headlands, offshore skerries, and/or park reserves, all typical of wildlife refugia. This point was alluded to by Knight (1908) for the Maine area, and is especially important in light of the apparent abundance of wintering habitat in eastern North America.

Vickery (1988) concluded that the status of Harlequin Ducks wintering in eastern North America historically had been rare. This conclusion masked a pattern of decline noted by many of the authors cited. I believe that Harlequin Ducks were more numerous historically and have declined throughout this region. This decline coincided with the depletion of many migratory birds in the western Atlantic area. Within the same geographic area in which Harlequin Ducks were known to over-winter, the Common Eider (Somateria mollissima) was virtually extirpated. Its special recognition under the Migratory Bird Convention Act, i.e., Article IV (1917) may have overshadowed the plight of the poorly studied Harlequin Duck. Both Phillips (1925) and Palmer (1949) linked hunting, more than any other factor, to the decline of Harlequin Ducks in eastern North America, because this species has been noted for its relative tameness compared to other sea ducks (see Norton 1896, Bent 1925, Phillips 1925, Palmer 1976).

Harlequin Ducks likely were never as numerous as other sea ducks wintering in eastern North America, i.e., hundreds of thousands. Goudie and Ankney (1986) implied that small body size might confer a "disadvantage" to this species relative to the larger scoters and eiders. However, other small-sized sea ducks have relatively large populations in the same geographic areas (e.g., Oldsquaw [Clangula hyemalis]). Surveys systematically reporting numbers (statistics) were scarce up to the early 1920s, so it is difficult to estimate how large the eastern North American population of Harlequin Ducks may have been. Dresser (1871–81) reported one Harlequin Duck for every 20 longtails (Oldsquaws) in the Bay of Fundy. Langille (1884) and Peterson and Fisher (1955) recorded hundreds of Harlequin Ducks at specific sites in Nova Scotia and Newfoundland, respectively. An estimate of 5000 to 10,000 Harlequin Ducks does not seem unreasonable for the former population of this sea duck in eastern North America. Given that the present population is less than 1000 individuals, one must conclude that the present status is precarious at best, and may be at or near minimum viable population size (see Shaffer 1981, Salwasser et al. 1984, Reed et al. 1986).

Acknowledgments.—Special thanks to R. Palmer and J. Zickefoose for helping to locate historical references, as well as for sharing their knowledge of Harlequin Ducks in the New England area. An earlier draft of this manuscript benefited from constructive criticisms by R. D. Elliot, A. J. Ershine, J. F. Piatt, and two anonymous reviewers.

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R. Ian Goudie, Canadian Wildlife Service, P.O. Box 9158, St. John’s, Newfoundland A1A 2X9, Canada. Received 18 May 1988, accepted 5 October 1988.

Additional records of birds from Cat Island, Bahamas.—During 11–15 March 1986, we visited Cat Island (34 km southeast of Eleuthera) in the Bahamas. Here we report on 27 species of birds whose status on Cat Island is poorly known (Buden 1987), including eight for which no previous records exist. Also included are our observations of several species on Eleuthera during the winter of 1985–1986, to aid in understanding their occurrence on Cat Island.

Double-crested Cormorant (Phalacrocorax auritus).—Seventeen were sighted near Orange Creek on 12 March, and 15 at Gambier Lake on 14 March. Although several Olivaceous Cormorants (P. olivaceus) spent the winter on Eleuthera, none were seen on Cat Island.

Herons.—During 11–15 March two Great Egrets (Casmerodius albus), one Snowy Egret (Egretta thula), and two Little Blue Herons (E. caerulea) were observed. All past records of these species are from late April to August (Buden 1987).

Blue-winged Teal (Anas discors).—The most numerous wintering duck on Eleuthera, a pair at Orange Creek on 13 March is the first Cat Island sighting.

Black-necked Stilt (Himantopus mexicanus).—Sixty-one near Orange Creek on 13 March were probably recently arrived summer visitors. On Eleuthera stilts were first observed on 24 February, the previous early date for that island being 5 March (Connor and Loftin 1985).

Other shorebirds.—Five species were observed that have previously been recorded on Cat Island only from May to August, including 12 Black-bellied Plovers (Pluvialis squatarola), 20 Greater Yellowlegs (Tringa melanoleuca), one Lesser Yellowlegs (T. flavipes), three Willets (Catoptrophorus semipalmatus), and four Least Sandpipers (Calidris minutilla). Spring migrant Willets on Eleuthera first were detected on 10 April; thus the three Cat Island sightings probably represent wintering individuals.

Laughing Gull (Larus atricilla).—None were seen on Cat Island, and only one was observed all winter on Eleuthera until a few appeared in mid-March. A similar pattern has been reported on New Providence (Brudenell-Bruce 1975), but this scarcity conflicts with findings by Buden (1987) on Cat Island (“common to very common resident”), and Connor and Loftin (1985) on Eleuthera (“more abundant in winter”).

Royal Tern (Sterna maxima).—One near Old Bight on 12 March either wintered locally or was an early migrant. On Eleuthera spring arrivals first were noted in early April.

Common Barn-Owl (Tyto alba).—The third Cat Island record was one flushed from a sinkhole near Old Bight on 12 March.

Gray Catbird (Dumetella carolinensis).—Three at Knowles on 13 March is the first report from Cat Island. This species was common on Eleuthera into early April.

Pearly-eyed Thrasher (Margarops fuscatus).—On 13 March one was seen briefly, 2 km northwest of New Bight, as it flew 30 m ahead of us across the road in dense brush habitat. It could not be relocated. This species was not found by Buden in May–July 1986, and breeding is unconfirmed in the Bahamas north of San Salvador (Buden 1987). One other Cat Island record (Paulson 1966).

Yellow-throated Vireo (Vireo flavifrons).—One at Old Bight on 12 March represents the first Cat Island record. This species was a rare winter resident on Eleuthera.

Cape May Warbler (Dendroica tigrina).—Four near Old Bight during 12–15 March are the first records on Cat Island.

Yellow-rumped Warbler (D. coronata).—Ten “Myrtle” Warblers (D. c. coronata) at three locations during 11–13 March are the first Cat Island sightings of this species, which was common on Eleuthera from mid-January to mid-March.
Yellow-throated Warbler (*D. dominica*).—Five were located at three locations during 11–13 March. One previous record (Buden 1987).

Black-and-white Warbler (*Mniotilta varia*).—One at New Bight on 11 March is the first Cat Island record.

American Redstart (*Setophaga ruticilla*).—One was at Arthur’s Town on 13 March, the second island record. Redstarts are fairly common in winter on Eleuthera (Connor and Loftin 1985, pers. obs.).

Ovenbird (*Seiurus aurocapillus*).—Despite only one other record (Buden 1987), this species is probably widespread on Cat Island in winter. We found two at Old Bight on 12 March, and one at Arthur’s Town on 13 March.

Northern Waterthrush (*Seiurus noveboracensis*).—One at Old Bight on 12 March, and two at Orange Creek on 13 March are the first island records. This species is common in winter on Eleuthera (Connor and Loftin 1985, pers. obs.).

Common Yellowthroat (*Geothlypis trichas*).—One was at Old Bight on 12 March, for the second island record.

Indigo Bunting (*Passerina cyanea*).—Apparently a common winter resident on Cat Island, as it is on Eleuthera. One previous record (Ridgway 1891), but we found 24 at three localities during 11–13 March, primarily foraging in casuarinas (*Casuarina equisetifolia*).

Northern Oriole (*Icterus galbula*).—A female “Baltimore” Oriole (I. g. *galbula*) at Old Bight on 12 March is the first report of this species on Cat Island. Two were located on Eleuthera in February 1986.

Observations of Cat Island birds have been limited; the eight additions reported here bring the island’s species total up to 105. Six of those (Blue-winged Teal, Gray Catbird, Cape May Warbler, Yellow-rumped Warbler, Black-and-white Warbler, Northern Waterthrush) are common winter residents in the Bahamas, whereas the Yellow-throated Vireo and Northern Oriole are scarce (Bond 1980). In four months on nearby Eleuthera we detected 56 bird species that are presently unknown on Cat Island, suggesting that further field work, particularly during migration and winter, will add many species to the known Cat Island avifauna.

**Acknowledgments.**—These observations were recorded during a U.S. Fish and Wildlife Service search for wintering Kirtland’s Warblers (*Dendroica kirtlandii*) in the Bahamas, from December 1985 to April 1986. We thank P. W. Sykes, Jr., and the staff of the U.S. Fish and Wildlife Service, Southeast Research Station, University of Georgia, for organizing the Cat Island visit. This note benefited from comments by D. W. Buden, F. L. Knopf, D. H. White, and an anonymous reviewer. Permission to conduct research in the Bahamas was granted by the Bahamas Ministry of Agriculture and the Bahamas National Trust.

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Notes on the rail *Rallus longirostris tenuirostris* in the highlands of central Mexico.—The King Rail/Clapper Rail (*Rallus elegans/R. longirostris*) complex is represented in the freshwater marshes of the highlands of central Mexico by a richly colored form described as *Rallus elegans tenuirostris* by Ridgway (1874). Warner and Dickerman (1959) provided the first natural history information on *tenuirostris* and greatly extended its known range, Hardy and Dickerman (1965) briefly noted these rails incidental to other studies, and Dickerman (1971) further clarified the range. As presently understood, *tenuirostris* occurs exclusively in freshwater situations at elevations of 800 m to 2500 m in the states of Nayarit, Jalisco, Michoacán, Guanajuato, San Luis Potosí, (Estado de) México, Tlaxcala, Puebla, and Guerrero and the Distrito Federal. With but one exception, all specimens reported as King Rails or Clapper Rails from the Central Highlands are referable to *tenuirostris* (Dickerman 1971, Banks and Tomlinson 1974). During my studies of waterbirds in Mexico, I observed *tenuirostris* on several occasions in the highlands of Jalisco and adjacent Guanajuato. These observations provide four new localities of occurrence, document the first reported nest of this race, extend the breeding season, and describe environmental factors governing the seasonal movements, breeding ecology, and status of this rail in central Mexico.

Taxonomic considerations.—The taxonomic position of *tenuirostris* is complicated by uncertainty about the status of King and Clapper rails with which *tenuirostris* shares characters. Noting that *R. elegans* and *R. longirostris* may interbreed, Dickerman (1971) suggested that the two were ecological replacements of each other and proposed lumping all races under *R. longirostris*, the older name. This treatment was also recommended by Blake (1977) and followed by Ripley (1977). However, the American Ornithologists’ Union (1983) retained *elegans* and *longirostris* as separate species. Oberholser (1937), who accepted *elegans* and *longirostris* as distinct species, was the first to consider *tenuirostris* a race of the Clapper Rail, noting that even though *tenuirostris* “is the form that most closely approaches *Rallus elegans* in [coloration]” (op. cit.:337), it presented “no characters that are not bridged over by individual variation when all the forms [of *R. longirostris*] are considered” (op. cit.: 314). The placement of *tenuirostris* as a race of *R. longirostris* has been generally accepted during the past 50 years (e.g., Ridgway and Friedmann 1941, Blake 1953, Deignan 1961, Anderson and Ohmert 1985) and I have followed this trend. The American Ornithologists’ Union (1983) still lists the form as a race of *R. elegans*.

Use of seasonal wetlands.—Warner and Dickerman (1959) found *tenuirostris* in many “extensive” marsh areas west of Mexico City, and I occasionally noted these rails at similar large permanent wetlands. However, I also found them in smaller seasonal wetlands in Jalisco after the onset of the summer rains, which typically begin in mid-June. In Jalisco, as throughout the range of *tenuirostris*, rainfall is the most pronounced seasonal variable. Guadalajara, located centrally in Jalisco, receives an annual average of 95 cm of precipitation, with 86% falling as rain during the June–September period (Wernstedt 1972). The effects
of such substantial precipitation are to expand the perimeters of permanent wetlands, create isolated seasonal wetlands, stimulate growth of wetland vegetation, and facilitate breeding by waterbirds. I observed *tenuirostris* in seasonal wetlands in Jalisco near El Molino (elev. 1550 m, 40 km SW Guadalajara), east of Laguna de Cajititlán (elev. 1500 m, 30 km S Guadalajara), in the vicinity of Ameca (elev. 1350 m, 75 km W Guadalajara), and near Atequiza (elev. 1500 m, 40 km SE Guadalajara). Water, vegetative cover, and rails were absent in each of these areas prior to the onset of the rains.

In the El Molino area in April through early June 1973, the valley was dry and barren and waterbirds were absent. After the rains began in mid-June, a shallow lake with an extensive marshy border of grasses, sedges, and forbs formed in the lower portion of the valley. This wetland was surrounded by wet pastures and muddy fields of corn and sorghum through which ran marshy ditches. I first noted rails there on 12 July 1973 and found them common there on 19–20 July; I last worked the valley on 1 August, at which time rails were still conspicuous. The El Molino site is about 25 km northwest of the west end of Lago de Chapala and about 15 km east of Laguna de Atotonilco.

The agricultural area east of Laguna de Cajititlán was similar to that of the El Molino valley, being dry and barren prior to the rains but wet and green in the rainy season. I recorded rails in grasses and sedges about seasonal *presas* (reservoirs) and in muddy, weedy sorghum fields on 30 July 1973, 9 and 12 August 1973, and 20 June 1974. The nearest potential rail habitat to this area is Laguna de Cajititlán, some 3–4 km distant. Near Ameca, I found a single rail in a seasonal wetland on 25 July 1973; the nearest extensive marsh habitat known to me is probably Presa de la Vega, some 30 km away.

*Nest and eggs.*—On the morning of 16 August 1973, I discovered an active nest in a seasonally wet pasture near Atequiza, approximately 6 km south of the Río Santiago, and near the outer edge of the river valley. I first found the nest when an adult rail flushed from it. It contained five warm eggs that were oval and whitish with brown spots. The nest was a domed structure made entirely of spikerush (*Eleocharis*), and it was situated in a seasonal stand of spikerush ranging from 45–60 cm tall. The following morning an adult flushed from the nest which still contained five eggs. I photographed the nest and eggs on 17 August, but did not return to the site again that year.

I visited the Atequiza site in May 1973, but found it devoid of water and vegetative cover. The aspect of lush greenness in August 1973 was a dramatic contrast to the pre-rainy season barreness. I also visited this site in May 1974 and May 1977, on the latter occasion equipped with tape-recorded rail calls, but I failed to find rails or suitable rail habitat. During a brief visit on 11 August 1975, however, I found at least three adult rails occupying comparatively extensive rail habitat.

*Breeding season.*—Based on specimens, Warner and Dickerman (1959) judged that the nesting season for this rail began in May and continued into July. My discovery of a nest with eggs extends the season into August; presumably, flightless young would occur well into September. It seems possible that egg laying could begin earlier than May in permanent marsh habitats, resulting in a breeding season extending from at least April into September. Such a lengthy breeding season would not be surprising, given the environmental regime of the Central Highlands region and the propensity of Clapper and King rails to renest if earlier efforts are disrupted or to initiate second nests after earlier successful efforts.

*Discussion.*—While *tenuirostris* apparently is resident throughout the year in the central Mexican highlands, my observations suggest that it is not strictly sedentary. I surmise that it occurs in permanent wetlands during the long dry season (October–April/May), with some dispersal to seasonal wetlands during the rainy season (May/June–September). This tendency to disperse has survival value, in that individuals are not restricted entirely to permanent marshes (many of which are in sadly degraded condition) and in that it probably serves to
extend the breeding season. It seems likely that these seasonal movements explain the lack of geographic variation within this race, the range of which extends some 700 km from west to east, and about half that distance from north to south. This is in marked contrast to certain other resident birds of the Central Highlands that are similarly dependent upon limited mesic environments but that tend to be sedentary in very local areas. However, the well-being of this highland race of rail is by no means assured. The overall range is limited, and suitable habitat becomes severely restricted toward the end of the typical dry season. Furthermore, the wetlands on which these rails depend may experience increasing agricultural, industrial, and urban development.

Although specimens apparently are lacking, _tenuirostris_ should be expected to occur in wetlands in the highland states of Querétaro, Hidalgo, and Morelos. In fact, there are May sight reports of _tenuirostris_ in rice fields near Cuernavaca, Morelos, which may be the basis for that state being listed in the range of the King Rail by the American Ornithologists’ Union (1983). The supposed occurrence of _tenuirostris_ in the coastal lowlands at Mazatlán, Sinaloa, has been properly discredited by Banks (1975). While _tenuirostris_ has been collected in Nayarit within 35 km of the Pacific Coast, that locality lies at an elevation of about 1000 m. Hence, there is apparently no contact with the grayish, lowland _R. l. nayaritensis_, which is resident in the coastal marshes and mangroves near San Blas.

_Tenuirostris_ is most often referred to as the Mexican Clapper (or King) Rail, but in light of the presence of several additional races in the Mexican lowlands, this name seems inappropriate. As the distribution of _tenuirostris_ corresponds quite closely to the general limits of the Central Highlands region of Mexico, and as this race occurs regularly at higher elevations than do any of the other races of Clapper or King rails, I suggest that Highland Clapper (or King) Rail may be a useful name for this distinctively marked race.

Acknowledgments.—I thank C. Blem, R. Dickerman, J. Hubbard, R. Ryder, and two anonymous reviewers for comments on the manuscript, and K. Lueder for his hospitality during my residence in Chapala, Jalisco. Field work was conducted while I was a student in the Department of Fishery and Wildlife Biology, Colorado State University. Financial support was provided by the Welder Wildlife Foundation, the National Audubon Society, and the U.S. Fish and Wildlife Service.

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Factors affecting the termination of breeding in Nuttall's White-crowned Sparrows.—A number of factors are known to affect the length of birds' breeding seasons, including intrinsic geographical factors, such as photoperiod and latitude (Miller 1960, MacArthur 1964, Ricklefs 1966, Wyndham 1986), and ecological factors, such as altitude and climate (Davis 1933, Skutch 1950, Immelmann 1971). Factors influencing the length of the breeding season can operate by affecting either the timing of the initiation or the termination of breeding or both. Climatic conditions are generally thought to affect the timing of the initiation of breeding by affecting the availability of food resources for the birds (Lack 1950, Skutch 1950, Snow and Snow 1964, Immelmann 1971, Wyndham 1986). However, climatic conditions may also affect the availability of nest sites or nesting material, particularly in areas with extensive winter snowfall (Morton 1978, DeSante, unpubl. data). Climatic conditions may also affect the termination of breeding through a relationship with food supply, but possibly in a more indirect or anticipatory manner. In migratory species, for example, the termination of breeding may occur well in advance of the time when food resources begin to diminish, presumably to allow the birds adequate time and an adequate food supply to raise their young to independence, complete their prebasic molt, and store fat for migration. In non-migratory birds, certain of these necessities may be somewhat relaxed, but the termination of breeding must still to some extent be controlled by the availability of food resources.

In situations where the environment provides predictive information as to the future availability of food resources (Immelmann 1973), the question arises as to what happens if the environmental cues lead to faulty predictions. If a predicted good food supply should suddenly fail, it seems obvious that the birds will either curtail breeding or fail in their breeding attempts if they persist. But what if a predicted failure of the food supply does not happen and food remains abundant? Wong (1983) presented circumstantial evidence to show that supplemental feeding with poultry mash extended the breeding season of Eurasian Tree Sparrows (Passer montanus) by two months at a site in Malaysia. Here we present data suggesting that a local superabundance of food will permit extended breeding by individual pairs that have access to that food resource.

Coastal central California experiences a Mediterranean climate characterized by mild wet winters and warm dry summers. Along the immediate coast, where both the Point Reyes Bird Observatory’s Palomarin Field Station and Golden Gate Park are located, the summer drought is ameliorated somewhat by the occurrence of persistent fog. Nevertheless, nearly 83% of the annual precipitation falls as rain during the 5 months November to March, while only 5% falls during the 5 months May to September. Virtually all of the annual plants,
including both introduced grasses and native forbs, as well as many of the perennial grasses and shrubs, and even certain trees, such as California buckeye (Aesculus californica), curtail primary production, dry up, turn brown and/or drop their leaves during the summer months. The timing of this browning of the landscape varies with the amount of winter rainfall that the area received. This occurs because increased amounts of winter rainfall tend to increase soil moisture content, ground water supplies, and spring-fed stream and seep flows, all of which permit vegetative growth later into the summer. Furthermore, winters of heavy rainfall are often followed by heavy spring rains that extend later than usual, thereby further delaying the onset of summer dry-up.

Because many breeding birds feed their young on herbivorous insects, and because most herbivorous insects feed on green growing plant material, it should be expected that the onset of the summer dry-up would bring about an abrupt termination to breeding activity in passerine birds. In order to test this hypothesis, we analyzed data from 247 Nuttall’s White-crowned Sparrow (Zonotrichia leucophrys nuttalli) nests monitored during an intensive 7-year study (1979–1985) of the breeding biology of this species at the Palomarin Field Station of the Point Reyes Bird Observatory. The timing of the termination of breeding was estimated by the mean clutch completion date of the latest 10% of the nests found each year, as well as by the clutch completion date of the latest nest found each year (Table 1). The clutch completion date for nests found after the clutch was already completed was assumed to be 12 days prior to hatching, the mean length of the incubation period for Palomarin White-crowndeds. For nests that were found after the clutch was already completed and that were preyed upon before hatching, the clutch completion date was estimated as the median date of the range of possible dates, again assuming a 12-day incubation period.

Figure 1 indicates that the timing of the termination of breeding, as determined by the mean clutch completion date of the latest 10% of the nests found each year, was directly related to the amount of winter rainfall during the previous year ($r = 0.820, P < 0.05$), such that breeding extended later into the summer following winters of heavier rainfall. A similar relationship existed using the single latest nest found each year, although it was not statistically significant ($r = 0.694, 0.05 < P < 0.10$), no doubt because the smaller sample size (7 rather than 26 nests) magnified the individual variation among the birds themselves. Nevertheless, these results indicate that the timing of the termination of breeding in Nuttall’s

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**Table 1**

**Timing of the Termination of Breeding of Nuttall’s White-crowned Sparrows at the Palomarin Field Station**

<table>
<thead>
<tr>
<th>Year</th>
<th>Annual (winter) rainfall (cm)</th>
<th>Number of nests</th>
<th>Mean clutch completion date for latest 10% of nests</th>
<th>Clutch completion date for latest nest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Date</td>
<td>Julian date</td>
</tr>
<tr>
<td>1979</td>
<td>67.16</td>
<td>9</td>
<td>28 June</td>
<td>179.00</td>
</tr>
<tr>
<td>1980</td>
<td>95.96</td>
<td>46</td>
<td>6 July</td>
<td>188.08</td>
</tr>
<tr>
<td>1981</td>
<td>63.40</td>
<td>42</td>
<td>30 June</td>
<td>181.20</td>
</tr>
<tr>
<td>1982</td>
<td>134.80</td>
<td>47</td>
<td>14 July</td>
<td>194.51</td>
</tr>
<tr>
<td>1983</td>
<td>151.69</td>
<td>44</td>
<td>12 July</td>
<td>192.50</td>
</tr>
<tr>
<td>1984</td>
<td>86.92</td>
<td>37</td>
<td>22 June</td>
<td>174.03</td>
</tr>
<tr>
<td>1985</td>
<td>79.20</td>
<td>32</td>
<td>30 June</td>
<td>181.40</td>
</tr>
</tbody>
</table>

*Measured from 1 July of the previous year to 30 June of the present year.*
White-crowned Sparrows is a function of local weather conditions and is probably related, in an anticipatory manner, to the availability of food for their young. Petrinovich and Patterson (1983) documented significantly reduced reproductive success in Nuttall’s White-crowned Sparrows in San Francisco in 1976, and attributed it to the severe drought conditions that year. This reduced reproductive success was likely caused, at least partially, by an early termination of breeding in response to the local browning of the vegetation.

It should also be noted that 1985 was characterized by rainfall during the previous winter (79.20 cm) that was somewhat below the 7-year mean (97.02 cm), and a termination of breeding (30 June; as determined by the mean clutch completion date of the latest 10% of the nests found) that was likewise slightly earlier than the 7-year mean (3 July).

Nevertheless, on 4 September 1985, Baptista was attracted by begging calls of a juvenile Nuttall’s White-crowned Sparrow near the California Academy of Sciences, Golden Gate Park, San Francisco, California, some 33 km from the Palomarin Field Station. A brief search produced a spotted juvenile being attended by an adult. The adult soon flew away and was followed by the fledgling. The fledgling’s tail was observed well and was judged to be no more than one-half of the tail length of the adult. The fledgling, therefore, could not have been out of the nest for more than 7 days, which would indicate that it fledged no earlier than 28 August.

On the following day, a spotted juvenile was again seen at the same spot accompanied by two adults. The juvenile continuously uttered begging calls and followed one of the adults, keeping within 15 cm of the latter as it foraged. Both the adults and the juvenile performed double scratches on the leaf litter. One adult (the female?) repeatedly pecked at objects on the leaf litter and three times inserted food items into the juvenile’s bill. Baptista immediately moved to the location where the adult was gathering food and feeding it to the juvenile, and began sweeping the leaf litter aside. Large numbers of terrestrial amphipods (Talitrus sylvaticus) were observed jumping in all directions as soon as the leaf litter was disturbed.
These amphipods were inadvertently introduced into Golden Gate Park from Australia, probably with soil attached to exotic plants. Larger individuals of these amphipods reach 15 mm in length and appear to be important food items for local birds. On numerous occasions, Baptista has observed White-crowned Sparrows eating them.

On 9 September 1985, Baptista observed two spotted juvenile White-crowned Sparrows being attended by adults near the Conservancy of Flowers in Golden Gate Park. This second site is about 0.5 km from the first. These juveniles had longer tails than the first one observed, and appeared to be slightly older. Still, because their tails were not fully grown, they could not have fledged earlier than 26 August.

For Nuttall's White-crowned Sparrows raised in central coastal California, fledging dates of 26–28 August correspond to clutch completion dates of 4–6 August, 35–37 days later than the mean of the latest 10% of the nests found at Palomarin in 1985, and fully 27–29 days later than the latest nest found at Palomarin in 1985. Moreover, these dates are 15–17 days later than the latest nest ever found at Palomarin, that being in the summer of 1983, the summer following the excessive rainfall (151.69 cm) associated with the 1982–1983 El Niño Southern Oscillation (Philander 1983).

It might be argued that the lateness of the observed fledglings at Golden Gate Park was an artifact of the amount of time and effort spent in observation, and of the ease of observation in open park habitat as compared to the dense coastal scrub habitat at Palomarin. We do not believe this to be the case, however. Nearly every nesting attempt of a population of some 20–25 pairs of Nuttall's White-crowned Sparrows was monitored at Palomarin over several thousand hours of observation. We are confident that we did not miss any late nesting attempts at Palomarin during the rather dry summer of 1985.

Thus we suggest that the superabundance of the introduced *Talitrus* amphipods in Golden Gate Park provided a readily available extra food source enabling certain individual pairs of Nuttall's White-crowned Sparrows to continue successful breeding activities well beyond that of nearby local populations.

Acknowledgments.—The actual monitoring of the 247 nests at the Palomarin Field Station from 1979 to 1985 was accomplished by the many field biologist interns of the Point Reyes Bird Observatory. Geoffrey R. Geupel supervised the work of these interns and provided helpful comments on an earlier draft of this manuscript. Financial support for this work was provided by the membership of the Point Reyes Bird Observatory and by the Chevron Corporation. We thank the administration of the Point Reyes National Seashore for their cooperation. This is PRBO Contribution Number 388.

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Inbreeding in Ospreys.—James et al. (1987) cite the scarcity of reports of inbreeding in natural populations of birds and report a case of mother-son mating in the Merlin (Falco columbarius). This and a case of mother-son mating in the Eastern Screech-Owl (Otus asio) (Van Camp and Henny 1975:37) appear to be the only published reports of inbreeding in raptors. Here, I report a case of full-sibling mating in the Osprey (Pandion haliaetus).

This pair was first noted in 1981 during my study of a color-banded Osprey population on a series of wildlife flooding around Houghton Lake, Roscommon County, in the north-central Lower Peninsula of Michigan (Postupalsky 1977). Most nests there occur on man-made platforms described by Postupalsky and Stackpole (1974).

Both members of the pair were raised on the same platform nest on the Dead Stream Flooding (also known as Reedsburg Dam Backwater) on the Muskegon River 4 km west of Houghton Lake. The female hatched in 1973, the male in 1974. Their mother was banded as a nestling in 1965 on Fletcher Pond, Alpena County, 100 km northeast of her breeding site, and nested on the same nest for seven seasons, 1970–76. Her mate during the 1972–76 breeding seasons was a banded male. Considering that the survival rate of adult males in my study area is 84% (N = 239; Postupalsky, unpubl. data), and that by 1973–74 very few individuals banded only with a FWS band were left in the population (most were either unbanded, or also had color bands), the probability is very high (84–100%) that the same male was involved in both 1973 and 1974. Therefore, the members of the pair reported here were at least half-siblings, and very likely full siblings.

The female was first found nesting in 1976 on a platform (designated P-2) on the east side of Backus Creek Flooding, 6 km east of Houghton Lake and 21.5 km ESE of her natal site. She nested there for five seasons, 1976–80, with unbanded male(s). The male was first observed nesting on another platform (P-1) near the west side of the same flooding in 1978; his mate during 1978–80 was another individually marked female.

In 1981 the female at P-1 was missing and was replaced by the female from P-2, which had moved about 0.5 km across the flooding, and had formed a pairbond with the resident male at P-1, her younger brother. An unbanded pair took over the P-2 territory. The sibling...
pair nested on the P-1 platform in subsequent years and was last seen there during the 1987 season. Both birds were then 21 km from their natal nest. In my study area, mean juvenile dispersal distance is 14.5 km for males (N = 37) and 38 km for females (N = 31). As some individuals, especially long-distance dispersing females, move outside the study area and are not found, the actual mean dispersal distances are probably somewhat longer than these preliminary estimates. Nevertheless, it is apparent that the male had dispersed farther than the mean distance for males, and the female had dispersed over a shorter distance than the mean for her sex.

The reproductive success of both siblings, together and with their respective previous, unrelated partners, is shown in Table 1. No obvious inbreeding depression, as was reported for other species (Greenwood et al. 1978), is evident here. To date, four young produced by these individuals have survived to reproductive age and have been found breeding elsewhere. All four were from the earlier matings with unrelated partners. I should add, however, that of 12 young fledged by the sibling pair to date (Table 1) at most seven would have reached the minimum breeding age by 1987. While most Ospreys start breeding at age 3, many do not until they are 4–6 years old.

I have followed the breeding of 157 individually marked adult Ospreys, and this is the only case of close inbreeding observed to date, suggesting that inbreeding is an uncommon occurrence in this Osprey population.

Acknowledgments.—My long-term Osprey population research in Michigan was at various times supported by Conservation for Survival, the National Audubon Society, and the Michigan Nongame Wildlife Fund. Additional support was provided by Thunder Bay Audubon Society (Alpena, MI), Alpena Power Company, Petoskey Regional Audubon Society, Chippewa Nature Center, Inc. (Midland, MI), and U.S., Inc. Among the numerous persons who assisted in the field over the years, J. Holt, Jr., J. Papp, and W. Robichaud helped with the banding and observations of the individual birds reported here. I thank S. Temple, C. Henny, and C. Stinson, whose comments improved this note.
LITERATURE CITED


Intraspecific nest parasitism by Sharp-tailed Grouse.—Intraspecific nest parasitism by species of Tetraoninae rarely has been documented. In 83 studies including more than 6000 clutches (Bergerud and Gratson, Adaptive Strategies and Population Ecology of Northern Grouse, Univ. Minnesota Press, Minneapolis, 1988), only two authors suggested that intraspecific nest parasitism had occurred. Darrow (in Bump et al., The Ruffed Grouse, Life History—Propagation—Management, The Holling Press, Inc., Buffalo, New York, 1947) stated... “a number of grous nests have been found in which there was every indication that two hens contributed to the clutch present,” after examination of more than 2000 Ruffed Grouse (Bonasa umbellus) nests in New York from 1930 to 1942. Martin (J. Field Ornithol. 55:250-251, 1984) gave evidence that 4 of >150 nests of Willow Ptarmigan (Lagopus lagopus) monitored over three years in Manitoba were parasitized. Here I report one instance of Sharp-tailed Grouse (Tympanuchus phasianellus) nest parasitism among approximately 120 nests (first through fourth) examined over a 4-year period in southern Manitoba, 49°10’N, 100°13’W.

On 18 May 1984 I approached for the first time the nest of a yearling I had captured and radio-tagged on 17 April at a lek 8 km away. The female flushed, and I numbered and measured the length and breadth of 17 eggs. I returned to inspect the clutch on 29 May after detecting that the female was no longer attending the clutch and remained 1.5 km away. An unbanded sharptail flushed from the nest and I numbered and measured each of five additional eggs. On 5 and 10 June I again returned and “flushed” an unbanded female from the nest; clutch size remained at 22. I returned on 17 June to capture the female and found that 20 of 22 eggs had hatched. An unbanded hen with >15, day-old chicks was within 10 m of the nest. Unfortunately, she did not respond well to a chick distress call and was not captured. I could not determine from egg dimensions which eggs were laid by which hen. Because of the number of eggs that hatched and the large number under the marked hen (only Hamerstrom, Wilson Bull. 51:105-120, 1939, reports ≥17 eggs for a clutch) I suspect that both hens were laying eggs simultaneously.
Financial support was provided by a Natural Sciences and Engineering Research Council of Canada grant to A. T. Bergerud; I thank A. T. Bergerud and the Wildlife Branch of The Manitoba Dept. of Natural Resources.—MICHAEL W. GRATSON, Dept. Biology, Univ. Victoria, Victoria, British Columbia V8W 2Y2, Canada. (Present address: Box 454, Mackay, Idaho 83251.) Received 16 June 1988, accepted 24 Aug. 1988.


Willow Flycatcher nestling parasitized by larval fly, Protocalliphora cuprina.—Blowfly larvae of the genus Protocalliphora (Diptera: Calliphoridae) are hematophagous parasites that feed on nestlings of nidicolous birds. With the exception of P. aenea (Halstead, unpubl. data) and P. hirudo which are subcutaneous parasites, all other Nearctic species of Protocalliphora are intermittent ectoparasites that live largely in the nest material (Gold and Dahlsten 1983, Wilson Bull. 95:560–572, 1983). Death of the host from infestation is uncommon (Whitworth 1976. Ph.D. diss., Utah State Univ., Logan, Utah; Gold and Dahlsten 1983). This note reports the first occurrence of P. cuprina on the Willow Flycatcher (Empidonax traillii).

On July 16, 1987, while banding Willow Flycatcher nestlings in Long Meadow, a Sierran montane meadow, elevation 2135 m, in Fresno County, California, we found a blowfly larva feeding near the cloaca of one nestling. The larva was collected, reared to adulthood, and sent to the Systematic Entomology Laboratory, USDA-ARS for identification. Since banding was initiated in 1983, 33 nestlings from 26 nests have been banded. No other blowfly larvae were noticed during this time.

Sabrosky (pers. comm., unpubl. data) reports 12 hosts for P. cuprina, of which two are flycatchers, the Dusky Flycatcher (E. oberholseri) and Western Flycatcher (E. difficilis). Our information adds the Willow Flycatcher to the hosts of P. cuprina.

Acknowledgments.—We thank the Kings River Conservation District for funding this publication and our Willow Flycatcher research, C. W. Sabrosky for identifying P. cuprina and for providing host information, and J. R. Single for reviewing this manuscript. This is Environmental Division Research Report No. 88-11 of the Kings River Conservation District.—STEPHEN P. BOLAND, JEFFREY A. HALSTEAD, AND BRADLEY E. VALENTINE, Environmental Division, Kings River Conservation District, 4886 E. Jensen Ave., Fresno, California 93725. Received 7 June 1988, accepted 30 Aug. 1988.


Flexible incubation system and prolonged incubation in New Zealand Snipe.—Shorebirds of the family Scolopacidae (Charadriiformes) have a wide variety of mating systems (Jenni 1974, Pitelka et al. 1974, Pienkowski and Greenwood 1979). Monogamy, with shared incubation of the same clutch, is presumed to be the primitive mating system (Jenni 1974, Pitelka et al. 1974). However, in a number of species, male or female emancipation has led to uniparental care by either sex (Hogan-Warburg 1966, Norton 1972, Pitelka et al. 1974, Reynolds 1987), or both sexes incubate different clutches simultaneously (Parmelee and Payne 1973, Hildén 1975, Pienkowski and Greenwood 1979). Species with shared incubation of the same clutch keep the eggs covered almost continuously (Norton 1972), while shorebirds
with single-sex incubation have an incubation constancy of 80–90% (Drury 1961, Parmelee 1970, Norton 1972, Cartar and Montgomerie 1985, Lofaldli 1985), because the incubating parent must divide time between nest attentiveness and food gathering (White and Kinney 1974, Lofaldli 1985). The incubating parent may take frequent foraging excursions which are short enough to maintain the eggs above physiological zero temperature (Lofaldli 1985, Kalas 1986), or it may take longer feeding trips, allowing the eggs to cool (Lill 1979).

New Zealand snipe *Coenocorypha* are typically monogamous, with shared incubation. However, in a study of 20 pairs of Snares Island Snipe (*C. aucklandica huegeli*) over six years, I observed simultaneous polygyny by two different males in separate field seasons. The remaining males were all monogamous. Here I document the incubation system associated with polygyny (three nests) and compare it with that of typical, monogamous pairs (37 nests). The polygynous males devoted almost all of their parental effort to one nest. The additional females incubated by themselves; thus, the incubation system became more like that found in other snipes (i.e., female, single-sex, intermittent incubation; Tuck 1972, Cramp and Simmons 1983, Lofaldli 1985). Both solo-incubating females paired monogamously and shared incubation with their mates in previous seasons.

**Study area and methods.**—Snares Island Snipe were studied in *Olearia* forest on the Snares Islands (48°01’S 166°36’E) south of New Zealand. Six visits to the study area were made each summer beginning in 1982. The most intensive work was carried out from 2 Nov. 1985 to 10 Mar. 1986, and from 22 Oct. 1986 to 20 Feb. 1987. All adult snipe within the 7.5-ha study area individually were color banded for the duration of the study. Territories and home ranges of snipe were plotted in relation to a 20-m grid system during daily surveys of the study area. Pairs were identified by mating, courtship feeding, or prolonged consorting. Snipe were sexed by measurements during handling (females are larger; Miskelly, unpubl. data) and by sex-specific calls and displays after marking. Most breeding attempts were detected during incubation; laying dates for nests with shared incubation were recorded directly, or calculated from hatching dates by subtracting 22 days for incubation (determined from three nests) and three days for egg interval (determined from five nests; the typical clutch is two eggs). Incubation length was taken as the time from laying of the second egg to hatching of either egg. Eggs, when found, were weighed to 0.5 g and measured to 0.1 mm. Fresh egg masses were obtained before incubation for 9 eggs. For nests with single-sex incubation, fresh egg masses were calculated using the equation: $M = 0.000526 \times L \times B^3$, where $M$ is initial egg mass (g), $L$ is egg length (mm) and $B$ is maximum egg breadth (mm). nests were checked at least once daily, and more frequently during hatching. If no bird was sitting, the eggs were touched to determine whether they were warm. Blinds were erected near four nests (one with female single-sex incubation), and five continuous 24-h watches were undertaken. A chart recorder, light beams and photo-electric cells were used to record incubation constancy at two nests with shared incubation in November–December 1987. Daily air temperatures were taken within the study area.

**Results.**—**Case 1.** Of 20 territory-holding males in the study area in 1985–86, one (Male A) had two mates simultaneously. Initially he courted only Female A, his mate of the previous three seasons. Female A was suspected to have commenced incubation about 24 Nov., as she was not seen during surveys of the study area after 23 Nov.; her nest (Nest 1) was not found until 5 Dec. The male commenced courting Female B on 22 Nov., the day after the estimated first egg-laying date of Female A. Male A and Female B shared incubation at Nest 2, which was found on 9 Dec. Both eggs in Nest 2 hatched on 21 Dec., giving estimated laying dates of 27 and 30 Nov. Female A at Nest 1 incubated by herself. No other birds were seen during 57 spot checks over 28 days at Nest 1. Female A frequently left the nest for extended periods to feed (over 100 min on one occasion), during which the eggs cooled to ambient temperature (7.5–19.0°C). Egg mass loss at this nest over 23 days averaged
TABLE 1
INCUBATION DETAILS FOR NEW ZEALAND SNIPE UNDER TWO DIFFERENT INCUBATION REGIMES

<table>
<thead>
<tr>
<th>Incubation regime</th>
<th>Shared N = 37</th>
<th>Solo</th>
<th>Case 1 (Nest 1)</th>
<th>Case 2 (Nest 4)</th>
<th>Case 3* (Nest 5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>% Female incubation</td>
<td>38c</td>
<td>100d</td>
<td>99.9f</td>
<td>100g</td>
<td></td>
</tr>
<tr>
<td>Incubation constancy (%)</td>
<td>100c</td>
<td>ca 69e</td>
<td>72f</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Egg mass loss (gd⁻¹)</td>
<td>0.182</td>
<td>0.125</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Incubation lengthd</td>
<td>22</td>
<td>37-39</td>
<td>Failed</td>
<td>Unknown</td>
<td></td>
</tr>
</tbody>
</table>

Male reproductive successb ≤ 2 3 ≤4h
Female reproductive success ≤ 2 1 ≤2b

* For first 5 days only, after which incubation was shared.
b Measured as number of young raised to fledging in one breeding season.
c Obtained from 24-h recordings at 5 different nests.
d From 57 nest checks over 28 days.
f Estimated from rate of egg mass-loss (see text).
g From two 24-h watches.
h From 7 nest checks over 5 days.
* Cases 2 and 3 refer to the same male and female in the same breeding season.

69% of that found for nests with shared incubation (Table 1). Using my equation to obtain fresh egg weights, and assuming a constant rate of water loss (Drent 1970, Rahn and Ar 1974), it appeared that incubation at Nest 1 started about 26 Nov. (cf. 24 Nov., determined by behavior). Water loss probably occurred mainly during active incubation in the humid environment of the Snares Islands, as a fresh egg which was deserted had lost no measurable mass after seven days in the nest; this suggests that incubation constancy at Nest 1 was approximately 69%. Both eggs in Nest 1 developed fully, although one chick died while hatching. Hatching occurred 28 days after the nest was found and 37–39 days after the estimated start of incubation, which is 68–77% longer than normal. The surviving chick from Nest 1 and both chicks from Nest 2 were raised to fledging.

Case 2. Male A and Female B disappeared between Mar. and Oct. 1986. In 1986–87 Male B from an adjoining territory defended an enlarged area which combined both males' territories. He courted three females: Female A, the solo-incubating female of 1985–86; Female C, his mate from 1985–86; and Female D, a female from another previously adjoining territory, whose mate had also disappeared. Male B was seen mating with Female A on 13 and 14 Nov. Female A laid eggs on 22 and 25 Nov. (Nest 3) and shared incubation with Male B; the eggs hatched on 17 and 18 Dec. Between incubation shifts at Nest 3, Male B courted Females C and D and was seen mating with Female D on 26 and 27 Nov. Female C probably laid eggs soon after 15 Dec. when she was captured and determined (by palpation) to be near egg-laying condition. Female C is presumed to have deserted early in incubation, since she was paired with another male by 21 Jan. Female D was found incubating two eggs (Nest 4) on 27 Dec., although she was suspected (by behavior and egg masses) to have commenced incubation about 16 Dec. Male B was caring for a nine-day-old chick from Nest 3 when Nest 4 was found. Female D incubated largely by herself for the next 11 days, although the male visited the nest up to four times a day and incubated for short periods (e.g., a 5-min shift during a 24-h watch on 30 Dec.). The female fed for long periods (up to
11 h 55 min) after replacement at the nest by the male; but as the male left the nest soon after the female, the eggs were uncovered for much of this time. Incubation constancies during 24-h watches at Nest 4 on 30 Dec. and 5 Jan. were 60% and 83%, respectively. Nest 4 was deserted about 7 Jan., about 22 days after incubation started. Both eggs contained half-developed embryos; I do not know if the embryos were alive when the nest was deserted.

Case 3. Female D relaid in a new nest (Nest 5) on 5 and 8 Feb. 1987, and incubated solo for the next five days. Male B continued to care for his 7.5-week-old chick from Nest 3 until 13 Feb., when he commenced his full share of incubation at Nest 5. Incubation at Nest 5 was continuing when I left the island on 20 Feb., so Male B potentially fathered four chicks during the breeding season (cf. a maximum of two for a monogamous male).

Discussion.—Other shorebirds have flexible mating and incubation systems. Spotted Sand-piper (Actitis macularia) (Hays 1972, Maxson and Oring 1980) and Eurasian Dotterel (Eudromias morinellus) (Kalas 1986) usually have male, single-sex, intermittent incubation, but females occasionally assist. Incubation constancy at Eurasian Dotterel nests where both sexes incubated was similar to nests where the male incubated alone; no decrease in incubation length with shared incubation was found (Kalas 1986). Solo incubating male Wilson’s Plovers (Charadrius wilsonia) increased their time on the nest significantly, but there was a decrease in total incubation constancy compared with nests where incubation was shared (Bergstrom 1981). There was no concomitant increase in incubation length with single-sex incubation in Wilson’s Plovers, possibly because the change in incubation pattern occurred late in incubation, and the ambient temperatures were much higher than on the Snares Islands (Bergstrom 1981). Lessells (1983) experimentally induced extended, successful incubation by one parent in Kentish Plovers (C. alexandrinus) analogous to the situation for New Zealand Snipe. Warriner et al. (1986) also recorded successful single-parent incubation by Kentish Plovers, for up to 10 days (by one male) and 7 days (one female), but this occurred only if the mate deserted after the 16th day of incubation. Erckmann (1983) found that neither males nor females were able to incubate alone in Western Sandpipers (Calidris mauri).

New Zealand Snipe incubating by themselves did not achieve incubation constancies of other scolopacids with single-sex, intermittent incubation (80–90%; Norton 1972, Cartar and Montgomery 1985, Lofaldli 1985), although solo-incubating females did increase the time spent at the nest compared with females at nests with shared incubation (Table 1). Eggs cooled to ambient temperature during feeding excursions and did not remain above physiological zero temperature as found during the shorter excursions of shorebirds with single-sex incubation (Lofaldli 1985, Kalas 1986). Decrease in incubation constancy at nests with single-sex incubation caused a concomitant increase in incubation length. Delayed development is also the main effect of egg neglect in other birds (Boersma and Wheelwright 1979, Boersma 1982 and references therein, Murray et al. 1983, Sealy 1984). However, increase in incubation length in New Zealand Snipe resulted from a change in incubation regime rather than by periods of egg neglect within the normal incubation pattern (as occurs in all other species with variable incubation length; see references above).

Female New Zealand Snipe incubating by themselves had low hatching success. Males benefited from emancipation as additional breeding opportunities increased their reproductive success compared with monogamous males. However, male emancipation was rare, and female single-sex incubation was observed only for two of 43 female-years. The change from shared to single-sex incubation resulted in a decreased incubation constancy and delayed embryonic development, with one female successfully hatching an egg after an incubation length 68–77% longer than normal.

Acknowledgments.—My research has been funded by the New Zealand Dept. of Lands and Survey (now Dept. of Conservation) with additional financial assistance from the Royal Forest and Bird Protection Society and the Ornithological Society of New Zealand. Expe-
ditions to the Snares Islands were organized through the Dept. of Zoology, Univ. of Canterbury; I thank the expedition members and staff of the department for logistical support. Evert Kampert assisted with field work in 1986–87. The manuscript was improved by comments from P. Bergstrom, C. Lively, I. McLean, P. Sagar, J. Waas, and K. Winnett-Murray. This is University of Canterbury Snares Islands Expeditions Paper No. 64.

LITERATURE CITED


Food sharing by sibling Common Barn-Owls.—Interactions among nestling Common Barn-Owls (Tyto alba) range from cannibalism (Baudvin 1975, Colvin 1984, Lenton 1984, pers. obs.) to food sharing (Bunn and Warburton 1977, Epple 1979). In this paper I present the first documented case of food sharing among siblings in the North American race of the Common Barn-Owl (T. a. pratincola).

I observed food deliveries of adult barn-owls and food consumption behavior of their young in an abandoned agricultural silo in Davis County, Utah. Observations were made at a distance of less than 1 m. I watched through a one-way mirror in the back of a nest box lighted from within by a small battery-powered bulb. I made 27 h of observations on five nights over a 4-week period in April and May 1983.

Initial observations occurred during 4 h on 14 April when the four nestlings ranged from 7 to 14 days of age. The adult female remained in the box with the young on this night and spent most of her time brooding. When the male delivered prey, she tore it into pieces and fed it to the young. On the second night of observation, 26 April, the young were 19–26 days old. Both adults brought food to the young but neither entered the box. Nine prey items, all small rodents, were delivered during the 9.5-h activity period. The two oldest young obtained most of the prey items because of their greater size and agility. I did not see the youngest owlet eat on this night. Observation was limited to the first 2 h of activity on 30 April during which the same pattern was seen as on 26 April. On 3 May all four young still survived and were 24–31 days old. The adults delivered a total of 15 prey items over 9.5 h, mostly rodents and shrews. Each time an adult arrived at the nest, all of the young rushed to meet it. Once an owlet had control of a prey item, there was little, if any, attempt by the others to wrest it away. The largest owlet obtained and ate prey brought in delivery numbers 1, 2, 3, 5, 7, and 9. The next largest young obtained and ate prey from deliveries 6 and 8, and the third largest ate item 4. One of the smallest two young ate the prey delivered 12th. Despite having eaten six prey items and apparently being satiated, the largest young persisted in rushing to meet adults arriving with food. It also managed to obtain the prey brought in deliveries 10, 11, 13, 14, and 15, but made no attempt to eat
any of them. Instead, it offered them intact to its siblings. The first four of these shared prey were voles (*Microtus* spp.) which the oldest owlet carried to one or the other of the two smallest siblings. The posture and vocalizations of the largest owlet during this food sharing were much like those of the adults when they offered food to the young, i.e., prey was picked up and carried by the owlet in its beak. As it approached a younger sibling, it leaned forward and presented the prey. During all of this activity, the older owlet uttered the rapid twitting described as the food-offering call by Bunn et al. (1982), but no food begging by the younger siblings was noted. This behavior left little doubt that the food was being presented to the other owlets. The final prey item of the night, a juvenile pocket gopher (*Thomomys talpoides*), was offered to each of the younger owlets by the oldest but was not accepted by any of them. Finding no interest, the owlet dropped the gopher which was ignored by all of the nestlings for the remainder of the night. A final short period of observation on 7 May produced results similar to early evening events on prior days of observation. All four young in the brood fledged by 15 June.

My observations of food sharing closely match those seen in two European subspecies of the Common Barn-Owl (Bunn and Warburton 1977, Epple 1979). Thus, it is clear that, although the frequency of occurrence of this behavior is not known, food sharing occurs in at least three races of this widely distributed species.

The significance of food sharing, however, is not clear. Seemingly, juvenile barn-owls do not guard food for later use once they are satiated. Younger owlets would thus have access to a prey item even if it was not given to them by their older siblings. Food sharing in juvenile barn-owls could be altruistic behavior consistent with kin selection theory (Kurland 1980). On the other hand, by giving food to younger siblings, older owlets may be merely storing food in living containers as a hedge against future food shortages (Bruce Colvin pers. comm.). Either behavior could contribute to the fitness of individuals exhibiting it.

Food sharing by juvenile barn-owls certainly differs greatly from siblicide commonly practiced by juvenile eagles (Edwards and Collopy 1983). Although cannibalism has been widely reported in barn-owls, there is little or no evidence of siblicide in the species. Death and/or disappearance of the youngest owlets has occurred in about 30% of the 250 nesting attempts that I have observed in northern Utah. In some cases, dead owlets have been consumed by their nest mates and in others they have not. I have not found any indication (i.e., injuries), though, of aggression having led to these deaths; starvation was apparently their cause.

Food sharing could have a survival advantage for younger members of large broods if the adult female must leave them to help the male hunt. Eggs in barn-owl clutches hatch at 2–3 day intervals (Smith et al. 1974, Wilson et al. 1986). Large broods, common in this species (Baudvin 1975, Lenten 1984, pers. obs.), thus may consist of young more than 2 weeks apart in age. If females with such broods leave to hunt before the smallest young can feed themselves, sibling feeding could play an important role in survival of the youngest brood members. However, unless older siblings tear up food before offering it to owlets too small to do so for themselves, the duration that food sharing is effective for the survival of smaller young would be brief. Nevertheless, it might provide the difference between surviving or not for some of the brood.

Strong selection for delivering and presenting food to their young by barn-owls would be expected because it is obviously a key to reproductive success. Development of this behavior in immatures is consistent with the overall reproductive pattern of the species. Barn-owls rapidly mature; most breed in their first year and individuals have been known to breed successfully at six months of age (Trollope 1971). Early development of food presentation could be especially important to the fitness of males because they give food to females to begin pair formation and continue to do so through incubation and brooding. Thus, food
sharing by nestling barn owls may be simply an early manifestation of a behavior important to their fitness.

Acknowledgments.—I thank B. Colvin, S. Zeveloff and G. Miller for constructive comments on earlier drafts of this paper.

LITERATURE CITED


Notes on the social behavior and mating system of the Casqued Oropendola.—Oropendolas (Psarocolius spp.) are of particular interest in studies of mating systems because they nest colonially and are among the most sexually dimorphic of all birds. Male oropendolas are 10–35% larger by wing length than females (Lowther 1975); in some species, males weigh more than twice as much as females (Robinson 1986c, unpubl. data). Extreme dimorphism is correlated highly with polygynous mating systems (Emlen and Oring 1977), and Robinson (1986c) suggested that some oropendolas may be harem polygynous. In this note we examine the mating system and social behavior of the Casqued Oropendola (Psarocolius oseryi), a previously unstudied species, in southeastern Peru and compare it with other closely related tropical Icterinae.

Study area and methods.—This study was conducted at the Cocha Cashu Biological Station in the Manu National Park (11°51’S, 71°19’W) in southeastern Peru. The study area consists of humid, undisturbed lowland forest (elevation 400 m) in the floodplain of the Manu River.
Observations were made from September through November at two colonies in 1988 (J. Leak) and at three other colonies in 1979, 1985, and 1986 (S. Robinson). In the 1987 field season, we censused an area of roughly 500 ha of floodplain forest in an effort to find all active colonies. Because colonies of *P. oseryi* are very noisy, we probably found all active colonies. Attempts to capture birds in mist nets resulted in only a single capture. Additional weights include three individuals captured in the Manu National Park (Robinson, unpubl. data), and five individuals from the Louisiana State Museum of Natural Science.

**Habitat selection and population density.**—Two active colonies containing 19 and 25 nests, respectively, were discovered in mid-September of 1987 in the 500-ha study area. One colony was located in the mid-successional (“transition”) forest and the other in the very old floodplain (“high-ground”) forest (see Terborgh [1985] for descriptions of habitats). These data suggest a population density of approximately eight breeding females per 100 ha. The colony located in 1979 (17 nests) was along the edge of a forest stream in mature floodplain forest, the colony located in 1985 (15 nests) was in mid-successional forest, and the colony located in 1986 (22 nests) was located in mature floodplain forest. Census data from 250 ha of upland or *tierra firme* (above the floodplain) forest revealed no colonies; flocks of *P. oseryi* were, however, observed foraging in this habitat. *P. oseryi*, therefore, nests or forages in most of the different kinds of forest present in the study area.

**Colony sites.**—The five *P. oseryi* colonies were located in *Cecropia* trees (see also Koeppcke 1972) isolated from the surrounding canopy. The *Cecropia* trees may have been protected by stinging ants (D. Davidson, pers. comm.); none of the colonies were clustered around paper wasp nests. *P. oseryi* seems to be a species of the forest interior unlike the Russet-backed Oropendola (*P. angustifrons*), which usually nests in isolated trees along the edges of open areas in the Manu floodplain.

**Interactions with predators.**—*P. oseryi* uses both active and passive defensive tactics against predators. One colony was destroyed by brown capuchin monkeys (*Cebus apella*) in 1985 (C. Mitchell pers. comm.), but some colonies were isolated from the surrounding canopy and seemed safe from primates. We saw brown capuchins approach a colony two times in 1987, but the monkeys seemed unable to find a way to reach the tree. Active defense against predators takes the form of mobbing. *P. oseryi* twice gave alarm calls at the approach of brown capuchins, and on one of these occasions, both males and females were seen diving at the monkeys closest to the colony. A group of about 15 *P. oseryi* were also observed at least 50 m from their colony mobbing Cuvier’s Toucans (*Ramphastos cuvieri*) which regularly attack colonies of colonial blackbirds (Robinson 1985a).

Oropendolas may have a sentinel-based defense against predators of adults. On several occasions, colonies were immediately evacuated by adults after loud, piercing alarm calls that appeared to be given by individuals perched in trees above the colony. Less than two sec after one of these alarms, a Black-and-white Hawk-Eagle (*Spizastur melanoleucus*) burst through the colony tree and narrowly missed catching a female that was leaving the colony tree. Black-and-white Hawk-Eagles have also been observed attacking colonies of *P. angustifrons* (Robinson, unpubl. data).

Piratic Flycatchers (*Legatus leucophalus*), which take over the nests of other colonial Icterinae (Robinson 1985c), were observed harassing females at two colonies. Both male and female *P. oseryi* chased the nest pirates. Eventually, the Piratic Flycatchers took over oropendola nests, but we were unable to determine if the nests had been abandoned due to harassment or for other reasons. We never saw Giant Cowbirds (*Scaphidura oryzivora*) visit a colony of *P. oseryi*. This species seems to parasitize only *P. angustifrons* in the Manu area (Robinson 1988).

**Intersexual interactions.**—Female oropendolas interacted aggressively at colonies. At one colony, six aggressive interactions were observed during 28 hours of observation; three
interactions involved prolonged midair grappling and chases. The other three involved one female supplanting another from a nest site. All six encounters took place during the early nest-establishment and nest-building phases. At least one female was observed robbing material from the nest of another female.

Aggressive interactions among males were observed (ten interactions during 28 hours of observation at one colony) and usually involved supplanting bouts in which one male supplanted another that was displaying to a female. The supplanting male subsequently displayed to the same female. One intense fight was observed between two males that grappled in midair and plunged into the understory before separating. Because we had no color-marked birds, we could not determine if there was a dominance hierarchy.

Sexual dimorphism.—Weights of Casqued Oropendolas from southeastern Peru indicate that males ($\bar{x} = 189.8 \pm 40.6$ [SD] g, $N = 5$) are roughly 90% heavier than females ($\bar{x} = 99.8 \pm 13.4$ [SD] g, $N = 4$).

Mating system.—Males appeared to consort with individual females, following them on flights to and from the colony during the late nest-building period. This system seems similar to the mating systems described for Yellow-rumped Caciques (Cacicus cela) (Robinson 1986c) and Chestnut-headed Oropendolas (P. wagleri) (Chapman 1928). Nesting synchrony may limit the number of females consorted by any one male. At the most intensively studied colony, all 19 nests were completed within a single week. During this period, as many as 12 females were consorted at the same time. The operational sex ratio (cf. Emlen and Oring 1977) therefore did not appear to be heavily skewed toward males. Because we had no color-marked individuals, we could not determine if males consorted the same female throughout the egg-laying period or if they switched among females. No copulations were observed at the colony.

Discussion.—The social behavior of the Casqued Oropendola has striking similarities to that of the Yellow-rumped Cacique (reviewed in Robinson 1986c). Both species nest in sites that are relatively safe from mammalian predators and both mob avian predators. Unlike caciques, Casqued Oropendolas also mob monkeys, perhaps because oropendolas are large enough to pose a significant threat. Both species also show evidence of intense intrasexual competition in males and females. In caciques, females compete for access to safe nest sites (Robinson 1986b), and fights between female Casqued Oropendolas may serve the same function. Interactions among male caciques, which have a mostly linear dominance hierarchy (Robinson 1986a), consist of frequent supplantings and occasional grappling fights (Robinson 1985b). It therefore seems possible that Casqued Oropendolas also engage in dominance interactions that determine priority of access to breeding females.

Caciques and Casqued Oropendolas also show a female defense-based mating system centered around consorting and guarding egg-laying females. Without color-marked birds, however, we have no data on the extent to which females are monopolarized. Males may consort each female for the two- or three-day egg-laying period, as is the case for the cacique, or they may switch among several females each day. Casqued Oropendola nesting is much more synchronous than that of the cacique (Robinson 1985b), and few males may therefore be able to monopolize more than one female (cf. Emlen and Oring 1977).

The mating system of the Casqued Oropendola differs from that of the Russet-backed Oropendola in that matings occur away from the colony and males appear to consort females individually. Russet-backed Oropendolas often copulate at colonies, and males sometimes accompany flocks of foraging females (Robinson 1986a). Dominant male Russet-backed Oropendolas therefore have the potential to monopolize most of the females in a colony, which may explain why they are more sexually dimorphic (Robinson 1985b) than Casqued Oropendolas.

Acknowledgments.—We thank K. Petren for his help with mist-netting. As always, we
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LITERATURE CITED


Diet of the Surfbird in southern Chile.—The Surfbird (Aphriza virgata) migrates during the boreal winter to the Pacific coast of Central and South America, mainly to Peru and Chile, and as far south as the Magellan Strait (Araya and Millie, Guía de Campo de las Aves de Chile, Edit. Universitaria, 1986). This report describes the diet of the Surfbird in the southern part of its wintering grounds, near Valdivia, Chile, and compares diet with food availability.

Foraging surfbirds were studied on rocky shores at Mehuín (39°24’S, 73°13’W), Valdivia, Chile. Diet could not be determined by direct observation, so 25 birds were collected in late February 1983 (18 males and 1 female) and in early March 1984 (3 males and 3 females).
Crop and gizzard contents of each bird were analyzed by counting all identifiable items and measuring maximum length of intact mussels to the nearest 0.1 mm. Also, 21 fecal pellets were collected at feeding areas in February 1983. Pellets were broken up in water and fragments placed in a Petri dish with a dot-matrix of 66 evenly spaced points. Dots covered by each item were counted and expressed as percent of the total number of dots covered. At feeding areas, food availability (percent cover of sessile species) was measured in 7 randomly placed quadrats (20 × 20 cm) during February 1983. In an additional quadrat, all mussels were removed and measured. In order to evaluate qualitative differences between the mussel species consumed by Surfbirds, shell strength (force necessary to break the shells) was measured with a Universal Testing Machine (N = 45 Semimytilus algosus and N = 48 Perumytilus purpuratus of different sizes), by applying pressure perpendicularly over the valve sides. R × C test (Sokal and Rohlf, Biometry, Freeman, 1969) was used to compare absolute frequencies, pooling categories when necessary to avoid zero frequency cells.

Flocks of 20 to 100 birds (mean = 68 ± 27 [SD], N = 12) were observed foraging on mussel beds in the mid- and low-rocky intertidal region. Prey were pulled from the rock and swallowed whole: no attempts to open the mussels were observed. Prey were crushed in the gizzard and hard parts were not regurgitated.

Stomach contents (crop plus gizzard) and feces showed that the mussel Semimytilus algosus predominated in the diet of Surfbirds during 1983, but in 1984 the mussel Perumytilus purpuratus was as important as S. algosus (Table 1). Stomach contents showed significant differences between years ($\chi^2 = 398$, df = 4, $P < 0.001$, pooling gastropods and excluding Choromytilus chorus—not present in 1984 stomach samples); thus it was not possible to pool both sets of samples for statistical analysis. Relative proportions of S. algosus and P. purpuratus in stomach contents varied significantly between 1983 and 1984 ($\chi^2 = 395$, df = 1, $P < 0.001$). Differences between years may be attributed to the tide level at the time of collecting the birds. In 1983, collection was done during low tide, while in 1984 birds were collected at the onset of low tide, when most of the S. algosus beds are unavailable to
### Table 1

**Prey Species Composition of Surfbird and Prey Availability on Rocky Shores of Mehuín, Valdivia, Chile**

<table>
<thead>
<tr>
<th></th>
<th>Stomach contents</th>
<th>Feces 1983</th>
<th>Environment 1983</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1983*</td>
<td>1984*</td>
<td></td>
</tr>
<tr>
<td><strong>Bivalvia</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Semimytilus algosus</em></td>
<td>92.9 ± 9.0**</td>
<td>46.4 ± 52.5</td>
<td>79.1 ± 39.5*</td>
</tr>
<tr>
<td><em>Perumytilus purpuratus</em></td>
<td>4.1 ± 5.8*</td>
<td>44.9 ± 42.9</td>
<td>0.7 ± 3.1**</td>
</tr>
<tr>
<td><em>Choromytilus chorus</em></td>
<td>0.1 ± 0.6</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>Gastropoda</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Littorina arauca</em>ana</td>
<td>2.3 ± 7.5</td>
<td>5.1 ± 10.7</td>
<td>—</td>
</tr>
<tr>
<td><em>Nucella crassilabrum</em></td>
<td>0.3 ± 1.3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Scurria variabilis</em></td>
<td>—</td>
<td>0.4 ± 1.0</td>
<td>0.2 ± 1.1</td>
</tr>
<tr>
<td><strong>Cirripedia</strong></td>
<td>0.2 ± 0.8**</td>
<td>3.2 ± 6.7</td>
<td>1.4 ± 3.5**</td>
</tr>
<tr>
<td><strong>Decapoda</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Emerita analoga</em></td>
<td>—</td>
<td>—</td>
<td>18.6 ± 39.3</td>
</tr>
<tr>
<td><strong>Algae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Iridaea boryana</em></td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>Number of samples</strong></td>
<td>19</td>
<td>6</td>
<td>21</td>
</tr>
</tbody>
</table>

* Significance of comparisons between environmental samples and consumption using Wilcoxon two-sample test: * = $P < 0.05$, ** = $P < 0.01$.

* No environmental figures for 1984 are available for comparisons with stomach contents.

* Species present but density figure not available.

* Includes *Chthamalus scabrosus* and *Jehlius cirratus*.

* Inhabits sandy beaches.
Surfbirds. Surfbirds, as well as other birds foraging in intertidal zones (e.g., Black Turnstones [Arenaria melanocephala] and Black Oystercatchers [Haematopus bachmani]), feed in various zones and prey in relation to tide levels (Frank, Ecology 63:1352–1362, 1982). The abundance of prey in the environment was different from that in stomachs and feces in 1983. The mussel *S. algosus* was taken by Surfbirds more frequently than it occurred in the environment, while *P. purpuratus* was ignored or taken in the same proportion as it occurred in the mussel beds (Table 1). The remaining prey species appeared at low frequencies. Occasionally when feeding on sandy beaches, Surfbirds preyed on the decapod *Emerita*.
analoga. In 1984 the actual prey items were almost the same as those taken during 1983, but *P. purpuratus* and *S. algosus* were equally represented in the stomach contents.

The size distribution of *S. algosus* consumed by Surfbirds (1983 sample) differed significantly from that found in the environment \( (x^2 = 61.8, df = 6, P < 0.005; \) test on absolute frequency of size classes, mussels >14 mm were pooled to avoid zero frequency cells). Medium-sized mussels, 6–12 mm in length, were frequent in stomachs, mussels in the length range 12–20 mm were rare, while those >20 mm were not found in stomach contents (Fig. 1A). *P. purpuratus* consumed during 1984 were mainly small-sized, 87.2% below 8 mm in length (Fig. 1B). Whole *S. algosus* and *P. purpuratus* were not found in the stomach contents of the 1984 and 1983 samples, respectively. Surfbirds foraging on mussel beds of *Mytilus californianus* and *M. edulis* on the coast of Oregon consumed mussels in the length range 2–10 mm (Marsh, Ecology 67:771–786, 1986), somewhat below the size range of mussels consumed in Mehuín.

Mussel shell strength increased exponentially with mussel length at the same rate in both species \( (F \text{ between slopes} = 1.90; 1.95 df; P > 0.1), \) but *P. purpuratus* had stronger shells than *S. algosus* \( (F \text{ between adjusted means} = 653.8; 1.94 df; P < 0.001). \)

The mussels *S. algosus* and *P. purpuratus* are the main prey of the Surfbird on rocky shores in Mehuín, Chile. The low frequency of consumption of other species suggests that they are swallowed incidentally, because most of them live on or among the mussels. The large number of small *P. purpuratus* consumed during 1984 (60% below 6-mm length) may have been swallowed incidentally because juveniles of this species recruit among the byssus of larger mussels (Moreno, Lunecke, and Lepez, Oikos 46:359–364, 1986).

Mussel species consumed by Surfbirds differ in their shell strengths, shells of *S. algosus* being more easily broken than those of *P. purpuratus* (Fig. 2). The same is true of byssuses of both species (pers. obs.). Although energy content of the mussels was not measured, the meat content of *S. algosus* is greater than in *P. purpuratus* of equivalent size (pers. obs.). These characteristics suggest that *S. algosus* is a more profitable prey than *P. purpuratus*.


**Historical breeding records of the Common Merganser in southeastern United States.**—The Common Merganser (*Mergus merganser*) breeds throughout the forested boreal portions of the Holarctic Region (Vaurie 1965), but presently nests only sporadically south of New England in the eastern United States (AOU 1983). In routine curating of the egg collection of the Western Foundation of Vertebrate Zoology (WFVZ) and during visits to other major museum collections, I recently discovered evidence of a formerly more extensive southerly breeding range for this species in the United States.

A clutch (WFVZ 124,806) containing 9 eggs was collected at Bishop’s Swamp, Mercer County, West Virginia, by David Willis on 19 May 1897. The set was acquired by the WFVZ from the private collection of Nelson D. Hoy of Media, Pennsylvania, who obtained
it from the J. Parker Norris collection, the largest turn-of-the-century egg collection in North America. According to the original data slip, the nest was 15 ft (4.6 m) high in a tree stub located a quarter of a mile from running water. The eggs are creamy-white, unmarked, subelliptical in shape, and have a smooth, almost oily texture. They average 64.5 (62.7-
67.1) × 46.1 (45.1–47.6) mm in size. In all of these details they agree with the published descriptions of eggs of this species (Bent 1923, Palmer 1976), as well as with >100 other Common Merganser eggs in the WFVZ collection, but differ in color, size, and shape from the eggs of Wood Ducks (Aix sponsa) and Hooded Mergansers (Lophodytes cucullatus), the two other cavity-nesting ducks in the southeastern United States (Bent op. cit.). Hall (1983) listed the Common Merganser as an “uncommon migrant and winter visitant” in West Virginia, and he did not allude to possible breeding within the state. Since Hall (op. cit.) was unaware of any West Virginia specimens of the Common Merganser, this egg set fills that void.

There are no previously published breeding records for Tennessee. A set of 9 Common Merganser eggs in the Field Museum of Natural History (FM 5132) was collected by J. T. Overstreet in Smith County, Tennessee, on 28 April 1899. Incubation was recorded as “very little,” and the nest was located in a cavity 15 ft (4.6 m) high in a cottonwood (Populus sp.) on the bank of a river. Average measurements of the existing 8 eggs are 61.9 (60.0–63.1) × 42.6 (41.4–44.5) mm, and they are creamy-white with a glossy texture. Two other sets of Common Merganser eggs from Tennessee are in the collection of the San Bernardino County Museum (SBCM). A clutch of 7 fresh eggs (SBCM 10628) was collected on 9 May 1898 in Smith County by James Jackson from “a hole in a tree.” The eggs average 62.4 (59.7–64.0) × 46.5 (45.4–47.6) mm. The other set (SBCM 11,293) was taken by J. T. Overstreet in April 1898, also in Smith County. It contains 9 eggs which were fresh when collected from a cavity 10 ft (3 m) high in a cottonwood tree. The eggs average 66.2 (64.8–
67.8) × 48.3 (47.4–49.4) mm. Both of the SBCM sets are creamy-white with the glossy, somewhat oily texture typical of Common Merganser eggs.

The WFVZ collection contains data cards for two additional Tennessee egg sets of this species, both collected by J. T. Overstreet in Smith County on 21 April 1897 and 30 April 1897, respectively. The 21 April nest contained 9 slightly incubated eggs and was located 18 ft (5.5 m) high in a broken limb of a beech tree. The 30 April nest contained 7 fresh eggs and was situated 7 ft (2.2 m) high in a hole in a cottonwood tree. Neither set was found in the WFVZ collection. Overstreet’s original data cards suggest that he did not place any distinctive marks on the eggs. This unfortunate practice by some “oologists” frequently resulted in the loss of such specimens as they changed hands from collector to collector. However, in view of the existence of the data cards, the details on them which are compatible with valid nesting records in regard to clutch size, breeding dates, and nest locations, and the existence of the other Smith County, Tennessee, sets at the FM and SBCM, there is justification to regard the records as authentic.

Common Mergansers nested south to western Pennsylvania until the end of the 19th century (Warren 1890), and Todd (1940) mentioned a single breeding record from Presque Isle as late as 1933. Indeed, the species may still breed in New Jersey and eastern Pennsylvania (Boyle et al. 1980). Farther south, broods of Common Mergansers were observed in the Shenandoah Valley of Virginia during the breeding seasons of 1947, 1953, and 1954 (Jopson 1956), and a pair with at least one young of the year was reported at Dyke Marsh, Hunting Creek, Fort Hunt, Virginia, during June–July 1965 (C. W. Carlson et al. in F. R. Scott 1965). Brimley (1941) reported a brood of Common Mergansers in Chowan County, North Carolina, in May 1938. These records, as well as those from Tennessee and West Virginia, give more credence to the claim of Audubon (1838) that this species bred in Kentucky in the early part of the 19th century, an assertion rejected by Mengel (1965).

It is difficult to interpret whether these scattered, presently extralimital records are merely
anomalous, or whether in aggregate, they represent the last vestiges of a relict historical breeding range which may have extended southward along the Appalachian Mountains. Bellrose (1976) implied that instances of nesting by this species far south of its usual breeding range are fortuitous, and he cited a curious isolated breeding record from Chihuahua, Mexico, by van Rossem (1929) as evidence for this. Phillips (1926) and Palmer (1976) acknowledged that this species formerly nested well south of its present breeding range in the United States and suggested that it may have disappeared from such areas as a result of man-induced habitat losses. However, it seems unlikely that a northward retreat on such a broad front could be attributed wholly to a single cause. Furthermore, a similar trend apparently exists in Europe, where several isolated populations south of the present breeding range have also disappeared in recent decades (Phillips 1926, Cramp 1977).

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ORNITHOLOGICAL LITERATURE


ALDO LEOPOLD/HIS LIFE AND WORK. By Curt Meine. Univ. of Wisconsin Press, Madison, Wisconsin, 1988: 638 pp. Illustrated. ISBN 0-299-11490-2. $29.50 hardcover.—There has been an outpouring from the American heartland of books about the most celebrated of American ecologists, Aldo Leopold. This may seem excessive but not for a man with his breadth of contributions to society and his profession. Leopold has long been celebrated by foresters, and in particular by wildlife managers who grew up with his classic textbook, “Game Management” (1933). When the environmental movement blossomed in the late 1960s it didn’t take long for a much larger audience to discover Leopold’s essays in “A Sand County Almanac” (1949), including his famous essay, “Land ethic.” Both of the books have been reprinted numerous times. As long ago as 1972–73, Susan Flader published two books about Leopold, “The Sand County of Aldo Leopold” (Steinhacker and Flader 1972) and “Thinking Like a Mountain/Aldo Leopold and the Evolution of an Ecological Attitude Toward Deer, Wolves, and Forests” (Flader 1973).

The occasion of the most recent publications, of which there are six, is the centennial in 1987 of the birth of Leopold. A symposium regarding Leopold was held by Iowa State University at Ames in October 1986 (Tanner, T., ed. 1987. “Aldo Leopold/The Man and His Legacy,” Soil Conservation Society of America). The university of Wisconsin Press has published a recent commemorative edition of “Game Management,” and Oxford has published a commemorative edition of “A Sand County Almanac.” Two additional volumes, including one of those reviewed here, have been published by the University of Wisconsin Press. (plus “Companion to A Sand County Almanac,” J. B. Callicott, ed., 1987) A two-day symposium called by Robert McCabe was presented by 17 of Leopold’s students in Madison in April 1987 (“Aldo Leopold: Mentor.” Richard E. McCabe, ed., 1988). Wisconsin Natural Resources magazine (Wisconsin Department of Natural Resources) has published Leopold articles in each issue of the commemorative year. Wisconsin Academy Review devoted an entire issue (34:Dec. 1987) to articles by those who knew him.

“Aldo Leopold/The Professor” was written and published by McCabe under the aegis of The Rusty Rock Press which McCabe named after his farm west of Madison. He has generously donated the proceeds to the Department of Wildlife Ecology at the University of Wisconsin, the department started by Leopold and later chaired for many years by McCabe.

One might think that such an outpouring of print about a single individual might lead to a great deal of redundancy but, for the most part, this does not appear to be the case. These two volumes are a good example; McCabe presents a highly personal statement of his experiences with Leopold for a period of ten years at the end of Leopold’s life, and Meine offers an objective, scholarly piece of research. Both authors write with clear love and respect for the man and his works.

McCabe’s intimate treatment of Leopold jumps from the pages from the beginning. For example, immediately under the covers, one finds facsimile copies of Leopold’s handwritten manuscripts of two of his essays which McCabe had rescued from oblivion and saved all these years. Leopold often signed memoranda and letters with his initials which are found, enlarged, on the title page. Among the excellent black-and-white photographs I counted 37 by Leopold and 4 others by members of his family. If this book has value as a historical
record, certainly these photographs will be one of the main reasons it does. Another personal
touch is the photographic treatment of the old frame house at 424 University Farm Place
in which the wildlife department at the University of Wisconsin was housed, including a
floor plan and two photos of the final demise of the building at the hands of the wrecker.
One I particularly like is a close-up of the iron numbers, 424, on the wooden pillar supporting
the porch of the building with McCabe's keys hanging below.

Both McCabe's and Meine's accounts have their historical beginning and ending, but in
between they differ substantially. McCabe starts with a brief background sketch of A.L. and
of himself when he arrived on the Madison campus of the University of Wisconsin seeking
graduate study. In between there and his account of Leopold's death in a grass fire near the
family shack, McCabe deals with the activities in which he and A.L. engaged, or which
McCabe observed; the department and its staff, including a notable and lengthy account by
Alice Harper Stokes, A.L.'s secretary during World War II; A.L.'s management of the
graduate program, his teaching, his personal and professional activities, the family shack
where Leopold applied his ideas of land use and where many of his essays were born, as a
scientist, A.L.'s friends, his role as a state conservation commissioner, as a hunter, and as
a writer.

Meine, on the other hand, takes Leopold's roots from his grandparents' emigration from
Germany, fitting their entrepreneurial experience into the settlement of the West during the
period of resource exploitation and national social responses leading to the conservation
movement at the turn of the century. Leopold, of course, was a leader and source of inspi-
ration and ideas for much of the movement. To understand McCabe's account of the final
decade of A.L.'s life, the reader will do well to read Meine's sensitive and more extensive
account first.

Because I shared enough of McCabe's experience to understand his portrayal easily, I
found few surprises. It is a portrait of a bust, not of a full length statue, largely because it
covers only one decade of a six-decade life and is mainly first-hand history. Meine, on the
other hand, presents us with a complete portrait, nearly all of it from astonishingly rich
second-hand sources, including fascinating vignettes from both A.L.'s family and his wife
Estella’s family. For me there were many surprises, but more importantly, he provided me
with a detailed background of the Leopold I knew first hand and that McCabe describes.
The three major professional phases of Leopold's life described by Meine are the 18 years
in District 3 of the U.S. Forest Service (Arizona and New Mexico, starting when they were
still territories) and at the Forest Products Laboratory in Madison, Wisconsin; four important
transitional years working on the Game Survey of the North Central States and, while
unemployed, writing "Game Management"; and lastly, his years on the faculty at the Uni-
versity of Wisconsin. Meine follows him through each of these, providing continuity by
tracing the development of his ecological ideas and the course of his family life.

The format of these two books is plain with few frills. The photographs in McCabe, many
by himself, are a significant contribution, and those in Meine are particularly well chosen
to illustrate significant aspects of Leopold's life. Both authors present their objectives in a
preface and conclude with an epilogue. The books both contain errors of fact and of typog-
raphy. I was bemused to find Aldo spelled "Also" twice within a few pages in Meine—
modern word processing doesn’t find all the errors. Both authors had difficulty keeping track
of the cast of characters and sometimes disagreed with each other on where they were and
when. There may be more errors of this nature than my records show; none that I found
detracts from the story. Professional historians of the future will have to check the facts for
themselves, especially in McCabe, who deliberately avoided documentation as much as he
could, relying on what he calls "cue words" to jog his memory.

The most unfortunate aspect of either of these books that I find is McCabe's entry into
the polemics of whether or not Leopold was the first recognized university faculty appointee designated in wildlife management; Leopold routinely kept thoughts of this nature out of print and McCabe, who candidly proclaims his hero worship, would have done well to follow his role model.

Both of these books are worthy contributions to the commemorative celebration of the 100th anniversary of the birth of America’s most celebrated conservationist and ecologist. Students of natural resource management, conservation, the environmental movement, and indeed the history of the country, will find these two books well worth their time. As we enter the era “beyond oil” we are going to need the kind of faith in ourselves and in the future that the words of men like Leopold provide. These two books will give us a fuller understanding of how he arrived at his deep commitment to a better relationship between man and the rest of the living community.—Fred Greeley.

The Skuas. By Robert W. Furness, illus. by John Busby. T & A D Poyser, Calton, England, 1987:363 pp., 30 black-and-white photos, 100 text figs., 65 tables. (Distributed in the U.S. by Buteo Books, Vermillion, South Dakota.) $45.00.—This attractive volume attempts to outline our knowledge of the skuas and jaegers. Although the “American Ornithologists’ Union Check-list of North American Birds,” Sixth Edition, places the skuas and jaegers within the Laridae, the author retains the six species as the Stercorariidae. Members of the family are probably poorly known to most North American ornithologists. This is because they are pelagic seabirds in the nonbreeding season and because they breed in polar and subpolar latitudes. The jaegers (or small skuas as they are called in this volume) of the genus Stercorarius have circumpolar and subarctic breeding ranges, although the Parasitic Jaeger (S. parasiticus) breeds south in the North Atlantic to Iceland and the northern British Isles. Most of the large skuas (Catharacta sp.) are distributed in a series of populations on Antarctica, subantarctic islands, and southern South America, but one northern hemisphere population, the Great Skua (C. skua skua) breeds in the eastern North Atlantic.

The taxonomy of Catharacta has been contentious. The author recognizes three species within the genus: the South Polar Skua (C. maccormicki), the Chilean Skua (C. chilensis), and C. skua, which includes the Great Skua of the North Atlantic, the Tristan Skua (C. s. hamiltoni), the Brown Skua (C. s. lomnbergii) and the Falkland Skua (C. s. antarctica). Hybridization is occurring between the South Polar Skua and the Brown Skua on the Antarctic Peninsula, and between the Chilean Skua and the Falkland Skua along the coast of Patagonia, but the amount of gene flow is not considered sufficient to alter the present taxonomy. The author considers that the Falkland Skua is the most likely source population of the northern race.

These species are attractive subjects for the study of evolutionary adaptation. All have strong hooked bills and show reversed sexual size dimorphism. Plumage polymorphism occurs in all members of Stercorarius (although very rarely in adult Long-tailed Jaegers [S. longicaudus]) and has recently been recognized in the South Polar Skua. Some of the jaegers and skuas are specialized kleptoparasites, particularly in the nonbreeding season. All the jaegers are predators in tundra ecosystems when breeding, except the maritime population of the Parasitic Jaeger, and feed on birds, bird eggs, rodents, insects, berries and carrion. The species show considerable opportunism in their feeding but one can generalize by saying that the Pomarine Jaeger (S. pomarinus) is an obligate lemming predator, the Parasitic Jaeger preys on small birds, including small shorebirds, and the Long-tailed Jaeger preys on rodents, small birds, mostly passerines, and insects.
The feeding ecology and territory systems of the large skuas (*Catharacta*) are remarkable for the variation between races and species. The South Polar Skua, the Chilean Skua and the Great Skua feed at sea away from small colonial territories. The three southern hemisphere races of the Great Skua (the Brown, Tristan and Falkland skuas) feed mostly on seabirds on large territories. The Brown and Falkland skuas forage by walking about at night and pouncing on any seabird they encounter.

This then is the rather unique group for which Furness has attempted to compile all our knowledge. His book contains 16 chapters headed: Early History and Classifications, Distributions and Populations, Migration Pattern, Reversed Sexual Size Dimorphism, Behaviour, Food and Feeding, Kleptoparasitism, Plumage Polymorphism, Breeding Systems and Social Organization, Breeding—Laying to Hatching, Breeding—Hatching to Fledging, Population Dynamics, Pollutants, Skuas and Agriculture, Skuas and Conservation.

The book reads well, although at times I thought the author's arguments moved too slowly. It is written for an informed general audience. Topics such as kleptoparasitism and reversed sexual size dimorphism are developed in a broad context which will appeal to undergraduates and graduate students in ornithology and ecology. John Bushy's drawings scattered through the text convey a good feel for the spirit of these birds.

The most obvious shortcoming of this work is that it does not live up to its inclusive title. The treatment actually given the several species is very uneven. This is in part because the species are not equally well known and in part because the North American jaeger literature is not well covered. The information presented on the Pomarine Jaeger and on the Parasitic Jaeger on its arctic breeding ground is largely from the work of Pitelka and Maher, although Pitelka's important paper on these two jaegers (Pitelka, Tomich and Treichel, Ecol. Monogr. 25:85-117, 1955) is not referred to. The information included on the Long-tailed Jaeger is largely from Northern Europe and northeastern Greenland, and a paper by Maher (Arctic 23:112-129, 1970) which would have added some important perspective to the discussion of the jaeger's territorial system and site fidelity is also not cited.

The author concludes that all the jaegers except the Pomarine Jaeger show mate and site fidelity from year to year. Yet populations of the Long-tailed Jaeger in northern Alaska and on Ellesmere Island, NWT, Canada, have showed dramatic increases in breeding density in response to increased microtine rodent populations, suggesting that this species is adapted to exploiting high microtine rodent population in a manner analogous to its larger congener, the Pomarine Jaeger.

Not all the available information from the North American arctic in the papers cited is used or consistently integrated into the text. For example, the chapter on egg laying and hatching is devoted to the Parasitic Jaeger in Britain, the Great Skua and some of the southern large skua populations, and a brief mention of work on the Long-tailed Jaeger from Scandinavia. There is good published information on egg-laying synchrony, egg loss, and hatching of the Pomarine Jaeger, which is not mentioned at all. The same focus occurs in the following chapter on hatching to fledging; again, relevant information from North America is lacking.

The author has worked intensively on the Parasitic Jaeger and Great Skua in Britain and in the southern hemisphere. The book appears to have been initially devoted to those two species and later expanded to include all members of the family. Indeed, the last three chapters of the book are concerned entirely with population histories and problems of conservation of the Parasitic Jaeger and Great Skua in the British Isles.

Despite the above I do recommend the book. It is a good and well-written compendium of much of our present knowledge of a fascinating family of seabirds. It will be of interest to informed laymen, and students in behaviour, population biology, and general ornithology as well as a useful reference for specialists. I just wish it came closer to being the comprehensive work that the title suggests.—William J. Maher.
NEOGENE AVIAN LOCALITIES OF NORTH AMERICA. By Jonathan J. Becker. Smithsonian Institution Press, Washington, D.C., 1987:171 pp., 3 figs. $14.95.—This book is a compilation of the fossil birds recorded from any Miocene or Pliocene locality in southern Canada, the United States, and northern Mexico. Following a brief introduction and checklist of species, the main section of the book is a list of fossil localities organized chronologically by land mammal ages, from the Late Arikareean through the Blancan. For each locality, Becker provides information in the following categories: geological formation, political state, land mammal age, radiometric dates, general references, avian references, avian taxa, and comments. This enormous amount of information is presented clearly and consistently. The index is indispensable.

This is a landmark study for several reasons. First, it is the first monographic treatment of the Neogene birds of North America. Second, it incorporates the latest information on biochronology and geochronology of the fossil sites. Third, it includes brief comments on previously unstudied material, especially that in the Frick Collection of the American Museum of Natural History. In the last two categories, Becker's book complements, corrects, or updates the standard references in avian paleontology (Brodorb, P. 1963, 1964, 1967, 1971, 1978, Catalogue of fossil birds, Bull. Florida State Mus. 7:180–293; 8:195–335; 11:99–220; 15:163–266; 23:139–228; Olson, S. L. 1985, The fossil record of birds, Avian Biology 8:76–252).

Becker makes no attempt to discuss the relationships of Neogene avifaunas to those of the Paleogene or the Quaternary. Although much taxonomic revision remains to be done, Becker has compiled so much information that the lack of a concluding section on the evolution and biogeography of Neogene avifaunas is disappointing. Regardless, anyone interested in the fossil record of North American birds will find Becker's book to be extremely useful. It is a major step in the movement to modernize the chronology of fossil birds.—

DAVID W. STEADMAN.


SPECIES-CHECKLIST OF THE BIRDS OF NEW GUINEA. By Bruce M. Beehler and Brian W. Finch. Australasian Ornithological Monographs, No. 1, Royal Australasian Ornithologists Union, Moonee Ponds, Vic., Australia, 1985:127 pp. No price given.—The appearance of this field guide is welcomed by all those studying the avifauna of New Guinea, and it is a boon to those who wish to visit the island. The two previous synthetic volumes on the New Guinea avifauna, Mayr's "List of New Guinea Birds" (1941) and the Rand and Gilliard "Handbook of New Guinea Birds" (RG), have each served to summarize the scattered literature. The Mayr volume provided the strong taxonomic background necessary for further meaningful studies and was the outgrowth of the numerous pre-World War II expeditions to the area. RG, using Mayr's list as its starting point, incorporated post-war taxonomic studies and produced the first comprehensive volume including the natural history of the avifauna.

Since 1967, many additional studies, both taxonomic and field oriented, have been made of New Guinea birds. In addition, the area has become accessible to birdwatchers and interested tourists. The need for an illustrated field guide has been felt for some years. "Birds of New Guinea" is such a guide. It has incorporated in its brief text much of the information gained in the last twenty years, both as the result of expeditions and long-term studies and of the valuable observations over the years by members of the Papua New Guinea Bird
Society, most of whom have been resident in Papua New Guinea (PNG) for varying amounts of time. (Most of these observations refer to birds occurring in PNG, the eastern half of New Guinea; West Irian, the western half of New Guinea and now a province of Indonesia, has had less recent field work and the birds are less well known.) These observations provide a perspective on seasonal variation in distribution and abundance. The authors and their text contributors (the late Harry Bell, Brian Finch, and Jared Diamond) have had extensive personal field experience in New Guinea; they are to be commended for packing so much information into so little space. The artists, Dale Zimmerman and James Coe, have also done a tremendous job of illustrating most of the 708 species described in the text, usually showing both male and female, when they differ, and sometimes immature plumages as well. Previous reliable illustrations did not exist for a large proportion of the species. Both artists have meticulously researched their birds, using museum specimens, field notes and labels, and the published literature to accurately depict colors of soft parts and details of plumage. The result is an up-to-date and reliable field guide, reasonably free of error. Color reproduction is, in general, good. The book is well made and my paperback copy has held up well during three field seasons.

The volume treats 725 species, 708 of which are known to occur (although some of these are “difficult” species known only from sight records). By way of comparison, RG listed 649 known species. Much of this increase is in the number of species of seabirds, shorebirds, and other migrants reported in the last 20 years by resident observers.

The introductory section, although necessarily brief, is good. The section on Nomenclature (p. 6) refers to English names, not scientific nomenclature, and discusses the difficulties of arriving at satisfactory English names, given the large number of sources. In general, the authors have followed a conservative course; and, while no-one will agree with all their choices, decisions were necessary and other names that have been used are given in the text. One ridiculous anomaly is that English names of birds follow Australian spelling, while the text uses North American spelling! For example, the “Blue-grey Robin” is “Uniformly blue-gray.” Surely, in the few cases where this is a problem, the spelling could have been made uniform without injury to regional sensibilities.

The chapter on Papuan natural history is an excellent short summary; however, I feel that Lord Walter Rothschild’s name and that of his curator, Ernst Hartert, should have been mentioned in the historical notes. It was Rothschild who hired and directed many of the collectors who are mentioned, and the taxonomic studies of the collections by Hartert and Rothschild, and of other early collections by Stresemann, formed a solid foundation for subsequent work.

On pp. 25–26 there is some confusion as to the boundary between the Northwest region and the Sepik-Ramu region, as the Torricelli Mountains are included in both. More properly, the Torricellis belong with the Northwest region. The In the Field section (pp. 37–42) is excellent and required reading for anyone planning to visit New Guinea for the first time.

Figure 21 is a map of New Guinea. In the paperback edition, it fills one page, follows the Gazetteer and is hard to find and practically unreadable without a magnifying glass. The hard-cover edition uses this same map as endpapers, and its larger size makes it much more usable. The information on where to acquire maps is useful. The Gazetteer is of more limited usefulness. Whereas, the Gazetteer in Mayr’s List primarily identified collecting localities, this one concentrates on birdwatching localities and recent Indonesian names, appropriate for a field guide. However, the cross-referencing of place names is incomplete and may cause the novice difficulties when referring to older literature. For example, Hollandia is the same place as Sukarnapura-Jayapura (=Djajapura), but it is not cross-referenced to the other three names. Sukarnapura is cross-referenced to Jayapura, but not vice-versa and Djajapura is only cross-referenced to Jayapura. If one looked up Jayapura, the present name, one would
be unaware of any of the others. The Snow Mountains are omitted although they are on the map on p. 243, and the Nassau and Oranje Ranges (the western and eastern parts of the Snows, respectively) are listed. In general, old names are cross-referenced to newer ones, but not vice-versa. This is particularly true where there is a newer Indonesian name. Most mountains are alphabetized under “Mt.,” but there are inconsistencies. Mt. Carstenz, the highest mountain in New Guinea, is listed under Carstenz Toppen, its Dutch name, and two mountains are listed under the Indonesia “Puncak.”

The bibliography is very spotty. A quick check revealed that reports on four Gilliard expeditions were omitted (three of these were post-RG) as were most papers by the Dutch on West Irian birds. None of Junge’s papers are listed, and only one by Mees, many of whose papers are post-RG. Filewood and Peckover (1978, “Scientific names used in Birds of New Guinea and Tropical Australia, Peckover & Filewood and Handbook of New Guinea Birds, Rand & Gilliard”) is omitted.

It is an enormous task to produce a first field guide, devising descriptions that both identify the species and give characters for differentiating it in the field from other species, not necessarily closely related. That the authors have succeeded so well is a measure of their own familiarity with the avifauna. And the plates almost always agree in detail with the descriptions. I would have found it handier to have the range given immediately following the description. Most of the errors are minor and will not interfere with identification.

The descriptions of the Green and the White pygmy-geese (Nettapus pulchellus and N. coromandelianus) could cause confusion. Presumably the lack of a “white leading edge to wing” is in contrast to the White-headed Shelduck (Tadorna radjah) in which the shoulder patch is white. The Green Pygmy-Goose male and female have a broad white terminal band on the secondaries (most of each secondary is white) and no white in the primaries. The White Pygmy-Goose has a narrow white terminal band on the secondaries. The large white patch in the primaries may be present or lacking in both male and female, adult and immature. The male and female of the Snow Mountain Quail (Anurophasis monorthonyx) are said to be similar, but Pl. 1 correctly shows the female to be more heavily marked.

The user of the guide should be aware that subspecies differences do occur that may not be noted; it would be impossible to do so in a field guide. For example, plumage of male Brown Quail (Coturnix australis) varies geographically and altitudinally, with the female either similar to or more (not less) heavily marked than the male. Pl. 1 correctly shows these differences, although plumbeus males may also be grayish.

On Pl. 21, 14a, the male and female symbols are reversed for the Painted Tiger Parrot (Psittacula picta). The descriptions of young Chestnut-breasted and Fan-tailed cuckoos (Cacomantis castaneiventris and C. flabelliformis) are correct, but under “Similar species” the young Fan-tail Cuckoo should be described as plain above. It usually does have a pale to yellowish eyering, but so may the immature Chestnut-breasted Cuckoo. All of the Bronze-cuckoos of the genus Chrysococcyx have iridescent bronze-green to green upperparts. This is mentioned only for C. lucidus and C. meyeri.

The confusion surrounding scrub-wrens of the species Sericornis beccarii and S. virgatus has been increased. While Diamond accepts the RG division of the populations into three species (including S. nouhuysi), his allocation of subspecies in the three is very different and also differs from the plate; i.e., S. beccarii weylandi and S. b. wonidiwoi of Pl. 36 are included by Diamond in S. virgatus. S. b. randi is the only bird illustrated that Diamond includes in S. beccarii. I have examined the Lake Kutubu specimen and it is S. b. randi. Reference should be made to Diamond (1969, AMNH Novitates no. 2362) for a complete description of his subspecies allocations. Differing interpretations may be found in RG and in Gilliard and LeCroy (1970, AMNH Novitates no. 2420). Field studies of these populations are much needed.
The Biak race of Dusky Myzomela (Myzomela obscura) is washed overall with a brownish red and no throat streak, red or dusky, is visible. Conopophila albogularis is also known from the Sepik (RG).

In the Species-checklist, Bechler and Finch have published a list of New Guinea birds used as the basis of the field guide. They have essentially chosen to follow the Peters’ “Checklist of Birds of the World” sequence with “crows last,” and have discussed how their list differs from those of Mayr, Rand, and Gilliard, and Peckover and Filewood. While no one working on the taxonomy of New Guinea birds will agree with all of their choices, a list was necessary in order to produce the field guide. Decisions and choices were unavoidable, and we should thank the authors for bringing together in one place the information on which their choices were based. It is a very useful summary for anyone working with birds in the Australasian region.

The following brief comments may perhaps be helpful. The first record of the Sanderling (Calidris alba) was in Hoogerwerf (1964, Bull. Brit. Ornithol. Club 84:144). The following were already listed in RG, and the record noted in the Species-checklist is the first for the eastern half of New Guinea only: Silver Gull (Larus novaehollandiae) and Gray’s Grasshopper-Warbler (Locustella fasciolata). Hydroprogne caspia has been known as H. tschegreva strema; Sterna bengalensis as Thalasseus bengalensis; Ectopus roratus as Lorius as well as Larus; Ptilorrhoa castanotus as Eupetes castanotus; Acrocephalus stentoreus as A. arundinaceus sumbae; A. arundinaceus as A. a. orientalis; Lichenostomus versicolor as Meliphaga virescens; L. chrysogenys as Oreornis chrysogenys. The family Acanthisiidae includes scrubwrens, thornbills, Australian warblers and allies, but Phylloscopus trivirgatus is included in the Sylviidae with the grassbirds and reed-warblers! Eugerygone is in the Eopsaltridae; Peltops is in the Cracticidae; the Timaliidae has disappeared. Meliphaga montana and albonotata populations have undergone yet another rearrangement as have Sericornis beccarii, S. virgatus, S. nouhuysi (see above). The specimen of Grallina cyanoleuca that I mentioned as having been collected by the Dentons in 1883 is in the Carnegie Museum, Pittsburgh, not AMNH. This record was called to my attention by K. C. Parkes some years ago.

It is in the nature of a book review to concentrate on errors and inconsistencies. I hope that the reader will realize that there are relatively few in this case and that the authors may find my comments helpful when a revision is produced. The field guide is necessary for anyone visiting New Guinea or studying the birds and while the species-checklist does not replace either of the two earlier volumes, it is a handy reference and a starting point for more detailed taxonomic studies, given the current state of flux of the taxonomy of birds in the region.—MARY LE CROY.
Dr. Kilham’s scientific background as a virologist shows through in the care with which he uses proper scientific names and terminology. He may be a bit too specific when he tells us exact dates on which he observed certain things. I doubt that professional ornithologists will find more in this book than some light reading (I finished the book in slightly over an hour). Beginning biologists and interested amateurs will find that this book offers rich descriptions of avian behavior and (often) insightful observations of the basis for the birds’ activities.

However, some of Dr. Kilham’s observations are not the sort of thing I would like young ornithologists to take too seriously. His hypothesis that Barred Owls (*Strix varia*) are not powerful enough to kill gray squirrels (*Sciurus carolinensis*) and that they sometimes scare the squirrels to death by caterwauling seems a bit far-fetched. His statement, “Although I used to find professional journals informative, I find almost nothing that I can use in the chart- and table-studded articles on behavior in the leading journals of today,” might lead one to think that scientific ornithology does not deserve the same quantitative approach that sciences such as virology enjoy. Another comment, “Reading is a poor way to start yourself on a scientific project, if you want to be original and a discoverer,” strikes me as an outrageous view. Finally, his statement, “When I think of all the tortured, complicated, and expensive experiments on animal intelligence that have been performed in laboratories, mostly with dubious result, I reflect on how much easier, simpler, and seemingly more meaningful were Davis’ experiments with his free-living birds.” (The Davis work cited consisted of teaching siskins to come into the house and get into the bed clothes.) This sort of careless comparison perpetuates a myth and implies that all of the work of the likes of Lorenz, Tinbergen, Skinner, Harlow, and dozens of other students counts for little and seems to be based on lack of knowledge of the field of comparative animal psychology. Such comments detract from an otherwise thoroughly enjoyable account of the natural behavior of birds.—C. R. Blem.

**Studies of Mascarene Island Birds.** Edited by A. W. Diamond. Cambridge Univ. Press, Cambridge, England, 1987:6 unnumbered introductory pages (including foreword) + 458 pp., 64 numbered text figs., 38 maps, 59 numbered text tables, and 3 appendices (including 3 tables). 53.25 pounds-sterling (approximately $100.00 U.S.).—Like all vertebrate faunas on islands devoid of native mammalian land predators, the avifauna of the Mascarene Islands was decimated after the arrival of humans and the animals they transported. To document the biology of what remains of this distinctive bird assemblage, the British Ornithologists’ Union (BOU) announced plans in 1972 for an expedition to the Mascarenes, three islands separated by several hundred km in the Indian Ocean east of Madagascar. This long-delayed volume reports the results of the 1974–1975 BOU expedition and chronicles the history, biology, and conservation of the Mascarene avifauna. Based on a large body of information from historical accounts, the BOU-sponsored field studies, reports of previous workers, and interviews with island residents, it provides a detailed summary of what we know and can reasonably infer about the Recent history of the Mascarene vertebrate fauna. In addition, it documents the population status, ecology, nesting, vocalizations, and measurements of the surviving endemic birds. Thus, the volume offers not only a useful guide for those charged with conserving what remains of the birds of Mauritius, Réunion, and Rodrigues, but a source of basic information for researchers interested in the ecology and evolution of island forms as well.

In the first chapter, Anthony Cheke recounts the history of the extinct, surviving, and introduced vertebrates and infers the time course of destruction and alteration of the islands'
habitats subsequent to the arrival of humans. Because so much information is discussed, readers will be grateful for the figures depicting the chronological history of Mascarene extinctions and the appendix listing the mammals, birds, and reptiles indigenous to the islands. In the subsequent chapter, Graham Cowles analyzes subfossil remains and presents the only unequivocal evidence for the existence of several endemics about which historical accounts are ambiguous.

The remainder of the volume concerns the surviving avifauna. Jennifer Horne discusses the vocalizations of the endemic landbirds and provides sonograms for each. She describes her methods fully and compares the vocalizations of the Mascarene forms with those of related, non-Mascarene taxa. The next chapters consist of detailed accounts of the population biology of the extant endemics of Mauritius and Rodrigues and of the complete indigenous avifauna of Réunion. Most were written by Cheke, but Carl Jones contributed prodigious sections on the Mauritius Kestrel (Falco punctatus, 39 pp.), the Pink Pigeon (Nesoenas [Columba] mayeri, 29 pp.), and the Echo Parakeet (Psittacula echo, 29 pp.), while Christian Jouanin provided brief accounts of the breeding of four species of shearwaters and petrels on Réunion. The accounts vary in quality, but each provides useful, basic data.

Characteristic of the text is the attention it gives to the claims of previous workers. For example, the date of extinction of the Mauritius Dodo (Raphus cucullatus) has usually been placed between 1681 and 1693. However, Cheke’s review of the original accounts indicates that the last Dodo on Mauritius was seen in the early 1660s, and that subsequent references to “Dodos” in fact pertain to the flightless Red Rail (Aphanapteryx bonasia), which died out several decades later. Captive Dodos probably expired in the 1660s as well. Cheke also identifies serious problems with the idea that the endemic tree Sideroxylon graminiflorum has become rare because its seeds require passage through a Dodo’s digestive tract to germinate.

The book ends with annotated tables of measurements and weights for the extant endemic birds and a list of the almost 1000 references cited in the text. I was glad to see a table summarizing the locations of museum specimens of Mascarene birds, including, among other items, the locations of two alcoholic specimens of the extinct Réunion “starling” (Fregilupus varius). However, for the Dodo, the same table inexplicably omits the foot in the British Museum and the head in Copenhagen and fails to spell out the abbreviation for the University Museum at Oxford, which also has a head and a foot. I found the appendix rather scant, considering the wealth of information contained in the text. Nonetheless, there are few such problems overall and almost no typographical errors. It is unfortunate that the steep price of the volume will discourage all but institutional buyers from purchasing it.

Reading between the lines of the foreword by Guy Mountford and the introduction by A. Diamond and Cheke, one gathers that this volume’s production was as threatened by limited funds as are the remaining birds by the factors that have obliterated over 60% of the archipelago’s endemic avifauna. Biologists and conservationists alike will be grateful both for the survival of the BOU effort and for the prospects it raises for the conservation of the 18 endemic species of birds remaining on the Mascarene Islands.—Anthony H. Bledsoe.

as other Ehrlich books; it is authoritative, exhaustive, and a real contribution to the education of bird students everywhere.

This is an unusual book: the left facing pages are devoted to summarizing behavioral, nesting, diet, and conservation information regarding each of the species of North American birds. (Most rarities are not included.) Illustrations are provided that tell one at a glance what type of nest is built, the normal clutch size, the role of each sex in care of the nest and young, composition of the nest, food items, habitat, and more. Recent references that discuss the species in question are cited.

On right facing pages essays are provided that discuss just about anything imaginable. Anatomy, physiology, advanced taxonomy, and the like are given thin or no coverage. However, most of the “hot” topics in ornithology are given authoritative, often exciting descriptions. I was impressed with the detail and quality of the information provided. In some instances the essay was essentially the same as papers I had heard by authorities at recent scientific meetings. Topics as diverse as salt glands, feathers, birds and the law, polyandry, fossil birds, urban birds, vocal development, and island biogeography are discussed. These are only a few of the essays; the total must be over 200. The authors also saw fit to give biographies of famous ornithologists, living and dead. The result is that an interested reader, professional or amateur, can quickly get an overview of the subject or person in the essay. The editorial treatment given the book was also of high quality. I found virtually no typographical errors. The typesetting and quality of illustrative materials are all first rate and the illustrations generally are relevant.

I thoroughly recommend this book to bird-watchers or listers who are considering learning more about ornithology. The presentations are given in such a clear and engaging fashion that I believe many will find themselves reading about subjects far from their previous interests. The net result will be that they will find themselves caught up in the developments of scientific ornithology and interested in how birds functions at all levels. The fact that the book also provides the best summary of the life history statistics of North American species is simply a big bonus. The relatively low price for a really substantial paperback book is frosting on the cake. —C. R. BLEM.

EXTINCT BIRDS. By Errol Fuller. Facts on File Publications, New York, 1988:256 pp., 59 color plates, 81 black-and-white figs. $35.—With the rate of extinction (or potential extinction) of birds increasing sharply in recent years some ornithologists have wondered if there will be anything left to study by the time their scientific careers have ended. Over the years there have been several attempts to catalog the depressing story of the extinctions. In 1907 Walter Rothschild published a sumptuous, copiously illustrated work entitled “Extinct Birds.” This long-out-of-print, and now long-outdated, book was hardly intended to be a popular account. Since that time Greenway’s “Extinct and Vanishing Birds of the World” (1958) and King’s “Endangered Birds of the World: the ICBP Bird Red Data Book” (1981) have outlined in a technical way the details of the disappearance of species. The present author has attempted to produce a popular, yet factual, successor to the Rothschild work. He has been quite successful in the attempt and has come up with a “coffee table” book that is more than that.

The book discusses in detail and gives a colored illustration of 74 species that have become extinct since 1600. The selection of that starting date eliminates the necessity of dealing with countless fossil and subfossil forms whose status is uncertain, but does lead to the inclusion of Aepyornis and three species of moa, as well as three didine species from the Mascarene Islands. The selection of this starting date is certainly defensible, but it does
allow the author to ignore the results of Olson and Steadman who have shown that the arrival of primitive man on many of the islands of the world resulted in wholesale extinctions of the avifauna.

The selection of species follows the list of Birds Known or Thought to Have Become Extinct Since 1600 given by King (op. cit.), except that the various extinct subspecies are not included if other races still exist. The extinct races are, however, listed in tables and occasionally mentioned in the family accounts. In a few cases Fuller is more optimistic than King in considering the possibility that a night-bird or a bird of the deep forest which has not been reported for 50 years or is known only from one specimen might still be extant.

The text is arranged with the species grouped in 17 orders. For each order there is an introductory account that gives in tabular form a listing of the rare, endangered, or little known forms of that order. Many of these are then discussed briefly in the introductory text. There follows a detailed account of each extinct species together with a colored illustration. A final chapter discusses several Hypothetical Species and Mystery Birds. This list includes Cooper's Sandpiper (Calidris ? cooperi).

The Railidae, with 11 species, lead the list of extinctions, with the Psittacidae following with 9 and the Columbidae with 6. There is also a list of 13 hypothetical extinct parrots. Twenty-four passerines are listed including 6 drepanidids. Fifty-three passerine subspecies are considered to be extinct and 18 passerines are listed as being known only from museum specimens.

The text of the species account is a mixture of interesting anecdote and the factual details about the species. There are occasional asides about the personalities of the people involved. Of interest is the account of the disputes between Lord Rothschild and Sir Walter Buller, particularly about the naming of the celebrated Stephen Island Wren (Xenicus lyalli).

The colored plates are selected from many publications of the past and are by 14 artists including Audubon, Lodge, Fuertes, and Gould. Twenty three of the plates are by J. G. Keulemans, many taken from the Rothschild book. Introducing the modern audience to the talents of this excellent, but almost forgotten, bird-artist is one of the major contributions of this book. The author has contributed his own paintings for 6 species.

While the classic cases, such as the Passenger Pigeon (Ectopistes migratorius) are covered in detail, the author has not really consulted the recent literature, and thus has not kept up with the exponential increase in extinctions. The bibliography lists only three papers published after the Red Data Book in 1981. In particular the author seems to be unaware of some of the American literature. How can anyone write an account of the Carolina Parakeet (Conuropsis carolinensis) without referring to the numerous publications of Daniel McKinley? Bachman’s Warbler (Vermivora bachmanii), Kirtland’s Warbler (Dendroica kirtlandii) and the Hawaiian Crow (Corvus hawaiensis) are listed as being rare or endangered; they are not discussed further. While the Culebra race of the Puerto Rican Parrot (Amazona vittata) is listed as extinct no mention is made of the dire straits of the nominate race. Seventeen corvids are listed as endangered but no additional comment is given for any of them, although some of these are close to the brink, e.g., the Guam (Marianas) Crow (C. kubaryi).

Despite these shortcomings the book is recommended for those interested in this gloomy subject. — GEORGE A. HALL.

900 ornithological publications, each containing at least 100 references. Entries are arranged alphabetically by first author and include "key word" notations as to the general subject of the work. There is also a list of personal bibliographies that have been published. There are three indices: Co-authors, Biosystematic, and Subject. The publication should be available in most research libraries.—GEORGE A. HALL.

BRIEFLY NOTED

OILED BIRDS: HOW TO SEARCH FOR AND CAPTURE OILED BIRDS AT OREGON INTERTIDAL AREAS. By Range D. Bayer. Studies in Oregon Ornithology No. 5, Gahmken Press, P.O. Box 1467, Newport, Oregon 97365, 1988:29 pp. 10 black-and-white photos. $3.50 (paperback).

The following books are unreviewed American reprints of Collins' Field Guides published in England some years ago. They are distributed by Viking Penguin, Inc., 40 West 23rd St., New York, New York 10010.


The following publications are available from the Publications Unit, U.S. Fish and Wildlife Service, Room 148 Matomic Building, Washington, D.C. 20240.


RESPONSE TO SIEGEL-CAUSEY (Wilson Bull. 100:708, 1988). “A Bibliography of Ornithological Translations, Current Ornithology, Vol. 4” performs a valuable service. My review of it (Wilson Bull. 100:149-150, 1988) was in no way designed to imply otherwise. However, its utility is reduced by indexing errors, some caused perhaps by mistakes in translation of common names or by back-formation of binomials. Yet it would seem difficult to explain most indexing errors in those ways. For example, 20 citations fall under “Recurvirostridae.” Three include the names “stilt” or “avocet.” The others refer to “woodcock” (11, 4 accompanied by “Scolopax rusticola”), “snipe” (3, one joined by “Gallinago”), “painted snipe” (one), “dowitcher” (one, joined by “Limnodromas griseus”), and “whimbrel” (one). Of these, only the latter two are listed elsewhere under an appropriate taxonomic heading; nowhere else are the others indexed taxonomically.

If the subject/taxonomic indices instead of the citations were meant to reflect the actual nature of the articles, then one would presume a fair bit of inaccuracy in translation. Perhaps a novel taxonomic classification was used instead. Perhaps there were actual mistakes in allocating citations to taxonomic headings. Regardless, the utility of the Bibliography is somewhat reduced, because most users will not find citations where one might expect them. Without scanning the full list of citations, users may miss pertinent papers. It was merely my intent to point out this problem so that readers can use the Bibliography to full benefit.—ANTHONY H. BLEDSOE.

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

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Major Papers, the address of each author should be given as a footnote at the bottom of the first numbered page. Three copies should be submitted. Xerographic copies are acceptable if they are clearly readable and on good quality paper. Copies on heavy, slick paper, as used in some copy machines, are not acceptable.

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Authors of accepted papers are urged to submit voucher photographs of their work to Visual Resources for Ornithology (VIREO) at the Academy of Natural Sciences of Philadelphia. Accession numbers from VIREO will then be published within appropriate sections of the paper to facilitate access to the photographs in subsequent years.

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The editor welcomes queries concerning style and format during your preparation of mss for submission to the Bulletin.—CHARLES R. BLEM, Editor.

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Illustration of the holotype of *Dysmorodrepanis munroi*, painted directly from the study skin before it was remade. Watercolor painting on illustration board, by Nancy Payzant, 1986.
DYSMORODREPANIS MUNROI
(FRINGILLIDAE: DREPANIDINI), A VALID GENUS AND SPECIES OF HAWAIIAN FINCH

HELEN F. JAMES, RICHARD L. ZUSI, AND STORRS L. OLSON

ABSTRACT.—A Hawaiian Finch that became extinct on the island of Lanai sometime after 1913 has been overlooked by ornithologists. Only one skin specimen of this bird was ever procured, and although it was described as the holotype of Dysmorodrepanis munroi Perkins, it soon fell into obscurity and was written off as a deformed example of Psittirostra psittacea. Our re-preparation and examination of the holotype indicates it is a valid genus and species. Dysmorodrepanis is probably most closely related to Psittirostra psittacea, and is distinguished by its unusual bill and associated modifications of the jaw apparatus, as well as by the plumage and external dimensions of the holotype. We speculate that the diastema between the bird’s tomia may have allowed the bill tips to act as pincers. Received 8 Oct. 1987, accepted 7 July 1988.

Considerably after R. C. L. Perkins completed his major contributions to the natural history of the Hawaiian Islands, he introduced a new genus and species of bird, Dysmorodrepanis munroi (Perkins 1919), based on a single specimen collected by G. C. Munro on the island of Lanai in 1913. This is the only Hawaiian bird that Perkins formally named as new, despite his having made one of the most scholarly and original contributions to Hawaiian ornithology (Perkins 1903). Because the period following the description of Dysmorodrepanis was a quiescent one in Hawaiian ornithology, Perkins’ new species was scarcely mentioned until Greenway (1939) examined the unique holotype and suggested that it was merely

an "aberrant young female" of the Ou, *Psittirostra psittacea*. Amadon (1950) concurred with Greenway, listing the species in the synonymy of *P. psittacea*. Until now there has been no further critical evaluation of this species, which had since been forgotten and ignored.

We initially were skeptical about the assignment of *Dysmorodrepanis munroi* to *P. psittacea* because of the external differences in bill form, plumage, and the smaller tarsus. We consequently had the holotype re-prepared following the procedure described by Olson et al. (1987), in which the skull is removed and replaced in the skin with a cast. This allowed us to examine the cranial osteology and, to a limited extent, the myology of the specimen. We found no osteological evidence of a pathological condition that might have caused deformation of the bill in *Dysmorodrepanis*: rather, the cranium and mandible show morphological modifications concordant with the unusual bill form. We conclude that *Dysmorodrepanis munroi* is a valid genus and species of uniquely specialized dreapanidine. Pending a more detailed character analysis of the Drepanidini, we consider *Dysmorodrepanis* to be a sister taxon of *P. psittacea*, and we tentatively cite the similar shape of the maxillary rostrum as a synapomorphous character linking these species. (Following Baumel et al. 1979), we refer to the external "mandibles" of the bill as the maxillary and mandibular rostra, and to the bony elements underlying these structures as the maxilla and mandible.)

**Genus Dysmorodrepanis** Perkins 1919:250

**Type Species.** — Dysmorodrepanis munroi Perkins 1919, by monotypy.

**Diagnosis.** — A medium-sized dreapanidine finch in which the decurved maxillary rostrum overhangs the mandibular rostrum. Compared to other drepanidines with this condition, the maxillary rostrum is sturdy and finch-like, similar to *Pseudonestor xanthophrys* and *P. psittacea* (frontispiece, Fig. 1); it is not weak and attenuated like that of *Hemignathus* spp. (sensu Amadon 1950). The mandibular rostrum is strongly recurved, so that only its tip enters the ventral trough of the maxillary rostrum, leaving a conspicuous diastema between the toma when the bill is closed (Fig. 2). The maxillary and mandibular rostra have deeply excavated internal surfaces. The tomal crest of both jaws from about the rostral third of the diastema to their tips are sharp and ridged as in *P. psittacea*; in the caudal two-thirds they curl inward to form broad, blunt surfaces that lie roughly parallel to each other at opposite sides of the diastema (Fig. 2). The articular cotylæ and medial process of the mandible are rotated strongly caudad compared to their orientation in most birds. The ramus (pars intermedia) is shorter than in *P. psittacea* (Figs. 1 and 3). The quadrate-squamosal articulation is located more rostrally on the skull, and in the resting position the quadrate is rotated farther rostrad compared to *P. psittacea* or *Pseudonestor xanthophrys* (Figs. 1 and 4). The medial condyle of the quadrate is more elongate than in *P. psittacea*, but much less elongate than in *Pseudonestor* (Fig. 4). The palatines are similar to those in *P. psittacea* but shorter (Fig. 4). Perkins (1919) described the tongue as nontubular.
**Fig. 1.** Lateral view of the crania and mandibles of *Dysmorodrepanis munroi* (above) and *Psittirostra psittacea* (below).

**Dysmorodrepanis munroi** Perkins

*Dysmorodrepanis munroi* Perkins 1919:251.—Richmond 1927:12; Mathews 1930:814; Greenway 1939:479; Bryan and Greenway 1944:140; Greenway 1958:9; Munro 1944:122; Munro 1960:191.

*Desmodrepanis munroii.*—Delacour 1928:22 (lapsus).


*Desmodrepanis munroii.*—Carlquist 1970:196 (lapsus, in synonymy).
Fig. 2. The bill of *Dysmorodrepanis*. A) Dorsal aspect of the mandibular rostrum, B) ventral aspect of the maxillary rostrum, and C) photograph showing the relation of the rostra in closed position.
HOLOTYPE.—Bernice P. Bishop Museum number BBM-4792, an unsexed skin of an adult bird collected and prepared by G. C. Munro on 22 February 1913. The fresh specimen measured six inches (152 mm) in length. J. P. Angle and F. V. Grady removed the skull and replaced it in the skin with an epoxy resin cast, December 1986, at the National Museum of Natural History, Smithsonian Institution. To preserve the unique morphology of the bill, the rhamphotheca were not removed from the two jaws. Archival-quality photographs and X-radiographs of the skin, taken before the skull was removed, are preserved in the photographic archives of the Bernice P. Bishop Museum, Honolulu, and at the Smithsonian Institution, Washington.

TYPE LOCALITY.—Kaiholena Valley, Island of Lanai, ca 20.83°N, 156.90°W, ca 2000 feet elevation.

DIAGNOSIS.—A drab Hawaiian finch with greenish olive plumage above and whitish yellow plumage below, with a yellowish superciliary stripe and whitish tips and inner vanes on the secondaries (frontispiece). The bird is the size of small females of *P. psittacea*, but the tarsometatarsus is proportionately short (Fig. 5). The non-overlapping dorsal and ventral nasal opercula resemble those of *P. psittacea* (Fig. 2).
Fig. 4. Ventral view of the crania of Dysmorodrepanis munroi (top), Psittirostra psittacea (middle), and Pseudonestor xanthophrys (bottom).

DESCRIPTION

Size and body proportions.—The lengths of the wing chord and tail of Dysmorodrepanis fall 1.3 standard deviations below the mean for a series of females of P. psittacea (Table 1), so that if wing chord is a reliable gauge of body size, the holotype of Dysmorodrepanis is similar in size to
small females of *P. psittacea* and larger than either sex of *Pseudonestor*. Among these species, the bill is absolutely and proportionately smallest in *Dysmorodrepanis*, whose bill dimensions are three to five standard deviations below the means for females of *P. psittacea*. *Dysmorodrepanis* differs further from *P. psittacea* and *Pseudonestor* in that the tarsus is shorter relative to the wing chord (Fig. 5).

**Plumage.**—The plumage of *Dysmorodrepanis* has been adequately described by Perkins (1919) and is illustrated in the frontispiece. The specimen is rather nondescript, greenish olive above, and whitish yellow below, with a faintly indicated yellowish superciliary stripe. The most striking feature is the conspicuous wing patches formed by the broad, whitish tips and inner vanes of the secondaries. Greenway (1939:479) maintained that this was due to the specimen being partially albinistic, and he asserted that “whitish feathers are scattered indiscriminately over nape, breast and belly.” In fact, there are no whitish feathers in the nape, although the feathers here have light-colored shaft streaks. The appearance of whitish feathers scattered over the ventral surface is caused by exposure of the whitish bases of the ventral feathers, but close examination shows all of these to be tipped with yellowish. The whitish patches in the secondaries

---

Fig. 5. Graph showing the short tarsus in relation to wing chord of *Dysmorodrepanis*, as compared to *Psittirostra psittacea* and *Pseudonestor xanthophrys*. 
Table 1
SKIN MEASUREMENTS (mm) OF DYSMORODREPANIS AND RELATED TAXA

<table>
<thead>
<tr>
<th></th>
<th>Culmen length</th>
<th>Culmen width</th>
<th>Wing chord</th>
<th>Tarsus</th>
<th>Tail</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dysmorodrepanis</td>
<td>13.0</td>
<td>5.0</td>
<td>86.3</td>
<td>21.4</td>
<td>52.0</td>
</tr>
<tr>
<td>munroi</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Psittirostra</td>
<td>15.5 ± 0.8a</td>
<td>6.6 ± 0.3</td>
<td>90.2 ± 3.0</td>
<td>23.9 ± 0.6</td>
<td>55.7 ± 3.1</td>
</tr>
<tr>
<td>psittacea,</td>
<td>(14.0–16.9)b</td>
<td>(5.7–7.0)</td>
<td>(84.2–96.2)</td>
<td>(22.8–25.7)</td>
<td>(49.4–62.3)</td>
</tr>
<tr>
<td>females</td>
<td>26c</td>
<td>18</td>
<td>26</td>
<td>26</td>
<td>28</td>
</tr>
<tr>
<td>Psittirostra</td>
<td>15.9 ± 0.7</td>
<td>6.6 ± 0.3</td>
<td>94.6 ± 2.1</td>
<td>24.2 ± 0.7</td>
<td>58.3 ± 1.7</td>
</tr>
<tr>
<td>psittacea,</td>
<td>(14.3–17.0)</td>
<td>(6.0–7.1)</td>
<td>(90.1–99.3)</td>
<td>(22.8–25.4)</td>
<td>(54.6–61.0)</td>
</tr>
<tr>
<td>males</td>
<td>35</td>
<td>28</td>
<td>37</td>
<td>39</td>
<td>35</td>
</tr>
<tr>
<td>Pseudonestor</td>
<td>16.4, 16.7</td>
<td>66.3, 66.4</td>
<td>21.1, 21.3</td>
<td>39.4, 39.9</td>
<td></td>
</tr>
<tr>
<td>xanthophrys,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudonestor</td>
<td>21.1</td>
<td>72.8</td>
<td>23.0</td>
<td>44.4</td>
<td></td>
</tr>
<tr>
<td>xanthophrys,</td>
<td>(18.9–23.0)</td>
<td>(71.4–75.1)</td>
<td>(22.4–23.8)</td>
<td>(43.2–45.9)</td>
<td></td>
</tr>
<tr>
<td>males</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

*a* Mean ± one standard deviation.

*b* Range.

*c* Sample size.

form intricate patterns with the darker central portions of the vanes that vary from one feather to the next but are symmetrical from side to side. These appear to be perfectly normal, and neither the secondaries nor any other aspect of the plumage appears to be affected by albinism.

After examining the holotype, Amadon (1950:172) speculated that: "Perhaps because of the abnormal bill and consequent inability to feed properly, its plumage is abraded, with evidence of retarded molt." This is also untrue. Although the drab coloration and somewhat disarrayed feathers give the impression of a rather worn, faded specimen, close inspection shows that the feathers are not abraded, the remiges in particular being quite fresh. We see no evidence of abnormality of molt or coloration in the specimen of *Dysmorodrepanis munroi*. Therefore, its principal differences from females of *P. psittacea*—white patches in secondaries, superciliary stripe, lighter and more yellowish underparts—must be regarded as characteristic of the species. The completely ossified skull of the holotype shows it not to be a juvenile; it may be an adult female, as suggested by the dull plumage. If so, the male in adult plumage may have been more brightly colored, as in *P. psittacea*. Yellow underparts and a distinct superciliary stripe occur in *Pseudonestor xanthophrys*, but *Pseudonestor* has no white in the wings, and its adult plumage is brighter in both sexes than in *Dysmorodrepanis*. 
External bill morphology.—Dysmorodrepanis resembles *P. psittacea* and *Pseudonestor* in its long, overhanging maxillary rostrum in combination with a sturdy, almost finch-like bill (Fig. 3), but it is set apart from these species by the diastema between its tomia. The maxillary rostrum of *Dysmorodrepanis* is more hooked and compressed laterally, with a more ridged culmen, than in *P. psittacea*. In this respect the bill shape is intermediate between *P. psittacea* and *Pseudonestor*. The external naris in *Dysmorodrepanis* is a slit between the dorsal and ventral nasal opercula (Fig. 2). The dorsal nasal operculum covers slightly more than half of the nasal opening and has a convex ventral margin. The opercula resemble *P. psittacea* but differ from *Pseudonestor*, in which the ventral operculum is lacking and the dorsal one has a concave margin. The upturned portion of the mandibular rostrum consists of rhamphotheca: it is not supported by bone. This is also true of the tip of the maxillary rostrum in both *Dysmorodrepanis* and *P. psittacea* (Fig. 3). The rhamphotheca of *Dysmorodrepanis*, especially of the maxillary rostrum, is darker brown than most individuals of *P. psittacea*, but lighter than the maxillary rostrum in *Pseudonestor*.

Within the trough on the ventrocaudomedial surface of the maxillary rostrum, there is a plate of thickened rhamphotheca. The plate is bounded laterally by distinct ridges that turn inward at about two-thirds of the distance to the tip of the maxillary rostrum and which meet each other at the midline (Fig. 2). Similar ridges are present in *P. psittacea*.

**Tongue.**—Munro saved the dried tongue of *Dysmorodrepanis*, but it was subsequently lost. Perkins examined the tongue when it was already in a poor state of preservation, and commented that it agreed in general with Gadow's description of the tongue in *Loxioides [bailleui]* (Gadow 1891:223), adding that the tongue of *Dysmorodrepanis* "is not acute at the tip and is apparently emarginate there, with the edges microscopically serrulate" (Perkins 1919:251). From this we gather that the tongue was of the primitive drepanidine form which is nontubular, fleshy above, corneous below and caudolaterally, and has a rounded tip edged with small papillae. This tongue morphology also occurs in *P. psittacea* and other finch-like drepanidines and in some cardueline finches (Raikow 1977).

**Cranial osteology.**—The fully ossified cranial vault (double-plated and trabeculated) indicates that the holotype of *Dysmorodrepanis* is a mature bird. It has the thick interorbital septum and associated features that characterize the Carduelinæ, including the Drepanidini (Zusi 1978). In *Dysmorodrepanis*, these features are: interorbital septum complete (not fenestrated), double-walled and supported by internal bony trabeculae throughout; ventral border of the cranial fenestra straight; the floor of the anterior cranial cavity (between the cranial fenestrae) broad and flat; and
TABLE 2
CRANIAL DIMENSIONS OF DYSMORODREPAonis AND PSITTIROSTRA PSITIACEA (MM)

<table>
<thead>
<tr>
<th></th>
<th>Dysmorodrepanis munroi</th>
<th>Psittirostra psittacea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cranium length without maxilla</td>
<td>18.8</td>
<td>20.9, 21.7</td>
</tr>
<tr>
<td>Orbit length</td>
<td>9.9 (0.53)*</td>
<td>10.1 (0.48), 10.4 (0.49)</td>
</tr>
<tr>
<td>Ventral length of pterygoid</td>
<td>5.4 (0.29)</td>
<td>6.6 (0.31), 6.7 (0.31)</td>
</tr>
<tr>
<td>Length of jugal bar</td>
<td>13.3 (0.70)</td>
<td>16.1 (0.77), 16.1 (0.74)</td>
</tr>
<tr>
<td>Palatine length (transpalatine process to prepalatine bar)</td>
<td>8.1 (0.43)</td>
<td>11.1 (0.53)</td>
</tr>
<tr>
<td>Nostril length</td>
<td>3.8</td>
<td>5.2</td>
</tr>
<tr>
<td>Height to length ratio of nostril</td>
<td>0.87</td>
<td>0.65</td>
</tr>
</tbody>
</table>

* Numbers in parentheses are ratios of the measurements to cranium length.

the caudal edge of the septum between the optic foramina broad. The palatine process of the premaxilla is fused to the prepalatine bar in the configuration of a lateral flange. This is an apomorphous condition that characterizes drepanidines with medium to heavy bills, but it also occurs in unrelated passerines (Bock 1960).

We compared Dysmorodrepanis to other drepanidines with similar bill shapes (Psittirostra psittacea, MVZ 122619 and USNM 111454; Pseudonestor xanthophrys, BPBM 240 and illustrations of BM S/1961.11.40 and S/1961.11.46). The skull of Dysmorodrepanis is slightly shorter than in P. psittacea, and the orbits of these species are similar in length (Table 2).

The most striking differences between Dysmorodrepanis and P. psittacea are in the mandible (Figs. 1 and 6). The articular portion of the mandible is rotated strongly ventrad in relation to the rest of the ramus, so that the surfaces of the mandibular cotylnae face caudodorsally. These surfaces face dorsad in most birds, including P. psittacea and Pseudonestor. The medial process of the mandible in Dysmorodrepanis is broader than in P. psittacea and, like the rest of the cranial articulation of the mandible, is directed more caudad compared to other drepanidines (Fig. 6).

Compared to P. psittacea, the mandibular symphysis of Dysmorodrepanis is much narrower and has the ventral surface angled strongly upward. The ramus (pars intermedia) is dramatically shorter and becomes thin and blade-like dorsally. The coronoid processes are directed more caudal than dorsad, unlike the condition in P. psittacea and other drepanidines. The mandibular fenestra of Dysmorodrepanis is smaller and more circular than in P. psittacea.

Dysmorodrepanis has a larger and more elongate medial condyle of the quadrate and a smaller posterior condyle than P. psittacea, while neither of the aforementioned species shows the extreme elongation of the medial
condyle and reduction of the orbital process seen in the quadrate of *Pseudonestor* (Fig. 4). Compared to *P. psittacea* and *Pseudonestor*, the quadrate-squamosal articulation is placed more rostrally on the skull in *Dysmorodrepanis* (Figs. 1 and 4). Moreover, when the bill is closed the quadrate is rotated farther rostrad, as reflected by the more obtuse angle between the body of the quadrate and the jugal bar (102° in *Dysmorodrepanis*, 96° in *P. psittacea*, and 78° in *Pseudonestor*). This forward position of the quadrate leaves relatively little space for the other bones of the palate, and the palatines and jugal bar are noticeably shorter in *Dysmorodrepanis* (Table 2, Fig. 4). The maxilla of *Dysmorodrepanis* is broadly similar to that of *P. psittacea* (Figs. 1 and 3), although *Dysmorodrepanis* has a shorter and more rounded nostril opening (Table 2) and, judging from the contour of the rhamphothecal covering, a much more domed ventral surface of the maxilla (Figs. 2 and 4).

**MYOLOGY**

Complete descriptions of drepanidine jaw muscles are available only for several species of "*Loxops*" (Richards and Bock 1973). To salvage myological information from the unique specimen of *Dysmorodrepanis* and to look for modifications related to its peculiar bill and lower jaw, we examined the dried muscles on the skull. These were fragmentary, the entire base of the cranium having been cut away. The condition of individual muscles, which are partially illustrated in Fig. 7, is detailed below.
Fig. 7. Jaw muscles of *Dysmorodrepanis munroi*. Above, right lateral view of skull. Muscle fibers of adductor mandibulae, depressor mandibulae, and pseudotemporalis muscles mostly or entirely removed. Aponeuroses and tendons shaded with dashed lines. Dotted
The skull caudal to the rhamphotheca was soaked in warm water to soften the muscles, which were removed after description. Terminology for the musculature and palate follows Richards and Bock (1973).

Lateral jugomandibular and postorbital ligaments were not found. (The postorbital process had been partially removed.) The medial jugomandibular ligament is strong, attaching on the ventral surface of the jugal bar just rostral to the lateral condyle of the quadrate. It wraps around the articulation to attach in a notch on the caudal edge of the articular, just lateral to the occipitomandibular ligament. A sesamoid is enclosed at a bend of the ligament caudomedial to the lateral cotyla of the mandible; the ligament and sesamoid anchor the caudodorsal and caudoventral portions of the articulation capsule.

*M. depressor mandibulae.* — The superficial portion (b [and c?], Richards and Bock 1973) had been removed except for part of the aponeurosis of insertion attaching along the caudoventral edge of the articular. A scar along the lateral surface of the tympanic wing of the exoccipital and adjacent surface of the cranium is similar to, but less well defined than that of *Psittirostra.* The deeper portion (a of Richards and Bock 1973) originates from an aponeurosis along the craniolateral rim of the tympanic wing of the exoccipital. It inserts by a sheet-like aponeurosis, attaching adjacent and deep (caudal) to that of the superficial portion on the rim of the articular. Attachment continues medially along the ventral border of the articular, superficial to the medial jugomandibular ligament and its sesamoid, to its limit on a knob of the medial process of the mandible caudal to the osteum tubae. Here, aponeuroses of origin and insertion meet and thicken into a ligament (occipitomandibular) from the ventral edge of the exoccipital.

---

line on mandible is limit of adductor mandibulae externus ventralis. Middle, left dorsolateral view of mandible. Tendons shaded with dashed lines, aponeuroses represented by parallel lines, fleshy attachments shown in black. Semidiagrammatic. Below, medial view of right quadrate and pterygoid. Abbreviations: A M E C a, b, M. adductor mandibulae externus caudalis (parts a, b); A M E R L, M. adductor mandibulae externus rostralis lateralis; A M E R M, M. adductor mandibulae externus rostralis medialis; A M E R T, M. adductor mandibulae externus rostralis temporalis; A M E V, M. adductor mandibulae externus ventralis; A M P, M. adductor mandibulae posterior; BM, M. branchiomandibularis; D M, M. depressor mandibulae; M J L, medial jugomandibular ligament; MY, M. mylohyoideus (=M. intermandibularis); P P Q, M. protractor pterygoidei et quadrati; P S P, M. pseudotemporalis profundus; P S S a, b, M. pseudotemporalis superficialis (anterior, posterior parts); PT, pterygoid; PT D L, M. pterygoideus dorsalis lateralis; PT D M a, p, M. pterygoideus dorsalis medialis (anterior, posterior parts); PT R, M. pterygoideus retractor; PT V L, M. pterygoideus ventralis lateralis; PT V M, M. pterygoideus ventralis medialis; QU, quadrate.
The depressor mandibulae is relatively large in the species studied by Richards and Bock (1973), occupying a major part of the lateral portion of the cranium and inserting, in part, on a long retroarticular process. To judge from muscle scars, the muscle in *Dysmorodrepanis* had a more restricted attachment on the cranium, and the retroarticular process is entirely lacking. The superficial part probably covered most or all of the deep part. The insertion is entirely aponeurotic, perhaps because the unusual orientation of the articular surfaces leaves only a narrow rim of the articular for attachment.

*M. adductor mandibulae externus.*—This muscle complex had been removed, except for some fibers of ventralis on the lateral surface of the ramus, and parts of the aponeuroses of insertion of rostralis medialis, rostralis lateralis, rostralis temporalis, and caudalis, on the mandible. The aponeuroses of insertion of rostralis temporalis and medialis converge from either side of the postorbital process to make a single, strong attachment on the anterior coronoid process. This “process” consists of a raised scar that begins on the dorsolateral surface of the ramus and extends caudally and somewhat medially along the dorsal rim of the ramus, almost to the posterior coronoid process.

Aponeuroses of insertion of caudalis are confluent but distinguishable; that of part b is longer and stouter, attaching on the caudodorsal surface of the posterior coronoid process. That of part a is continuous ventrally with aponeurosis a, forming a vertical sheet shorter and thinner than the latter; it attaches on a vertical crest of the lateral surface of the ramus continuous with the caudal face of the posterior coronoid process.

The attachment of ventralis is not marked on bone except for its caudoventral border along the ventrolateral ridge of the ramus. Scattered muscle fibers indicate that it occupied the lateral surface of the ramus, immediately rostral and ventral to the mandibular fenestra, and much of the mandibular surface caudal and caudodorsal to the fenestra.

Rostralis lateralis inserts by a slender aponeurosis that parallels the dorsolateral edge of the ramus and attaches rostral to the mandibular fenestra.

*M. adductor mandibulae posterior.*—The muscle had been removed, except for a thin sheet of fibers from the ventral edge of the base of the orbital process of the quadrate. The fibers attach on the dorsal and dorsolateral surfaces of the ramus, between the lateral protuberance of the ramus (just rostral to the lateral cotyla) and the pseudotemporal tubercle.

*M. pseudotemporalis superficialis.*—The muscle had been removed, except for parts of the tendons of insertion and some fibers of origin attached to depressions on the rostral wall of the cranium and on aponeuroses
from two intraorbital crests. This muscle has both anterior and posterior portions. Attachment of the posterior portion is by a complex of strong aponeuroses to the pseudotemporal tubercle of the mandible. The anterior portion inserts by a thin, sheet-like aponeurosis and some fleshy fibers along the dorsomedial surface of the ramus between M. pseudotemporalis profundus and the coronoid processes. Its linear attachment extends from the pseudotemporal tubercle to the rostral limit of the anterior coronoid process.

*M. pseudotemporalis profundus.*—A large muscle arising fleshy from the ventrolateral and ventromedial surfaces of the distal two-thirds of the orbital process of the quadrate and by strong aponeurotic sheets from the tip, ventral edge, and medial surface of at least the distal half of the process. The aponeurosis from the tip of the orbital process lies along the rostral surface of the muscle. Fibers attach on the medial surface of the mandible around the mandibular fenestra, with strongest attachment by an aponeurotic sheet on the thickened, ventral portion of the ramus.

*M. pterygoideus.*—Much of the muscle mass had been cut away ventromedially and in the orbit; the left pterygoid bone had been cut and the mediopalatine processes removed. All descriptions are incomplete.

Dorsalis lateralis has an extensive attachment on the lateral surface of the palatine blade, base of the prepalatine bar, and dorsolateral surface of the transpalatine process and its aponeuroses. Its mandibular attachment is by an aponeurotic sheet along a narrow line ventral to the ventral attachment of M. pseudotemporalis profundus, and between points slightly rostral and caudal to the mandibular fenestra.

Ventralis lateralis attaches by aponeuroses to the transpalatine process and palatine blade. The mandibular attachment is fleshy on the caudoventral, caudomedial, and caudolateral portions of the ramus and on the base of the medial process. Species studied by Richards and Bock (1973) showed little or no attachment on the lateral surface of the mandible.

Ventralis medialis extends from the tip of the transpalatine process to the tip of the medial process of the mandible. Both attachments are aponeurotic.

The anterior part of dorsalis medialis extends from the palatine hasp and pterygoid to the medial surface of the mandibular ramus, bounded by insertions of pterygoideus dorsalis lateralis, pseudotemporalis superficialis (posterior portion), pterygoideus ventralis lateralis, and by the jaw articulation. The posterior part extends from the dorso-caudal portion of the pterygoid bone to the tip of the medial process of the mandible (caudalmost angle of the blunt-tipped medial process).

The retractor portion originates on the ventral surface of the braincase
rostral to the basitemporal plate. It inserts on the rostrodorsal portion of the pterygoid and on the retractor process of the pterygoid and dorsal surface of the prepalatine process.

*M. protractor pterygoidei et quadrati.*—Origin of the pterygoidei portion is from a marked depression on the wall of the interorbital septum, between the cranial fenestrae and palatine hasp. It extends rostrad halfway between the rostral limits of the cranial fenestra and optic foramen (on an imaginary transverse plane perpendicular to the jugal bars). Insertion is by a short tendon on the dorsal process of the pterygoid. Origin of the quadrati portion on the skull had been removed. Its insertion is marked by a depression on the medial surface of the body of the quadrato extending to the dorsal edge of the base of the orbital process. Fibers of the two parts of this muscle merge.

*M. branchiomandibularis.*—Most of this muscle had been removed. Part (?) of its mandibular attachment remained. The origin is partly fleshy and partly tendinous along a narrow line on the dorsomedial surface of the ramus, lying ventral to the attachment of *M.* mylohyoideus and extending from the caudal limit of the rhamphotheca halfway to the rostral limit of the mandibular fenestra.

*M. mylohyoideus (=M. intermandibularis).*—The muscle had been removed except for part (?) of its mandibular attachment. It originates fleshy along a narrow line on the dorsomedial surface of the mandibular ramus just dorsal to *M.* branchiomandibularis. Its origin extends rostromedially almost to the midline of the mandibular symphysis just ventral to the rhamphotheca. The caudal limit of origin appears to be close to that of *M.* branchiomandibularis.

Scars of neck muscles on the occiput (*M.* complexus, *M.* biventer cervicis, *M.* splenius capitis), are comparable in strength and position to those of *Psitirostra psittacea.*

To judge from the incomplete material examined, *Dysmorodrepanis* shows no major departure from the general pattern of jaw musculature of the drepanidines studied by Richards and Bock (1973), although the adductor muscles of the mandible are relatively larger and the depressor of the mandible relatively smaller. The adductor muscles of *Dysmorodrepanis* appear to be somewhat less strongly developed than in *Psitirostra psittacea,* but the protractor of the upper jaw was probably at least as well developed (based on muscle remains, on the limits and depth of muscle scars, and on the prominence of crests and processes). The mandibular depressor is, perhaps, less strong than that of *Psitirostra psittacea.* In contrast to *Pseudonestor xanthophrys,* the retractor portion of *M.* pterygoideus is not enlarged (Zusi 1989).
Fig. 8. The skull of *Dysmorodrepanis munroi* showing hypothetical kinetic movements of the jaws.

**FUNCTIONAL ANATOMY**

After soaking the skull of *Dysmorodrepanis*, we were able to move the upper jaw well above and below the closed position. We made no attempt to measure this movement, but the positions illustrated in Fig. 8 are probably representative of movements in the living bird. In the closed bill, about 40% of the tomial length of the maxillary rostrum extends beyond the lower mandible, but in the opened bill the tips of the rostra oppose each other like ice tongs (Fig. 8). The tips can be made to meet when both jaws are depressed beyond the resting position.

The blunt surfaces of the tomial crests, which extend over the caudal two-thirds of the diastema on both jaws, lie opposite each other with the bill in closed position. If either jaw moves independently, or if both are depressed beyond the closed position, the blunt surfaces are no longer opposite. They remain more or less opposite if both jaws open or close simultaneously. Neither the tips nor the tomia showed irregularities or noticeable wear, and the flattened surfaces were not abraded.

It is unlikely that the bird crossed its bill tips in the manner of crossbills (*Loxia*) even occasionally. The tips are not asymmetrical or worn in the area of potential crossing, they are not laterally compressed, and the jaw articulations are not asymmetrical. Certain features of the jaw articulation imply that lateral rotation of the mandibular rostrum was extremely limited as discussed below. The diastema was thus a permanent feature of the closed bill.

The mandible of *Dysmorodrepanis* slopes ventrally relative to the long axis of the jugal bar, both rostral and caudal to the mandibular fenestra (Fig. 8). The rostral slope relates to the “open-mouthed” position of the closed jaw required by the recurved rhamphotheca. The caudal slope has several consequences. One is that the surfaces of the mandibular cotylae
lie at an angle of about 60° to the long axis of the lower jaw (from the articulation to the tip) in lateral view. The comparable angle in Psittirostra psittacea is 13°. In the latter species, lateral motion of the lower jaw requires unilateral sliding of the articular on the quadrate; this sliding is possible because the planes of motion of the jaw and articular surface are approximately coincident. In Dysmorodrepanis the planes are widely divergent; lateral motion of the jaw would lift the articular of the opposite side off the quadrate. Unilateral sliding of the jaw on the quadrate would produce rotation of the lower jaw about its median axis.

Configuration of the condyles of the quadrate and cotylae of the lower jaw further suggests that sliding occurs in P. psittacea but not in Dysmorodrepanis. The profile of the medial cotyla in longitudinal section is convex upward in the former—concave upward in the latter. The larger medial condyle of the quadrate of Dysmorodrepanis occupies most of the medial cotyla in a loose ball-and-socket arrangement. Reduced capacity for sliding is further reflected by the short lateral cotyla. Manipulation of the lower jaw on the skull confirms that the articulation acts essentially like a pin hinge. This would ensure that the mandibular rostrum closed into the groove of the maxillary rostrum without damaging the tomia.

**DISCUSSION**

Several facts suggest that the bill of Dysmorodrepanis was not used often for strong biting or crushing or forceful manipulation of the substrate: the adductor musculature is not highly developed, the flattened portions of the tomia of the lower jaw are not supported by bone, and the domed lingual contours of the rostra provide poor surfaces for biting. The shape of the rostra and the presence of a diastema appear unsuited for insect gleaning or handling of small seeds. Munro (1944) noted that when he collected Dysmorodrepanis the stomach and throat were full of the small ripe berries of Urera glabra, a widely distributed native Hawaiian shrub. Dysmorodrepanis may have used the pincer action of its bill tips to pluck berries or flowers, and the blunt tomial surfaces of the diastema could have functioned to carry or to crush fruit such as medium-sized berries. On the other hand, the berries in the stomach of Dysmorodrepanis could represent an opportunistic meal rather than the mainstay of its existence. A diet of berries is an unlikely source for the selection that produced the unusual bill of Dysmorodrepanis, considering that a great many avian species feed on berries and none of them has developed a similar adaptation.

Another possibility, albeit a highly speculative one, is that Dysmorodrepanis was a specialized snail-eater. Native land snails were once an abundant source of potential nourishment in the Hawaiian islands before
human habitat disruptions drastically reduced their numbers and distribution. These were both arboreal and terrestrial and ranged in adult size from a few millimeters up to several centimeters in length. Other Hawaiian passerines may take small snails on occasion, but the only species known to feed on them frequently is Melamprosops phaeosoma on Maui (Baldwin and Casey 1983), a drepanidine with an ordinary but rather weak finch-like bill. Dysmorodrepanis could have used the pincer action of its bill or the diastemal tomia to transport snails. The hooked maxillary rostrum may have been capable of spearing the body and drawing it out of the shells of larger snails as Snail Kites (Rostrhamus sociabilis) do. The incurled tomal crests of the diastema could have crushed the shells of medium-sized snails, and the fleshy tongue might then have maneuvered the broken shells out the open sides of the bill, and the meat into the throat.

There is no reason to assume that the natural distribution of Dysmorodrepanis was limited to the island of Lanai. Fossil evidence has shown that the distribution of many endemic Hawaiian birds was wider in the past. Dysmorodrepanis is most likely to be found as a fossil on Maui or Molokai, two adjacent islands that were connected to Lanai as recently as 17,000 years ago. No fossils of Dysmorodrepanis have been identified to date, however (Olson and James 1982, 1984; James 1987; James et al. 1987).

Despite the general reluctance among ornithologists to give due consideration to taxa that are known from unique specimens, the case of Dysmorodrepanis is not at all singular or unexpected. Over the past century, the decline of native birds on Lanai has been so dramatic that seven of the eight endemic Hawaiian species known from non-fossil specimens are now apparently extinct there (Scott et al. 1986). Only three specimens of the Lanai Akialoa (Hemignathus lanaiensis) were procured before that species became extinct. Elsewhere in the Hawaiian islands, Myadestes oahuensis and Hemignathus lichtensteini are each known from two specimens, Chaetoptila angustipluma is known from four, Ciridops anna is known from five, and Porzana sandwichensis is known from seven. Similar cases from the southwest Pacific are Aplonis mavornata from the Cook Islands (Olson 1986) and Aegothelies savesi from New Caledonia (Olson et al., in press), each known from a single specimen. What these rare specimens reflect is the acceleration in avian extinctions that accompanied human proliferation in the Pacific basin.

ACKNOWLEDGMENTS

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Dysmorodrepanis. N. Payzant painted the frontispiece and rendered the inked illustrations of Dysmorodrepanis based on R. L. Zusi’s pencilled originals. Stippled illustrations of P. psittacea and Pseudonestor are by J. Schulz, and Fig. 5 is by J. Clark. One of V. Krantz’s many photographs of Dysmorodrepanis is reproduced in Fig. 2. We thank A. Berger and R. Raikow for reviewing the manuscript. The specimens referred to in the text are from the following museum collections: British Museum (Natural History), Tring (BM), Bernice P. Bishop Museum, Honolulu (BPBM), Museum of Vertebrate Zoology, Berkeley (MVZ), and National Museum Natural History, Washington (USNM). We thank the appropriate curators and curatorial assistants at these museums for the loan of specimens.

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COLOR PLATE

The frontispiece painting by Nancy Payzant has been made possible by an endowment established by George Miksch Sutton.
COMPARATIVE BIOLOGY AND EVOLUTION OF TITMICE

THE CENTENNIAL SYMPOSIUM OF THE WILSON ORNITHOLOGICAL SOCIETY

This volume of The Wilson Bulletin is devoted to papers on the evolution and comparative biology of titmice, including the invited papers of the Centennial Meeting. Their appearance here continues a long Wilson Bulletin tradition of seminal papers on the biology of chickadees and titmice.

Chickadees and titmice (Parus) are among the most popular birds for ornithological study. The extensive literature on these small passerine birds, however, does not mean that research opportunities are nearly exhausted. Quite the opposite. The rapidly growing body of knowledge of their behavior and ecology makes chickadees and titmice excellent subjects for both descriptive and experimental studies in the field and in the laboratory. Parids are ideal for comparative studies, the basis for insights concerning many evolutionary problems. Increasingly, also, we are entering an era of synthesis in which knowledge of parid social behavior, communication, morphology, physiology, foraging behavior, reproductive biology, population ecology, community ecology, and systematics blends into an integrated understanding of adaptations and evolution of whole organisms. No other set of birds is known so intimately and so coherently as are the titmice. This taxonomic group provides ideal "model species" for investigating important questions concerning many aspects of avian biology. For example, few other groups have been the subject of such extensive long-term studies of local populations as those conducted by workers on several European species. For another example, as the result of field and laboratory studies, parids now feature in biological research concerning the nature of memory and its relationship to brain structure.

The Centennial Meeting of the Wilson Ornithological Society at the Academy of Natural Sciences of Philadelphia on June 9, 1988 provided an opportunity to further research on Parus. This is a large avian genus (about 43 species), with a distribution spanning four continents. By organizing an international symposium devoted to the comparative biology of titmice, we hoped both to increase communication among experts from North America and Europe and to launch a new era of cooperation, stimulation, and, especially, synthesis. To this end, we invited seven plenary speakers—André Dhondt from Belgium, Jan Ekman from Sweden, Svein Haftorn and Olav Hogstad from Norway, Jack Hailman from
the U.S., Christopher Perrins from England, and David Sherry from Canada—renowned leaders in the study of titmice. Each plenary speaker addressed a topic of his choice, reviewing recent advances, and setting the stage for further research. As important as the plenary talks, however, were the informal discussions and workshops that ensued that week in Philadelphia. It was an exciting event that clearly launched the next decades of parid research.


Editor's note: Frank Gill organized and conducted the symposium. Frank and Millicent S. Ficken gathered the authors' manuscripts, read and edited them, and negotiated revisions, deletions, and corrections. We express our gratitude to Millicent and Frank for producing a synthesis that will be a valuable source for students of the biology of Parus.—C. R. BLEM.
PROTEIN RELATIONSHIPS AMONG TITMICE (PARUS)

Frank B. Gill,1 David H. Funk,1 and Bengt Silverin2

Abstract.—As a first step toward understanding the evolutionary and biogeographical relationships among species of Parus, we compared allozymes at 34 loci of nine North American and six Eurasian species representing six subgenera. The results of this electrophoretic survey provide the first broad summary of genetic relationships among species of the genus Parus. Distance Wagner and UPGMA analyses suggest that: (1) the crested North American titmice (subgenus Baeolophus) are only distantly related to the other parids examined; (2) the Bridled Titmouse (P. wollweberi) is closest to Baeolophus titmice and convergent in appearance to the Crested Tit (P. cristatus); (3) the Marsh Tit (P. palustris) and Willow Tit (P. montanus) probably are sister taxa, but the Carolina Chickadee (P. carolinensis) and Black-capped Chickadee (P. atricapillus) may not be; (6) the Black-capped Chickadee is genetically closer to the Mountain Chickadee (P. gambeli) and Mexican Chickadee (P. sclateri) than to the Carolina Chickadee and (7) the Boreal Chickadee (P. hudsonicus) and Chestnut-backed Chickadee (P. rufescens) are sister taxa related in turn to the atricapillus species group.

The titmice of the world (Paridae) are a well-defined taxonomic group. All but two of the 46 species are classified in the genus Parus (Snow 1967). The 11 North American species apparently are descendents of Eurasian lineages that crossed the Bering land bridge during interglacial epochs of the Pleistocene (Mayr 1946, Parkes 1958). Following range expansions in North America, the populations of some of these colonists underwent repeated fragmentation and vicariant speciation due to the advance and retreat of the glaciers (Selander 1965, Brewer 1963, Dixon 1978). The current view of relationships among species is suggested by the subgeneric classification of Thielcke (1968) (Appendix I). The three large, crested, North American titmice (Plain Titmouse, P. inornatus; Tufted Titmouse, P. bicolor; and Black-crested Titmouse, P. [bicolor] atricristatus) constitute the subgenus Baeolophus. The Bridled Titmouse (P. wollweberi) is an enigmatic species assigned to the subgenus Lophophanes with two Old World species, the Crested Tit (P. cristatus) and the Gray-crested Tit (P. dichrous). The North American chickadees (subgenus Poecile) include a “brown-capped” superspecies (Chestnut-backed Chickadee, P. rufescens; Boreal Chickadee, P. hudsonicus; Siberian Tit, P. cinctus), and a “black-capped” species group (Black-capped Chickadee, P. atricapillus; Carolina Chickadee, P. carolinensis; Mountain Chickadee, P. gambeli; and Mexican Chickadee, P. sclateri) (Mayr and Short 1970). Superficially, these


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"black-capped" chickadees appear close to certain Eurasian forms, especially the Willow Tit (*P. montanus*), with which the Black-capped Chickadee has been considered conspecific (see Snow 1956).

In this paper we explore the relationships among North American chickadees and titmice and selected Eurasian species based on electrophoretic surveys of genetic loci that code for enzymes that function in intermediary metabolism. Differences among species allow us to construct hypotheses of evolutionary relationship and biogeographical history (Wilson et al. 1977, Barrowclough 1983, Barrowclough et al. 1985, Nei 1987).

**MATERIALS AND METHODS**

We surveyed allozymes present in tissues of nine North American species and six Eurasian species of *Parus* (Appendix 1). With the exception of Boreal Chickadee (N = 4) and the Coal Tit (*P. ater*) (N = 3), we used five individuals of each species, or in the case of the Black-capped Chickadee, five individuals from each of two geographically distant populations (*P. a. atricapillus* from Pennsylvania and *P. a. occidentalis* from Washington). A White-breasted Nuthatch (*Sitta carolinensis*) served as the outgroup, but in hindsight this nuthatch was too different genetically to help resolve most issues of character polarity.

Tissue samples were preserved on dry ice or liquid nitrogen in the field and transferred to freezer storage at −70°C until analysis. Methods were similar to those of Braun and Robbins (1986), except that we used horizontal rather than vertical starch gel electrophoresis. Most of the 34 presumptive genetic loci we examined (Appendix 1) matched theirs. We could not obtain satisfactory results with four of their loci (Alat-1, Alat-2, Glud, Pro-1), which included diagnostic alleles, and we scored six additional loci (Ck-3, Pgm-2, Me, Np, Gda, Ald). Alleles at each presumptive genetic locus were scored with reference to their mobility from the origin, and labelled *a*, *b*, *c*, etc. in sequence from the one closest to the anode. Allelic frequencies were calculated from the individual genotypes scored from banding patterns on the gels.

We used the computer program BIOSYS-1 (Swofford and Selander 1981) for calculations of gene frequencies and genetic distances, as well as construction of distance Wagner trees and UPGMA phenograms based on both Rogers’ (1972) and Cavalli-Sforza and Edwards’ (C-S&E) (1964) chord distances. The analysis of evolutionary relationships based on electrophoretic surveys of allozyme compositions is controversial (Felsenstein 1982, 1983, 1984; Lanyon 1985; Farris 1986; Swofford and Berlocher 1987). Distance Wagner trees and UPGMA clustering methods based on Rogers’ (1972) genetic distances are the most commonly used procedures. Tests of the different tree building procedures by Nei et al. (1983) suggest that C-S&E chord distances produce the most accurate branching topologies in both distance Wagner trees and UPGMA phenograms. UPGMA phenograms give the most accurate trees when small numbers of loci are analyzed, but assume constant evolutionary rates (Rohlf and Wooten 1988). We also used Felsenstein’s (1981) unrooted maximum likelihood networks, specifically the CONTML program in PHYLIP 2.8. In modelling tests that assumed constant evolutionary rates, this approach produced the most accurate trees when large numbers of loci (e.g., over 50) are analyzed (Rohlf and Wooten 1988). Kim and Burgman (1988) also found maximum likelihood to perform better than either maximum parsimony or phenetic clustering in simulations with unequal evolutionary rates that corresponded to a genetic drift model with population bottlenecks, as may be appropriate for birds (Barrowclough et al. 1985). Character state polarities of alleles refer to their distributions among the hierarchy of clusters in the distance Wagner tree (Richardson et al. 1986).
RESULTS

Twelve of the 34 loci (35%) were monomorphic in Parus, including five that were monomorphic in both Sitta and Parus (*): Aat-2, Ck-1*, Ck-2, Pgm-1, Ldh-2, Mdh-1*, Mdh-2, Sordh*, Sod-2, Hb*, Mb, G3pdh*. Distinct alleles characterized Sitta at 26 loci. In Parus, fixed interspecific differences characterized 16 of the 22 informative loci. The number of alleles per locus averaged 1.1. Across species, an average of 9.2% of the loci were polymorphic (range = 0.0–17.6; 0.95 criterion).

Nei's (1978) genetic distances (\(D\)) between species pairs ranged from 0.005 to 0.396. Distances between subgenera, using Black-capped Chickadee to represent the subgenus Poecile and Tufted Titmouse to represent the subgenus Baeolophus, averaged three–four fold greater (\(\bar{D} = 0.22 \pm 0.09\) SD, \(N = 15\)) than distances between species pairs of Poecile (\(\bar{D} = 0.06 \pm 0.05\) SD, \(N = 28\)). Distances between the two species of Baeolophus titmice (\(\bar{D} = 0.06\)) were the same as the average among pairs of Poecile chickadees. Braun et al. (1984) reported the distance between Black-crested Titmouse and Tufted Titmouse to be \(\bar{D} = 0.063\), the same as we found between Tufted Titmouse and Plain Titmouse. Distances between North American chickadees and Baeolophus titmice (\(\bar{D} = 0.29 \pm 0.04\) SD, range 0.2–0.4) were higher than those estimated for all other combinations of species. The protein distance between Tufted Titmouse and Carolina Chickadee is 0.28, not 0.09 as erroneously reported for this pair of species by Mack et al. (1986). The Marsh Tit (P. palustris) was genetically the most divergent of all chickadees. Among North American species of chickadees, Carolina Chickadee and Mexican Chickadee were the most different. Chestnut-backed Chickadee and Boreal Chickadee were particularly close to one another (\(\bar{D} = 0.004\)) and to Black-capped Chickadee (\(\bar{D} = 0.004\), 0.007). The two races of Black-capped Chickadee from opposite sides of the continent were virtually identical (\(\bar{D} = 0.00\)).

Relationships among subgenera.—Distance Wagner trees (Fig. 1), UPGMA phenograms, and the maximum likelihood network (Fig. 2) all suggested the following relationships among subgenera, regardless of whether Rogers’ or C-S&E genetic distances were used: (1) the North American crested titmice (“Baeolophus” plus Bridled Titmouse) represent a distinct parid lineage; (2) Bridled Titmouse is not allied to the Crested Tit, rather it is convergent in appearance; (3) the Crested Tit is the closest of the Eurasian taxa to Poecile chickadees; (4) the Eurasian subgenera represent distinct lineages without clear affinities among themselves.

Two major ambiguities persist in the topological relationships among subgenera. First is the arrangement of Coal Tit (subgenus Periparus), Blue Tit (P. caeruleus) (subgenus Cyanistes), and Great Tit (subgenus Parus).
Both distance Wagner trees based on C-S&E chord distances, and the shortest distance Wagner tree based on Rogers’ distances, projected a hierarchical sequence of Blue Tit-Great Tit-Coal Tit, as illustrated in Fig. 1. A slightly longer, alternative distance Wagner tree based on Rogers’ distance linked Coal Tit and Blue Tit, as did UPGMA phenograms based on both Rogers’ and C-S&E distances. The second ambiguity concerns the relationship between the Crested Tit and Poecile chickadees. Distance Wagner trees and the maximum likelihood networks consistently placed the Crested Tit outside the cluster of Poecile species. UPGMA phenograms clustered the Crested Tit between Marsh Tit and Carolina Chickadee.

One to three unique alleles characterized all but one of the subgenera (Fig. 1). Fixed differences separated Parus from Sitta at 17 loci, and combinations of the Eurasian lineages from the North American crested titmice at five loci. At one of these five loci (Gpi), the North American crested titmice retained plesiomorphic allele a (also present in Sitta), whereas all other species had the alternative (derived) allele b. At the other four loci (Np, αGpdh, 6Pgd, Mpi), the alleles distinguishing the North American crested titmice differed from Sitta but still may have been plesiomorphic: (1) locus Np—the North American crested titmice shared allele d with Great Tit and Blue Tit, whereas other species exhibited the derived state c, or (Crested Tit only) the derived states f and g; (2) locus αGpdh—the North American crested titmice were united by allele
Among the North American crested titmice, Tufted Titmouse and Plain Titmouse are sister taxa distinguished from Bridled Titmouse by derived alleles at two loci (Ada, Me). Braun et al.'s (1984) data suggest that the Black-crested Titmouse has the same allele as the Tufted Titmouse at one of these loci (Me). The other locus (Ada) was polymorphic in their samples of Black-crested Titmouse and Tufted Titmouse, with a strong frequency difference between the two species. The derived allele prevailed (96%) in Tufted Titmouse, whereas the primitive allele, which was fixed in Bridled Titmouse and all chickadees, prevailed in Black-crested Titmouse (92%). Allele c present as a polymorphism at a third locus (Pro-2) also distinguished Tufted Titmouse and Plain Titmouse from Bridled Titmouse, but the same (or an indistinguishable) allele was present in two species of chickadees (see below).

Few synapomorphies linked the other subgenera. Alleles at locus Me appear to link Bridled Titmouse and Crested Tit with the subgenus Poecile (Me) and Blue Tit with Great Tit (Me), but this variable locus requires further study. Allele c at locus 6Pgd also linked Great Tit and Blue Tit.
Fig. 3. Distance Wagner tree of genetic relationships among species of *Poecile* chickadees using Cavalli-Sforza and Edwards' genetic distances. This tree is a subset of the full set of species rooted with *Sitta*, but only *bicolor* is included here as an outgroup for reference (total length of full tree = 2.86; percent standard deviation = 10.99). Synapomorphies and autapomorphies indicated as in Fig. 1.

**Relationships among chickadees.**—Similar allozyme compositions characterized the *Poecile* chickadees, resulting in short branch lengths (Figs. 3 and 4) and topologies that varied with tree length and algorithms. Two species combinations, however, consistently clustered together: (1) Mexican/Mountain and (2) Boreal/Chestnut-backed. Marsh Tit and Willow Tit linked as sister taxa in distance Wagner trees, but not in the UPGMA phenograms or the maximum likelihood network, which positioned Marsh Tit outside all other *Poecile* species. Carolina Chickadee did not cluster with Black-capped Chickadee, but rather placed outside all other species in the distance Wagner trees, and outside all species, except Crested Tit and Marsh Tit, in the UPGMA phenograms and the maximum likelihood network. The distance Wagner trees and maximum likelihood network clustered Black-capped Chickadee most closely with Mountain Chickadee and Mexican Chickadee, but the UPGMA phenograms suggested a closer tie to the brown-capped species, Boreal Chickadee and Chestnut-backed Chickadee. Tentatively, we suggest that Fig. 3 represents the best available working hypothesis of relationships among chickadees.

Shared alleles distinguished some sets of species (Fig. 3). Me<sup>b</sup> characterized Crested Tit (and Bridled Titmouse) plus all *Poecile* chickadees except Marsh Tit, which retained or reverted to allele *a*. Dip-2<sup>c</sup> distinguished the *Poecile* chickadees from all other subgenera. So did allele *d* at Me, with the caveat that Marsh Tit either retained or reverted to the
primitive allele $b$ which was present in the North American crested titmice. Black-capped Chickadee, Mountain Chickadee, and Mexican Chickadee shared a unique allele at the one locus (Dip-1$^d$). This allele was fixed in both Mountain Chickadee and Mexican Chickadee but not in Black-capped Chickadee, which retained the primitive allele ($c$). No unique states linked Boreal Chickadee and Chestnut-backed Chickadee. One synapomorphy (locus Ada$^d$) linked Willow Tit and Marsh Tit. Fixed autapomorphies at one locus each distinguished Carolina Chickadee (Gda$^b$) and Marsh Tit (Aat1$^d$) from all other chickadees.

**DISCUSSION**

The results of this electrophoretic survey provide the first broad summary of genetic relationships among species of the genus *Parus*. The protein data support some, but not all, of the current classification of...
parids based on morphology and vocalizations (Snow 1967, Thielcke 1968, Eck 1988). First, the crested North American titmice (subgenus *Baeolophus*) constitute a distinct lineage. The substantial genetic distance (Nei’s $\bar{D} = 0.31$) between these titmice and chickadees (subgenus *Poecile*) is comparable to that distinguishing many genera of passerine birds (Johnson et al. 1988). Also, Tufted Titmouse mitochondrial DNA (mtDNA) was markedly different (9%) from the mtDNA of two species of chickadees (Mack et al. 1986). The relationships of these titmice to the superficially similar Gray-crested Tit of the coniferous forests of western China and Tibet warrant study, because this species stands out as perhaps the best candidate for the modern Eurasian representative of this distinct lineage. Thielcke (1968) and Eck (1988) both allied Bridled Tit to the Gray-crested Tit as well as to Crested Tit. Our data establish that Bridled Titmouse is not closely related to Crested Tit ($D = 0.213$), but, instead, may be more closely related to the *Baeolophus* lineage ($D = 0.134, 0.201$). It remains to be resolved whether Bridled Titmouse is more closely related to the *Baeolophus* titmice than to other Eurasian lineages, and how many invasions of North America occurred. The subgenus *Lophophanes* as constituted by Thielcke (1968) is paraphyletic.

The other parid subgenera examined in this study appear to be distinct lineages separated by substantial genetic distances. Coal Tits (subgenus *Periparus*) and Blue Tits (subgenus *Cyanistes*) may be sister lineages, but further study of these two Eurasian species groups is required. We were surprised that Crested Tit appears to be the closest of the Eurasian lineages to *Poecile* chickadees ($\bar{D} = 0.118$, compared to $\bar{D}$s of 0.150 [Coal Tit], 0.220 [Great Tit] and 0.275 [Blue Tit]). To our knowledge, this relationship has not been indicated previously.

Few differences in allozyme compositions were evident among the species of *Poecile* chickadees we examined. Phylogenetic hypotheses among these closely related taxa based on such data are weak and volatile, influenced both by sampling error and specifics of alternative clustering algorithms. A conservative view would be to present the relationships among the North American chickadees as an unresolved polytomy. With this caution, we make the following, potentially controversial observations. Among North American taxa, the close relationships of Mexican Chickadee/Mountain Chickadee and of Chestnut-backed/Boreal were the two clearest results. A derived chromosome arrangement also supports the relationship between Mexican Chickadee and Mountain Chickadee (Holly pers. comm.). The protein data also suggest that: (1) phenotypically confusing (sibling) species, i.e., Carolina/Black-capped chickadees and Marsh/Willow tits, are genetically divergent and are not necessarily sister taxa as we have presumed; (2) the “brown-capped” species (Chestnut-backed, Boreal) are close relatives of the Black-capped Chickadee species group; (3)
the North American taxa probably are more closely related to each other than any is to Willow Tit or Marsh Tit of Eurasia; and (4) the genetic distinction between Black-capped Chickadee and Willow Tit supports earlier conclusions (Snow 1956) that these two taxa are not conspecific and may not be sister taxa.

The lack of genetic differentiation between Pennsylvania and Washington state populations of Black-capped Chickadees is perhaps surprising, given the marked (subspecific) geographical variation in plumage color in this species (Duvall 1945). Our samples from Washington state were of the distinct race P. a. occidentalis, not the eastern Washington race P. a. fortuitus, which is remarkably similar in appearance to P. a. atricapillus from Pennsylvania. Genetic uniformity over such a large region suggests recent geographic expansion of the species (Wake et al. 1978).

One of the principal conclusions evident from these taxonomic comparisons is that species most similar in visual appearance are not necessarily closest genetic relatives. In this regard, perhaps the most controversial result of this protein study pertains to the relationship between the hybridizing species, Black-capped and Carolina chickadees, which are so similar in morphology, vocalizations, and behavior that they are viewed by some as potentially conspecific (Robbins et al. 1986). Distantly related species have converged in the evolution of plumage color patterns and ornamentations, such as crests, which mediate their social interactions. Vocal repertoires may also exhibit such convergence. Head color pattern differences between closely related species, such as Black-capped Chickadee and Mountain Chickadee suggest that such plumage color patterns diverged flexibly and are poor guides to phylogenetic relationships.

Mengel (1964) and Hubbard (1969) developed models of Pleistocene speciation events for North American wood warblers, models which pertain to Parus because the evolution of both groups of species is tied to the historical distribution of boreal, cordilleran, and (Pacific) coastal coniferous forests. Mengel's model for wood warblers, however, centered on a Madro-tertiary forest refugium in the southeastern U.S., which was appropriate for some autochthonous New World groups, but may not be fully applicable to an allochthonous Eurasian group such as Parus. How many separate invasions are responsible for the modern North American species of chickadees remains unknown. One specific hypothesis (Brewer 1963) is that the ancestor of two species, Black-capped Chickadee and Carolina Chickadee, invaded North America across the Bering land bridge in the late Pliocene or early Pleistocene and separated into an eastern form (Carolina Chickadee) and a western (montane) form (Black-capped Chickadee) during one of the early Pleistocene glaciations. Brewer suggested that expansion of Black-capped Chickadee into the east took place during a subsequent interglacial period, resulting in secondary contact
with Carolina Chickadee, followed by latitudinal shifts in distribution. The protein data suggest a more complex scenario that includes the evolution of Mountain and Mexican chickadees.

Our results are largely consistent with previous allozyme comparisons of parids, e.g., Tufted and Black-crested titmouse (Braun et al. 1984) and Black-capped, Carolina, and Mountain chickadees (Braun and Robbins 1986). The most significant discrepancy was the fixed allelic difference distinguishing Carolina from Black-capped Chickadee at the Gda locus which was not examined by our predecessors. A survey of this locus in both Carolina Chickadee (PA, NJ, GA, N = 33) and Black-capped Chickadee (PA, WA, ONT, N = 26) confirmed this difference in samples from distant localities in the distribution of each species (Gill unpubl. data). The fixed difference at the Gda locus increased the genetic distance between Carolina Chickadee and Black-capped Chickadee from $\bar{D} = 0.001$ (Braun and Robbins 1986) to $\bar{D} = 0.027$. These two species hybridize extensively in a long, narrow zone of contact (Brewer 1963, Rising 1968, Robbins et al. 1986).

We failed to find the differences between Black-capped Chickadee and Mountain Chickadee reported by Braun and Robbins (1986), substantially reducing our estimated genetic distance between these two species. Despite repeated efforts we could not score the locus (Alat-2) at which Braun and Robbins reported a fixed difference. They also found a large frequency difference between Black-capped Chickadee and Mountain Chickadee at Pro-1, but we could not score this locus either. This may have been due merely to differences between laboratories, or to the fact that their sample of Mountain Chickadee was of the distinct California race, P. g. baileyae, whereas ours was of the Rocky Mountain race, P. g. gambeli. Such discrepancies illustrate how subject to sampling errors allozyme comparisons of closely related taxa may be (Nei 1987).

Two future efforts will provide better resolution of genetic relationships among these chickadees. First will be analyses of mtDNA base pair sequence divergence which enables better discrimination among closely related passerine birds, including species of Parus, than do allozymes (Mack et al. 1986, Avise and Zink 1988). The mtDNAs of Black-capped Chickadee and Carolina Chickadee, for example, exhibit a 4% divergence, which suggests separation about two million years ago. Second, genetic comparisons should include Sombre Tit (P. lugubris) of Eurasia plus White-browed Tit (P. superciliosus) and Pere David's Tit (P. davidi) of southwestern China. The White-browed Tit resembles the Mountain Chickadee, and Pere David's Tit may be related to either the Sombre Tit or the Black-capped Chickadee (Eck 1988). Some populations of Sombre Tit (and also of Willow Tit, e.g., the songarus group—Vaurie 1959, Snow 1956), have brown caps and resemble Siberian Tits. Any one of these
species could be a close relative of North American taxa. Once these two efforts are complete, and a comprehensive picture of genetic relationships among chickadees is available, we should be able to develop a realistic analogue of Mengel's warbler speciation model for North American parids.

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LITERATURE CITED


# APPENDIX I

## Alleles Scored at Variable Loci for 15 Species of *Parus* plus *Sitta*. Frequencies of Secondary Alleles are Indicated in Parentheses

<table>
<thead>
<tr>
<th>E.C. #</th>
<th>Locus</th>
<th>Buffer</th>
<th>Alleles of each species*</th>
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<tr>
<td>1.1.1.1</td>
<td>$\alpha$-glycerophosphate</td>
<td>D</td>
<td>e            e            e            e            e            e</td>
</tr>
<tr>
<td></td>
<td>dehydrogenase ($\alpha$Gpdh)</td>
<td></td>
<td></td>
</tr>
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<td>Lactate dehydrogenase</td>
<td>A</td>
<td>a            a            a            a            a            a</td>
</tr>
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<td></td>
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<td></td>
</tr>
<tr>
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<td>Malate dehydrogenase</td>
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</tr>
<tr>
<td></td>
<td>(Mdh-2)</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>Malic enzyme (Me)</td>
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</tr>
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<td>Isocitrate dehydrogenase</td>
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<td></td>
<td>(Isdh-1,2)</td>
<td></td>
<td></td>
</tr>
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<td>A</td>
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<tr>
<td></td>
<td>(6pgd)</td>
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<td>Superoxide dimutase</td>
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<td>(Sod-1,2)</td>
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<td></td>
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<td></td>
<td>B</td>
<td>b            b            b            b            b            b</td>
</tr>
<tr>
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<td>Myoglobin (Mb)</td>
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Monomorphic loci: Sorbitol dehydrogenase (Sordh) [1.1.1.14], Buffer A; Malate dehydrogenase-1 (Mdh-1) [1.1.1.37], Buffer A; Glycerdehyde-phosphate dehydrogenase (G3pdh) [1.2.1.12], Buffer E; Creatine Kinase-1 (Ck-1) [2.7.3.2], Buffer D; Hemoglobin (Hb), [no E.C. #]; Buffer D.

Buffers: A = TC-7.5 (0.2 M tris/0.058 M citric acid/pH 7.5), B = TEB-8.1 (0.2 M tris/0.26 M boric acid/0.005 M EDTA/pH 8.1), C = PC-6 (0.2 M sodium phosphate (monobasic)/0.55 M citric acid/pH 6.0), D = TM-7.5 (0.2 M tris/0.087 M maleic acid/pH 7.5), E = P-7 (0.67 M sodium phosphate (monobasic)/0.133 M sodium phosphate (dibasic)).

*Species: 1 = P. atricapillus; 2 = P. carolinensis; 3 = P. rufescens; 4 = P. hudsonicus; 5 = P. gambeli; 6 = P. sclateri; 7 = P. palustris; 8 = P. montanus; 9 = P. ater; 10 = P. major; 11 = P. caeruleus; 12 = P. cristatus; 13 = P. wollweber; 14 = P. inornatus; 15 = P. bicolor; 16 = Sitta carolinensis.
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ECOLOGICAL AND EVOLUTIONARY EFFECTS OF INTERSPECIFIC COMPETITION IN TITS

ANDRÉ A. DHOND'T

Abstract.—In this review the evidence for the existence of interspecific competition between members of the genus Parus is organized according to the time scale involved. Competition on an ecological time scale is amenable to experimental manipulation, whereas the effects of competition on an evolutionary time scale are not. Therefore the existence of competition has to be inferred mainly from comparisons between populations. Numerical effects of interspecific competition in coexisting populations on population parameters have been shown in several studies of Great and Blue tits (Parus major and P. caeruleus) during the breeding season and during winter, and they have been suggested for the Black-capped Chickadee (P. atricapillus) and the Tufted Titmouse (P. bicolor). It is argued that the doubly asymmetric two-way interspecific competition between Great and Blue tits would have a stabilizing effect promoting their coexistence. Functional effects on niche use have been experimentally shown by removal or cage experiments between Willow (P. montanus) and Marsh (P. palustris) tits, between Willow and Crested tits (P. cristatus) and Coal Tits (P. ater) and Goldcrests (Regulus regulus), and between Coal and Willow tits. Non-manipulative studies suggest the existence of interspecific competition leading to rapid niche shifts between Crested and Willow tits and between Great and Willow tits. Evolutionary responses that can be explained as adaptations to variations in the importance of interspecific competition are numerous. An experiment failed to show that Blue Tit populations, subjected to different levels of interspecific competition by Great Tits, underwent divergent micro-evolutionary changes for body size. It thus remains unclear what time scale is involved in the presumed adaptations to interspecific competition.

The problem with interspecific competition is that some people believe it is such an important force which is a transient phenomenon that can be observed only rarely in nature, whereas others think it is so important that it permanently influences coexisting species-populations. This difference in opinion, also concerning titmice, existed 35 years ago. Kluyver (1951, 1966) wrote that interspecific competition between Great Tits (Parus major) and Blue Tits (P. caeruleus) existed, but that since intraspecific competition among Great Tits was more important than interspecific competition between the two species, he would only consider the first. From the context of these statements it seems he meant that Blue Tit numbers influenced some aspect of Great Tit population dynamics. Unfortunately, he did not present evidence to support his claim.

Lack (1945) argued that closely related species coexisting in the same habitat differ in ecological niche, especially in foraging niche, in order to avoid competition. These niche differences are the result of their evolu-

tionary history, during which interspecific competition did occur. Forty years ago this was an important new idea, since it was then that the so-called Hypothesis of Gause, that closely related species must differ in their ecological niches in order to coexist, was being substantiated. Several of Lack’s students (Hartley 1953, Gibb 1954, Betts 1955) provided data showing that, indeed, the five members of the genus *Parus* coexisting in Wytham Wood differed in their foraging niches. The large overlap in foraging niches in the breeding season was explained by stating that food was so superabundant then that no competition would take place. During winter, when food abundance was thought to be limiting, niches diverged, supporting the idea that birds avoided competition for food.

The most convincing, but not easiest, way to demonstrate the existence of interspecific competition is through field experiments. Schoener (1983) listed 164 experiments published before 1982. Only seven concerned birds, two of which were about titmice. Tits have, therefore, played an important role in the experimental study of interspecific competition in birds, a role they continue to play.

WHAT IS COMPETITION?

Competition is a biological interaction between individuals or populations (belonging to the same or to different species) for a limiting resource, resulting in a reduced fitness of all parties involved. Recently it has become fashionable to enlarge the definition and to include amensalism in the definition of competition, meaning that if only one of the parties involved is affected, this should also be called competition. Evidence for the existence of competition can either be provided by changes in population size (numerical response) or by a niche shift (Thomson 1980).

In the published literature, interspecific competition is accepted as having been demonstrated if an effect is shown on population size as such or on one of the population processes such as reproduction, survival, recruitment, immigration, or emigration (cf. Schoener 1983, Connell 1983). Competition can also influence the age structure of a population (Hairston 1980). The usual implicit assumption is that if there is an effect on one of the population processes, this will eventually influence population size also. Alternatively, if the age structure has changed, this must have been caused by a change in one of the population processes. I will therefore consider all such responses as belonging to the category of numerical responses. Thomson (1980) further subdivided niche shifts into two groups, nonevolutionary shifts of behavior which are functional responses to competition, and evolved shifts such as character displacements which are evolutionary responses.
Most students of interspecific competition are satisfied that competition is present if an effect can be demonstrated for one of the populations studied (amensalism). Very rare are the publications that provide evidence that both populations were affected. Another way to regroup the effects of interspecific competition is by considering the time scale which is involved. Numerical responses and “functional” responses occur rapidly on an ecological time scale, and they can thus be reversed immediately when conditions change. If competitive effects exist, they can be demonstrated by experimentation, and positive experiments would indicate that interspecific competition is a force that can be observed. Evolutionary responses operate over a longer time scale, and when conditions change, the populations respond more slowly. They are therefore not amenable to short-term experimentation. If demonstrated, they would support the idea that interspecific competition is an important evolutionary force shaping the composition of communities. One exception concerns competitive exclusion, which could be demonstrated experimentally through introductions of species absent from certain habitats or geographical ranges. I prefer to discuss the effects of interspecific competition according to the time scale over which they operate and will consider “ecological” effects and “evolutionary” effects. I realize that it is not always easy to separate between them, that given sufficient time one will lead to the other, and that several responses may occur together (Thomson 1980). Tit studies provide examples of all types of responses, although not all are equally convincing nor have they all been explained in the same way.

ECOLOGICAL EFFECTS OF INTERSPECIFIC COMPETITION

Numeric responses.—Although it is now considered that niche shifts are sufficient to conclude that interspecific competition does exist (see below) the older competition theory, based on equations such as the Lotka-Volterra equations, implied that numeric responses were needed before one could conclude as to the existence of competition. Very little literature showing such effects in birds, however, is available, perhaps because such data can be collected only over a much longer time period than data on niche shifts.

The Black-capped Chickadee and the Tufted Titmouse

One very interesting example is the study of the dynamics of a Black-capped Chickadee (Parus atricapillus) population for over 25 years by Loery and Nichols (1985). In the course of their study, the Tufted Titmouse (Parus bicolor) became established in their study site through natural expansion. They found that, following the establishment of the titmouse population, the chickadee population showed a short term (one
Fig. 1. Changes in population size (numbers), adult survival rate (survival) and numbers of immigrant birds (recruits) in a Black-capped Chickadee population before (filled symbols) and after (open symbols) the invasion by Tufted Titmice. The large circles indicate the value for the first year of the invasion. Horizontal lines represent average values for five-year periods before and after the invasion. Numbers and significance values as given by Loery and Nichols (1985).

year) but significant reduction in population size caused by a reduction of both the survival rate and the number of recruits (Fig. 1). They found, however, no long-term effect on population size, although when comparing the five-year periods before and after the establishment of the titmouse, a significant decrease in survival rate and a significant increase in number of recruits was found. As they pointed out (p. 1201), this
“natural experiment,” although highly suggestive for the existence of one-way interspecific competition between the Tufted Titmouse and the Black-capped Chickadee, is not conclusive. If we assume, for the sake of argument, that interspecific competition caused the changes in the population parameters of the Black-capped Chickadee, then we would conclude that the immediate numeric effect in the year following the establishment of the Tufted Titmouse was quite strong because both adult survival and recruitment of new birds was very low. The birds responded, however, very rapidly to the new situation whereby from the second year onwards, the number of recruits increased significantly but adult survival remained low. From the second year onwards after the settlement of the Tufted Titmouse, the increase in recruitment quantitatively compensated for the reduced survival, so that population size before and after the arrival of the titmouse were similar again, although the proportion of juveniles in the breeding population would have increased.

Great Tits and Blue Tits during the Breeding Season

The second example of interspecific competition between two tit species, the Great Tit and the Blue Tit, stems from my own work. The interesting aspect of this case is that, because these two species breed easily in nest-boxes, data are relatively easy to collect, and experimental manipulations have been carried out in the field. Furthermore, it is a rare case of a two-way doubly asymmetric interaction whereby during the breeding season the smaller Blue Tit is competitively superior (Dhondt 1977), and whereas during the non-breeding season the larger Great Tit has the upper hand (Dhondt and Eyckerman 1980a, b). Most probably this double asymmetry is a powerful stabilizing force which makes the coexistence of Great and Blue tits stable. This idea is supported by the analysis of Parus assemblages in European passerine bird communities by Herrera (1981). He found that in 78 out of 85 communities, in which at least two tit species were present, both Great and Blue tits were observed. In five communities, the Great Tit was present without the Blue Tit, and in one neither was present. In three communities, in which only one Parus species was present, neither Great nor Blue tits were found. These two species are thus both present in almost all situations throughout Europe in which tits are able to live.

During the breeding season, the Blue Tit has a negative effect on the reproduction of the larger Great Tit through exploitative competition for food. Both species feed mainly on the same species of caterpillars, but the Blue Tit eats the smaller instars, thus eating the food of the Great Tit before it becomes available for the larger species. Dhondt (1977) has shown for the Ghent study that significant negative correlations exist between Blue Tit breeding density and Great Tit reproductive rate (number of fledglings per pair and per season), mainly through an increased
nestling mortality in first broods and a reduction in the proportion of breeding pairs that start a second brood after having successfully raised a first brood. No reverse effect was found. Minot (1981) confirmed Dhondt’s conclusions in part for the Oxford populations, showing that fledging weight, a good predictor of juvenile survival, was also inversely related to Blue Tit density. He also provided experimental evidence by manipulating Blue Tits. He removed all Blue Tit nestlings from one section of the woods and added them to another, keeping a third area as a control. He found that Great Tit young were significantly heavier in the area from which Blue Tits had been removed, compared to the two other areas, but he found no difference between the supplemented area and the control area. Török (1987) performed an interesting experiment in which he manipulated densities of Great and Blue tits in three plots, so that in the control plot both species could breed, and that in each of the experimental plots only Great or Blue tits bred. Over the three years of the experiment, he found no adverse effect of the Great Tit on the Blue Tit, confirming what Dhondt (1977) had found. He found no effect on the clutch size nor on the fledging success of the Great Tit and showed that Great Tit fledging weight was lower in the plot with Blue Tits compared to that without. This was, however, true only in two out of three years, which suggests that the importance of interspecific competition for food during the breeding season varies according to local conditions.

Additional effects of interspecific competition during the breeding season have also been found (Table 1). Thus Clobert et al. (1988) demonstrated non-experimentally that survival rate of male (only first year birds) but not of female Great Tits is negatively related to density of Blue Tits. Den Boer-Hazewinkel (1987) found that by experimentally removing Blue Tits before the start of the first brood, a higher proportion of the Great Tits will produce a second clutch, thus raising more young in a season. This suggests that some effects of competition operate over a longer time period. All these effects are probably the result of exploitative competition, although the result obtained by Clobert et al. (1988) is puzzling. They explained it as being caused by interference competition, whereby male Great Tits would have to expend more energy in territory defense, when Blue Tits are more numerous. My data from the Antwerp study showed that in the period 1979–1982, the adult survival rate of breeding Great Tits of both sexes differed between two experimental plots differing in Blue Tit but not in Great Tit density. Thus in Plot T (low Blue Tit density) adult survival was 54.5% (N = 220), but it was only 45.7% (N = 278) in Plot B (high Blue Tit density) (3-way G-test with Williams correction, effect sex: partial G = 0.135, 1 df NS; effect Plot: partial G = 3.845, 1 df, P < 0.05; Dhondt, unpubl. data).

No effects of Great Tit on Blue Tit reproduction have as yet been
Table 1
A Summary of the Effects of Blue Tit on Great Tit During the Breeding Season

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<td>Fledglings/egg</td>
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<td>Percent two broods</td>
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<td>Fledglings/pair</td>
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<td>NS</td>
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<td>+&lt;sup&gt;b&lt;/sup&gt;</td>
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Notes: NS: no effect shown; +: significant effect; 0: effect not considered.
<sup>a</sup> Effect detected in two years out of three.
<sup>b</sup> Effect detected in yearling males only.
<sup>c</sup> Effect detected in both sexes.

...demonstrated when nest sites are superabundant, although Löhrl (1977) and Minot and Perrins (1986) have shown that the two species compete for nest sites if these are a limiting resource. This would be the result of interference competition, whereby the larger Great Tit would be more successful at securing nest sites than the smaller Blue Tit. Löhrl (1977) observed in several cases that when he hung a very low density of large-holed boxes in an optimal habitat, Blue Tits were killed by the Great Tits inside the nestboxes, emphasizing that interference competition could be rather vicious.

The data on interspecific competition between Great and Blue tits during the breeding season in six different studies, four of which are experimental, and in four different countries, all show that Blue Tits adversely influence one or more Great Tit population parameters (nestling survival, nestling weight, proportion of second broods, reproductive rate, adult survival). It can thus be concluded that there is strong evidence, both correlative and experimental, that during the breeding season Blue Tits adversely affect Great Tit reproductive output or effort. The exact parameter which is influenced, however, varied between studies, and competition could not be demonstrated in all years. Competition during the breeding season seems to be the result of exploitative competition for food.

Great Tits and Blue Tits outside the Breeding Season

Dhondt and Eyckerman (1980a, b) have shown experimentally that when Great Tits were excluded from the nestboxes in a plot by reducing
the size of their entrance hole to 26 mm, which made the boxes unsuitable for Great Tits but not for Blue Tits, the breeding density of the Blue Tit increased in the following breeding season by a factor of almost two and remained high for at least five years (Dhondt 1985). Although they showed that the number of Blue Tits roosting in nestboxes during winter increased when Great Tits had been excluded, their data were inadequate to determine what changes in population parameters caused this increase in Blue Tit density. A similar experiment by Löhrl (1977) gave a similar result, although he had no control area. He concluded, however, that the breeding density he observed (almost 4 pairs per ha) had never been found in any other study. That food could be involved in this winter competition was shown experimentally by Krebs (1971) who found that in a study plot in which food was added during winter, Blue Tit breeding numbers had increased in the next breeding season, whereas they had decreased in a control plot. Källander (1981), however, repeated a similar experiment in two different years and found that in one year Great Tit numbers increased in the plot with extra food, but he found no influence on Blue Tit population size. The importance of winter competition for food between Great Tits and Blue Tits therefore, seems to be limited. Intraspecific competition among Great Tits for food during winter also depends on the amount of natural food (beech mast) available and does not seem to influence all age classes in the same ways (van Balen 1980).

I started the Antwerp tit project in 1979, using the earlier conclusions to manipulate the level of interspecific competition. This allowed me to determine what differences, other than density, exist between Blue Tit populations in optimal habitat, exposed to or protected from Great Tit interspecific competition. The mechanism of winter competition is to a limited extent for food, but there certainly is greater competition for roosting sites. When nestboxes were made unsuitable for Great Tits, Blue Tits suddenly used them for roosting during winter in large numbers (Dhondt and Eyckerman 1980a, Dhondt, unpubl. data).

Dhondt et al. (1982) have shown that in a high density area, Blue Tit territories covered the entire plot, whereas in the low density plot open space remained between the territories. In such low density areas, therefore, Blue Tits seem to be winter limited (through interspecific competition), whereas in the high density areas they seem to be summer limited (through intraspecific competition). Although the complete analysis of the results has not yet been performed, I will present some conclusions that are already clear. These are based on the comparison of two study plots, about 600 m apart, both of about 12 ha (B and T) in the Peerdsbos, a wooded estate of ca 150 ha near Antwerp. In both plots, nestboxes were superabundant. In Plot B the nestbox configuration remained unchanged
throughout the study period, with 118 large-holed and 59 small-holed nestboxes which provided Blue Tits with a refuge from the winter competition by Great Tits. This resulted in Great and Blue tit populations at high densities. In Plot T 80, 120 large-holed nestboxes were available later in the breeding seasons of 1979–1983, and 120 small-holed nestboxes since then. In Plot T, during the first five years, Great Tit densities were high, and Blue Tit densities low compared to Plot B (1.83 pairs per ha, and 2.42 in Plot B). In the following four years, Great Tit density was very low, and Blue Tit density high (2.75 per ha compared to 2.46 in Plot B). The breeding densities of Blue Tits were thus as expected from the experimental results obtained by Dhondt and Eyckerman (1980a) at Ghent and reflected the expected effects of interspecific competition. Nearly all breeding birds were trapped on the nest, so that complete data were available on reproduction, local recruitment (recruitment of locally born breeding birds into the breeding population), immigration (recruitment of non-local birds into the breeding population), and adult survival.

This experiment provides information on the effect on interspecific competition of Great Tits on Blue Tit population parameters. Plot B is kept as a control. Plot T was changed from a low density, high interspecific competition situation (first period) to a high density, low interspecific competition situation (second period). The main findings are that (Dhondt, unpubl. data): (1) there is no clear difference in reproductive rate (number of fledglings per pair and per season) between the plots, nor between the periods in Plot T; and (2) there is a difference in adult survival rate. For both sexes combined the survival in Plot B was 35.6% (N = 191) in period 1 (1979–1982) and 27.6% (N = 225) in period 2 (1983–1986). This decrease in survival, that was also observed for Great Tits and in a third Blue Tit area, was probably caused by three severe winters. In Plot T, however, the survival increased from 34.5% (N = 139) in period 1 to 37.6% (N = 223) in period 2. During period 1 the survival rate did not differ between the plots ($G = 0.040, 1$ df, NS), but during period 2, survival was significantly higher in Plot T ($G = 5.207, 1$ df, $P < 0.05$). This suggests that through the experimental reduction of the interspecific competition by Great Tits in the second period in Plot T, adult survival of the Blue Tits increased, although Blue Tit density had also increased. (3) In males, but not in females, the proportion of local recruits in the breeding population increased in Plot T in the second 4-year period (1984–87) compared to the first 4-year period (1980–1983), although it decreased in Plot B. A two-way ANOVA on the proportion of local recruits (angular transformation), with plot and period as the factors, yields a significant plot × period interaction ($F = 14.106, 1,15$ df, $P < 0.01$), showing that through the change in the experimental setup in Plot T, local born males made
up a larger proportion of the breeding recruits. (4) In males, but not in females, the proportion of immigrant recruits decreased in Plot T but increased in Plot B. A two-way ANOVA again shows that a significant interaction plot × period existed ($F = 11.177, \text{df} = 1,15, P < 0.01$). Immigrant males thus formed a smaller proportion of the breeding population in Plot T during the second period when breeding density had increased through a reduction of the interspecific competition, whereas this was not the case in Plot B.

The effect of Great Tit interspecific competition on Blue Tit population parameters thus operates mainly on the juvenile males, since fewer juveniles recruit locally in the low density situation with interspecific competition, and a larger proportion of the breeding population has therefore emigrated. Adult survival of both sexes also seems to be higher in the high density situation. A low density Blue Tit population suffering from interspecific competition by the Great Tit, therefore, has a larger genetic turnover compared to a high density population protected from the Great Tit.

It is interesting to underline that, in essence, this is the same result as the one obtained by Loery and Nichols (1985), who found that the Black-capped Chickadee population had a lowered adult survival, but an increased immigration after the Tufted Titmouse arrived. In their case, these changes compensated one another, so that local population size remained unchanged. In the Blue Tit, changes in the population parameters did not compensate one another, so that an increase in the breeding population was observed.

The Foraging Niche of Tits in the Presence and Absence of Congeners

Changes in foraging niche have been used extensively to provide evidence that interspecific competition exists and were recently reviewed by Alatalo (1982) and Alatalo et al. (1986). In the context of the reasoning developed in this paper, I want to differentiate between “functional” and “evolutionary” responses.

Examples of functional responses are relatively few. If they exist, they must be found in single study plots in which on different territories the flock composition differs. The advantage of studying tits is that many species defend group territories in winter and that the group territories of many species overlap to a large extent. The differences in flock composition may be natural or experimental.

A first example is provided by Alatalo (1981). He observed that in mixed-species winter flocks in one study area in northern Finland there was a clear niche shift of the Willow Tit (P. montanus) in relation to the
presence/absence of individuals of a more dominant species (Crested Tit [P. cristatus]), in which the Willow Tit shifted away from the species of trees occupied by the Crested Tit in flocks in which it was present, as compared to neighboring flocks in which it was absent. Similarly, Willow Tits shifted away from the parts of the trees occupied by the Great Tit or by the Crested Tit when these were present in the same flocks. Alatalo et al. (1985, 1987) experimentally confirmed the existence of interspecific competition for foraging sites in winter. In an area in which Willow, Crested, and Coal tits (Parus ater), and Goldcrest (Regulus regulus) spent the winter together in mixed-species flocks of constant composition, they reduced the number of Willow and Crested tits which mostly use the inner parts of the trees (Alatalo et al. 1985) and reduced the smaller species which mainly feed on the outer parts of the tree in a second experiment (Alatalo et al. 1987). In both experiments, they observed an increase in the use of the tree parts vacated by the removed species. Thus, the smaller Coal Tit and Goldcrest increased their foraging in the inner canopy when the larger Crested and Willow tits had been removed. They repeated this experiment in three experimental plots, having at the same time observations from three control plots. This convincingly showed that interspecific competition existed against the smaller species. The reverse experiment, i.e., the removal of the smaller species resulted in an expansion of the foraging of the larger species at the end of winter towards the outer parts of the tree. This was true for both Willow and Crested tits in pine trees but for the Crested Tit only in spruce trees. Alatalo et al. (1985) have thus shown that in winter there is two-way interspecific competition between Crested and Willow tits on the one hand and between Coal Tits and Goldcrests on the other. Exploitative competition was certainly involved in the niche shift of the larger species. In the smaller species, it could have been interference competition, exploitative competition, or both. In a cage experiment, Alatalo et al. (1986) showed that the smaller Coal Tits used the outer parts of the tree in the presence of Willow Tits but used inner parts in their absence. Willow Tit tree use did not differ in relation to the presence or absence of Coal Tits. It should be emphasized that in these examples no experimental evidence is given for competition between Willow and Crested tits (but see below).

A second example stems from observation in Belgium. It demonstrated that at high wind velocities tits shift their foraging sites. Such a niche shift also happens in relation to temperature (Grubb 1978), but the interesting feature of the wind effect is that strong winds are usually of short duration, so observations on different days are, on the whole, independent of one another because they are separated by days with normal wind. The studies of Ysenbaardt (1987) and Lens (1988) on Crested and Willow tits
in a pine forest in northern Belgium showed that on days of low wind velocity, the foraging niches of the two species were not affected by the presence of the second one. However, on days of high wind velocity (>10 m/sec) Willow Tits in territories without Crested Tits significantly shifted their foraging sites to lower and more inner parts of the trees. Crested Tits also shifted their foraging sites to a lesser extent, towards lower and more inner parts of the tree; but Willow Tits on territories with Crested Tits moved up and out. Lens (1988) simultaneously observed an increase in the number of chases of Willow Tits by Crested Tits, suggesting that interspecific intolerance was the direct cause of the displacement of Willow Tits from more preferred parts of the tree, but only under conditions of environmental stress.

These examples show that, in coniferous habitats at least, interspecific competition between tits exists in ecological time. Although the observed changes in niche use were not related to changes in survival, it is probable they would have such an effect, since two experimental studies have shown that overwinter survival increased when additional food was offered dur-
ing winter. This shows that small tits in climatically extreme environments are food limited during winter (Willow and Crested tits in Sweden: Jansson et al. 1981; Black-capped Chickadee in Wisconsin: Brittingham and Temple 1988).

Evolutionary Effects of Interspecific Competition

Evolutionary effects cannot normally be experimentally demonstrated because of the time scale involved. Evidence, therefore, must be circumstantial, but if this evidence shows a pattern that is as predicted from the ecological effects of competition, it can become very convincing. In some of the examples below it is unclear what is the exact time scale involved. I have included them in this section because no experimental evidence is available yet which shows that interspecific competition does actually occur between the species discussed. Four categories of evidence are normally used: (1) Allopatric distribution of sibling species, (2) Habitat segregation and non-random assemblage of congeners in communities, (3) Niche segregation in sympathy and divergence of niches in sympathy compared to allopatry, and (4) Character displacement. Many of these arguments are discussed in detail by Lack (1971), and I will refer only to arguments published since then. Lack concluded (p. 36): “The European tits were selected for ecological study because of their apparent complexity, and in particular because several species usually coexist in the same habitat. Nevertheless, each species is segregated from every other, in a few cases by geographical range, in many by habitat, and in yet more by a difference in food and feeding stations in the same habitat. Differences of this last type are associated with adaptive differences in overall size and in size of beak, the larger species tending to feed lower down, and on larger insects and harder seeds, than the smaller species. Likewise the species which live in coniferous forest have longer and narrower beaks than those in broad-leaved woods. Some species have a different, or unusually wide, habitat in a small part of their range, often linked with the absence of another species, and the beak may be appropriately modified.” Lack believed that segregation by range or by habitat is the result of competitive exclusion. This exclusion need not be because of competition with congeners alone, but it can also be the result of competition with a group of other passerines. A nice example of interspecific competition for space between the Great Tit and the Chaffinch (Fringilla coelebs) on a small island off the coast of Scotland was recently described by Reed (1982).

Community Composition of Tits in Europe

Herrera (1981) analyzed 88 European passerine bird communities in which at least one species of Parus was present. He found that only about
one third of all possible combinations with the six available species were observed, whereby mean interspecific difference in bill length was significantly higher in the combinations which were observed. He concluded that the _Parus_ assemblages were the result of competitive interactions for “some sort of complex combination of prey size, prey type and micro-habitat,” whereby species absent from assemblages were excluded through interspecific competition.

The Foraging Niche of Tits in Sympathy and in Allopatry

Sympatric species of tits often use different habitats and are thus, in Lack’s terminology, ecologically segregated by habitat. Among European tits, 32% are isolated by habitat (Lack 1971, p. 59). Habitat use differs, however, over the geographic range of the species. Thus, for example, Blondel (1985) has shown that the three tit species that breed on the island of Corsica strongly broadened their habitat niche compared to those on the mainland. Other examples concern the Willow Tit, that is limited to coniferous habitats in Scandinavia, but is a regular breeder in deciduous habitat in Western Europe, and of the Crested Tit that occasionally uses broad-leaved habitat in western and southern Europe but never in Scandinavia. Such species are ecologically segregated from congeners by habitat in part of their range but by feeding niche in others (cf. Lack 1971, p. 261). These observations give no solution to the problem of whether competition exists today, or whether the actual situation is the result of adaptation to local situations under the influence of competition in the past. However, Alatalo and Lundberg (1983) concluded, as a result of aviary experiments in which Marsh (_Parus palustris_) and Willow tits were given a choice to forage on oak or spruce branches, that in Scandinavia, Willow Tits would be competitively excluded from deciduous habitat by the presence of Marsh Tits.

The foraging niches of tits, especially during winter, are very well studied. Essentially all authors find that the average foraging niche differs between coexisting species but that there is a considerable amount of overlap. Lack calculated that 43% of the European tits are ecologically segregated by feeding station (Lack 1971, p. 59). The interpretation of such non-experimental data can be that these differences are the result of interspecific competition in the past, and permits coexistence with no significant competition (Gibb 1954, Lack 1971) or that they still lead to interspecific competition for food in the present day. This latter point of view is the more popular today, and evidence for it has recently been reviewed by Alatalo (1982) and by Alatalo et al. (1986). The argument is that when one compares the foraging niche of a species in sympathy and in allopatry with a second species, a divergent niche shift in sympathy is suggestive of the existence of interspecific competition in sympathy. Ala-
talo et al. (1986) accept that "differences in the biotic or abiotic environment, irrespective of the presence or absence of putative competitors, may produce changes in foraging sites. The question is whether environmental causes can create general tendencies toward divergent rather than convergent changes." Alatalo et al. (1986) found such a general tendency towards divergence in sympathy and therefore concluded that non-experimental data demonstrate that interspecific competition does exist between sympatric tits. The problem with this kind of evidence is that, although it will convince the convinced, researchers who do not believe that interspecific competition is continuously important on an ecological time scale, might argue that the differences one finds when comparing sympatric and allopatric foraging niches could be the result of an evolutionary response rather than of an ecological response as defined above, and simply confirm Lack's thesis.

In conclusion then, during winter some species of sympatric tits living together in the same habitat compete interspecifically for preferred foraging sites. This conclusion is supported by all categories of arguments summed up above, i.e., segregation by range, by habitat or by feeding station, which can all be interpreted as having come about because of interspecific competition. This implies that the composition of passerine communities would be affected, to an important degree, by interspecific competition. These arguments by themselves do not tell us how often this competition takes place.

Character Displacement

The final part of this review addresses evolutionary changes in tit population which could be explained through effects of interspecific competition. Lack (1971) summed up the examples of character displacement known in tits, in which the clearest example was that of the Blue Tit in the Canary Islands (Lack and Southern 1949). Two more recent examples have also been found.

Herrera (1978) described a situation in southern Spain in which he studied tits in two neighboring evergreen broad-leaved oak woodlands 175 km apart. In one locality he found only Great and Blue tits and in the other also the Crested Tit, although the passerine communities of the two areas were otherwise identical. He found a clear example of a character shift in the bill lengths mostly of Blue Tits. In zones of sympathy, the bill length of Blue Tit and Crested Tit differed by 0.75 mm, whereas in allopatri the difference was only 0.1 mm. Great Tits showed no differences in bill length between the two populations. These changes in morphology coincided with niche shift in foraging sites, in which the Blue Tit food niche was more compressed in the three-species locality. Surprisingly, the numeric response was not as expected, since in the two-species locality
Blue Tits were relatively more abundant and Great Tits relatively less abundant than in the three-species locality.

A second example concerns the Coal Tit on the Swedish island Gotland (Alatalo et al. 1986). There, Coal Tits are larger than on the mainland, in the absence of demonstrated competitors, since both the larger Crested and Willow tits are absent on Gotland. Again, the change in morphology coincides with a shift in foraging niche, in which the larger Coal Tits of Gotland forage more on the inner parts of the trees, while on the mainland they feed mostly on the outside of the tree and on needles.

Both examples show that when tit communities differed, this coincided with a change in morphology in allopatry so that the smaller species was larger. The most likely explanation of these observations is that through the absence of competitors of different species, there was a selective pressure for the smaller species to become larger. In Spain, the larger species (the Great Tit) did not change in morphology. In Gotland, the effect of increased intraspecific competition was illustrated very nicely, with the larger males showing the strongest change in foraging niche. A question that has not been answered yet is, how rapidly does such a change occur, or, in other words, can such a morphological change in relation to interspecific competition be experimentally induced?

In order to answer this question consider my Antwerp studies of Blue Tits, experimentally subjected to different levels of interspecific competition by Great Tits. When I began investigations in 1979, I knew that body size was heritable, at least in Great Tits (Garnett 1976), and that environmental changes could result in micro-evolutionary changes in Great Tit body size (Dhondt et al. 1979). I confirmed experimentally that Blue Tit tarsus length was heritable in my populations (Dhondt 1982, 1988). If interspecific competition were a powerful selective force on body size, I expected a rapid divergent micro-evolutionary change in body size between populations subjected to different levels of interspecific competition. I therefore studied the between-year variations in tarsus length of Blue Tits in three populations subjected to different levels of intra- and interspecific competition. My study started after an extremely cold winter (1978–79), and during the course of the study, four other cold winters were observed. I did observe relatively large between-year variations in nestling tarsus length that, however, were parallel in the three plots, but I found no differences between the plots (Dhondt 1988). These differences were the result of differences in body size of the recruits into the breeding population in relation to winter cold; after cold winters, both male and female recruits were larger, and since recruits made up between 50 and 70% of the breeding population, the body size of nestlings was larger after cold winters (Dhondt, unpubl. data). Since no differences could be demonstrated between plots, interspecific competition could not be shown to
have had an effect on the body size of the birds. In this situation of non-isolated populations subjected to different levels of interspecific competition, it did not cause divergent micro-evolution between the plots.

In conclusion, I think there is a considerable body of evidence that among tits interspecific competition exists in ecological time. A population suffering from interspecific competition shows a larger population turnover caused by a reduction in adult survival, a reduction in juvenile local recruitment, and an increase in recruitment through immigration. The effect may influence only one sex (males) or age-class (juveniles). If population size is limited through intraspecific competition during the breeding season, this will not cause an increase in the size of the breeding population but only a change in the age composition. In one of the two examples a decrease in population size in the population with interspecific competition was observed, in the other, this was not observed. This suggests that interspecific competition acts via a reduction in apparent habitat quality to the species suffering from this interaction. If, as is the case for Blue Tit and Great Tit, the interspecific competition influences both species but in an asymmetric way and in different seasons. This competition seems to have a stabilizing effect that promotes coexistence. In order to stand, however, this conclusion will have to be tested in appropriate models (P. Chesson pers. commun.).

Interspecific competition also leads to a narrowing of the niche space available, mainly in the winter season when food is probably limiting. Some experimental evidence proves this for a small number of European tits living in conifers. Much circumstantial evidence suggests that this is generally true. The effect of interspecific competition during only one season, in which the larger species usually are dominant, may have a destabilizing effect, which can lead to competitive exclusion of the subordinate species. In Scandinavia, some habitats contain only one species of tit (Hogstad 1978). Recent experiments in Norway (Steinar Helle, in litt.) suggest that on small islands, Willow and Crested tits competitively exclude one another. Willow Tits introduced on islands of the west coast of Norway, on which only Crested Tits lived, nearly all disappeared. Two that remained did not breed. The size of the Crested Tit population was not affected.

ACKNOWLEDGMENTS

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SEASONAL AND DIURNAL BODY WEIGHT VARIATIONS IN TITMICE, BASED ON ANALYSES OF INDIVIDUAL BIRDS

Svein Haftorn

ABSTRACT.—The main aim of this study was to test different graphical models showing possible patterns of seasonal and diurnal body weight cycles in passerines as proposed by Lehikoinen (1987). About 13,300 weight records of five different European tit species (Great Tit Parus major, Blue Tit P. caeruleus, Coal Tit P. ater, Marsh Tit P. palustris, Willow Tit P. montanus) were collected in the period from August 1987 to April 1988 at two study areas in central Norway (61°40' and 63°15'N). To get sufficient weight data at desirable times of the day (in the early morning, at noon, and in the evening), an electronic balance was used as a bird table. The data collected allowed an analysis of the weight cycles for individual birds. Most birds, regardless of species, followed the “winter fattening strategy,” i.e., both the morning weight, noon weight, and evening weight increased during autumn, reached a midwinter peak (usually in December), and then declined. One dominant Great Tit male deviated from this pattern and decreased in weight from September onwards, apparently for reasons other than starvation or competition with other birds. This trend may be related to its high-ranking status in the social hierarchy. It is argued that the weight variations in titmice are controlled by the photoperiod and air temperature, with photoperiod as the prime factor.

For quite some time it has been known that the body weight of many birds living in the northern temperate zone increases during the autumn, reaches a peak in midwinter and declines as springtime approaches. This trend applies, for example, to titmice (e.g., Haftorn 1951, 1976, 1982; Kluyver 1952; Owen 1954; Lawrence 1958; van Balen 1967). It is generally agreed that these variations in weight mainly are due to changes in fat content (Lawrence 1958, Chaplin 1974, Lehikoinen 1986; see also King 1972). Superimposed on this seasonal variation in body weight there is a marked diurnal variation. The birds build up a fat reservoir during the day for use during the coming night.

In some recent studies Lehikoinen (1986, 1987) has put forward four graphical models to illustrate the possible relationship between the seasonal and the daily variation in body weight (Fig. 1). According to model a, the birds only compensate for the nightly weight loss. Consequently, the morning weight decreases in winter, while the evening weight remains stable. If, however, the bird overcompensates, other possibilities exist. In model b, the bird makes only a partial compensation for the expected weight loss during the following night. The amplitude of the daily weight

1 Dept. Zoology, the Museum, Univ. Trondheim, N-7004 Trondheim, Norway.
cycle increases, but the morning weight still falls. In model c, there is a full compensation for the expected weight loss, and consequently the morning weight remains stable. In all three models there is a daily stable point in body weight, either in the evening (a), on average (b), or in the morning (c).

Models a and b seem to be unrealistic because the safety margins are smallest in midwinter, just when the environmental conditions presumably are severest. Model c, on the other hand, seems to be biologically relevant. If, however, the bird overcompensates excessively, both the daily minimum, the average, and the maximum weight will increase in winter (model d). As Lehikoinen (1987) points out, true winter fattening can be achieved only through model d. In practice it is not easy to distinguish between models c and d. Lehikoinen (1987) emphasizes that an analysis based on weight records made at random times during the day can easily give an impression of true winter fattening, although the bird might be following model c, which assumes that the morning weight is stable. Both models assume an increase in the average winter weight. So, by simply looking at weight curves that show daily average weights, it is impossible to discern which of the two models the bird follows.

Birds whose weight pattern fits model d are considered by Lehikoinen (1987) to have adopted the "winter fattening strategy." This strategy presumably improves the survival chances for birds faced with unstable or unpredictable food resources in winter. On the other hand, the condition for adopting model c, the "constant morning weight strategy," is secure access to food throughout the winter.

Up to now, weight data for titmice have been obtained by catching the birds in traps or nets. In this way it is very difficult to get enough records at desirable times of the day, and in practice it is impossible to record weight curves for individual birds. Researchers have therefore been compelled to pool the data for several individuals and deal with the problem on a population level. Nevertheless, by using regression analyses Lehikoinen (1987) was able to establish substantial support in favor of model d, i.e., that both the morning and the evening weights increase in winter.

However, a safer way of testing the weight models would be to avoid estimated weight data and instead to weigh the birds at the correct times of day. These would include weighing the same birds in the early morning, just after roosting time, and then once again in the evening, just before the end of the daily activity period. To obtain enough data of this kind, it is hopeless to rely on usual methods of catching birds. Birds become shy after having been handled a few times. Furthermore, frequent handling disturbs them and may lead to an abnormal weight development. So it is necessary to find an alternative method of obtaining weight data for
Fig. 1. Four graphical models showing the possible relationship between seasonal and diurnal variations in body weight. Horizontal broken line symbolizes an assumed constant minimum weight level which the birds just can tolerate. The daily weight amplitude is considered to be a direct function of night length, while air temperature is assumed constant. Further explanation in the text. (After Lehikoinen 1987).

free-living birds. Fortunately, such a method is readily obtainable. One can simply use an electronic balance as a bird table.

The main aim of this paper is to test the graphical models proposed by Lehikoinen (1987) and to look for possible interspecific differences.
STUDY AREAS, MATERIALS AND METHODS

I collected data regularly throughout the winter at two different sites in central Norway, in a conifer-dominated forest at Klaebu (63°15’N) near Trondheim at about 160 m above sea level, and in the birch region at Venabu (61°40’N) at about 900 m above sea level. Altogether 13,291 weight records were collected from August 1987 to April 1988 inclusive, for the following five species of titmice, the Great Tit (Parus major), the Blue Tit (P. caeruleus), the Marsh Tit (P. palustris), the Willow Tit (P. montanus), and the Coal Tit (P. ater) (Table 1). These are all common resident birds in Scandinavia. The Coal Tit is definitely the smallest, weighing only about 9–10 g, and the Great Tit the biggest, weighing about 17–21 g. All five species were present at Klaebu. At Venabu only the Willow Tit was recorded.

The electronic balance used for recording the body weights was a battery operated Sartorius model with an accuracy of 0.1 g. This was placed in a windshield, a box with one side open, outside the observer’s house or hut. I could thus sit behind the window and read the data from a distance of a few meters. To attract the birds, a piece of solidified fat embedded with sunflower seeds was placed on the balance. All visiting birds were individually colorbanded. I used a flashlight to see the birds and the balance properly in the poor morning and evening light during the winter. Only birds which remained on the balance until it had stabilized were recorded.

I obtained weights at both study areas during the first and the last hour of the birds’ daily activity period. At Venabu, I also collected weight data during one hour around noon (12:00 h ± 30 min). Only the weights of birds which regularly visited the balance are used in the present paper.

When calculating daily weight gain and nightly loss, respectively, I used principally the records made the first and the last 20 min of the daily activity period. Because of the geographical latitude of the study areas, in midwinter the birds had only 6–7 h at their disposal for foraging.

The climate during the winter 1987–88 was unusually mild, with little snow in the Klaebu study area. The average temperature of the coldest month (February) was −3.4°C and never fell below −20°C. At Venabu the temperature was somewhat lower, with a mean of −7 to −8°C for the coldest months (during my periods of stay in December–March), but even here only a few really cold spells occurred, with temperatures down to about −20°C. On the other hand, there were heavy snow falls, 1–2 m deep, at Venabu.

RESULTS AND DISCUSSION

In the present paper I deal with the birds individually and have in no cases pooled the data for different birds.

Seasonal weight variation.—The weight of most of the birds I studied, regardless of species, increased gradually toward a midwinter peak in December. As seen in Figs. 2–4 the winter increase does not apply only to the mean daily weight, a result in line with earlier findings (e.g., Haftorn 1951, 1976, 1982; Kluvyer 1952; Lawrence 1958; van Balen 1967; Lehikoinen 1980), but also to the morning and evening weights, as well as to the noon weight (Fig. 2A–C). This pattern is consistent with Lehikoinen’s (1987) model d, or “the winter fattening strategy.” On the other hand, I found no clear evidence that any birds adopted the “constant morning weight strategy,” although in some cases the morning weight was
Table 1

Number of Body Weight Records from August 1987 to April 1988, Inclusive

<table>
<thead>
<tr>
<th>Species</th>
<th>Klaebu</th>
<th>Venabu</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great Tit</td>
<td>2309 (16)*</td>
<td>—</td>
<td>2309 (16)</td>
</tr>
<tr>
<td>Blue Tit</td>
<td>356 (5)</td>
<td>—</td>
<td>356 (5)</td>
</tr>
<tr>
<td>Coal Tit</td>
<td>875 (4)</td>
<td>—</td>
<td>875 (4)</td>
</tr>
<tr>
<td>Marsh Tit</td>
<td>2648 (6)</td>
<td>—</td>
<td>2648 (6)</td>
</tr>
<tr>
<td>Willow Tit</td>
<td>3860 (16)</td>
<td>3243 (14)</td>
<td>7103 (30)</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>—</td>
<td>13,291 (61)</td>
</tr>
</tbody>
</table>

* Number of different individuals is in parentheses.

relatively stable (Figs. 2D and 4A, C). This concerns especially one female Willow Tit, the morning weight of which showed no significant variation from November to April inclusive (analysis of variance, $P = 0.13$), but unfortunately, weight data from the period before November are completely lacking for this particular bird (Fig. 2D).

The degree of winter fattening can be illustrated by the difference found between the relatively low autumn weight and the winter peak weight. On the whole, the tits in this study increased their body weight by 2–8% from September–October to December. The question then arises as to whether any interspecific differences exist in the degree of winter fattening. According to Lehikoinen (1987), tits which store food increase their winter weight less than those which do not store. The tentative explanation is that food-storing tits have predictable food resources and are, therefore, less dependent on body fat deposition.

Fig. 5, however, lends no immediate support to this hypothesis. None of the Great Tits, a species which does not store food at all, increased their weight proportionally more than did the Marsh Tits or the Willow Tits, both of which are known to be food storers (Haftorn 1944, 1956b; Löhr 1955; Cowie et al. 1981). Of course, it may be claimed that even the Great Tits had a predictable food resource in the present study, because they were being artificially fed. It is doubtful, however, that such an arbitrary situation would have completely masked a strategy which presumably is inherited.

Whatever the interspecific relationship is, Fig. 5 shows another striking feature, namely the great variation between individuals of the same species. In fact, one male Great Tit did not put on weight at all during the period from September to April, but gradually lost weight throughout the winter (Fig. 4D). Does this mean that the bird suffered from a lack of food or from competition with other birds? Certainly not, this specific male Great
Fig. 2. Seasonal body weight variation (mean ±2 SE) of six Willow Tits. N = number of weight records.
Tit was, in fact, the dominant bird and chased all other birds from the table and always had free access to the food supply.

Two things can be learned from Fig. 4D. First, this particular male Great Tit does not fit any of the models proposed by Lehikoinen (1987). Second, the weight-change pattern of such odd birds would have remained totally undetected if all the data had been pooled and dealt with at a population level.

Diurnal weight variation. — I found the diurnal weight cycle to be of a considerably higher magnitude than the winter fattening cycle. The daily variation has been expressed as the difference between the evening and morning weights as a percentage of the morning weight. Whereas the degree of winter fattening by the tits usually amounted to only 2–8% of their autumn weight, and for some individuals was even negative, the daily weight increase was about 7–12% of the morning weight. Interestingly enough, some differences between species were noted in this respect.
Fig. 4. Seasonal body weight variation (mean ± 2 SE) of four Great Tits, one Blue Tit, and two Coal Tits. N = number of weight records.
Fig. 5. Increase of the morning and evening body weights, respectively, of four Great Tits, five Marsh Tits, and four Willow Tits, from October on to the weight peak in December (expressed in percentages).
(Fig. 6). The Great Tit, Blue Tit, and Coal Tit all showed a proportionately greater diurnal amplitude in body weight than the Marsh Tit and the Willow Tit, viz. 9–12% and 7–8%, respectively. The difference between the two groups is statistically significant (Mann-Whitney U-test, \( P < 0.001 \)).

It is noteworthy that the Coal Tit and the Great Tit, which are the smallest and the largest, respectively, of the present species both belong to the group showing the greatest weight variation. If this trio, the Great Tit, Blue Tit, and Coal Tit need relatively more energy than the Marsh Tit and the Willow Tit, as indicated by the present data, this would possibly have a negative impact on their winter survival rates. It may not be a mere coincidence that the former species lay relatively larger clutches and are fairly regular double-brooders, in contrast to the Marsh Tit and the Willow Tit. Another feature which characterizes the two groups is the degree of sedentariness. The Marsh Tit and the Willow Tit are known to be much more sedentary than the others. On the other hand, representatives of food-storing species are found in both groups, since in addition to the Marsh Tit and Willow Tit, the Coal Tit also regularly stores food (Haftorn 1956a).

As the days get shorter and the nights longer during the early winter,
Fig. 7. Mean (± 2 SE) daily gain and nightly loss, respectively, of the body weight of two Marsh Tits, one Great Tit, and three Willow Tits. Day length is the duration of the tits' activity period (monthly means).
<table>
<thead>
<tr>
<th></th>
<th>Daily weight gain in relation to</th>
<th>Nightly weight loss in relation to</th>
<th>Rate of daily weight gain in relation to</th>
<th>Rate of nightly weight loss in relation to</th>
</tr>
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<tbody>
<tr>
<td>Great Tit</td>
<td>juv ♀</td>
<td>0.55***</td>
<td>−0.37**</td>
<td>−0.11</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>0.60***</td>
<td>−0.07</td>
<td>−0.26</td>
</tr>
<tr>
<td></td>
<td>ad ♀</td>
<td>0.72</td>
<td>0.03</td>
<td>0.19</td>
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<td>juv ♀</td>
<td>0.74***</td>
<td>−0.39*</td>
<td>0.02</td>
</tr>
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<td></td>
<td>♀</td>
<td>0.85***</td>
<td>−0.24</td>
<td>−0.49*</td>
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<tr>
<td>Blue Tit</td>
<td>♀</td>
<td>0.80</td>
<td>−0.53</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>0.38</td>
<td>−0.34</td>
<td>−0.25</td>
</tr>
<tr>
<td>Coal Tit</td>
<td>♀</td>
<td>0.44***</td>
<td>−0.33**</td>
<td>−0.08</td>
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<tr>
<td></td>
<td>♀</td>
<td>0.59**</td>
<td>−0.40*</td>
<td>−0.43*</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>0.58***</td>
<td>−0.38*</td>
<td>−0.16</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>0.56*</td>
<td>0.06</td>
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</tr>
<tr>
<td></td>
<td>♀</td>
<td>0.77*</td>
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</tr>
<tr>
<td></td>
<td>♀</td>
<td>0.77*</td>
<td>−0.01</td>
<td>0.10</td>
</tr>
</tbody>
</table>

**Note:** The table presents Pearson correlation coefficients for the relationship between daily/nightly changes in body weight and duration of daily activity (day length), roosting time (night length), and air temperature. The entries represent the correlation coefficients, with significance levels indicated by *** (p < 0.001), ** (p < 0.01), * (p < 0.05), and signs indicating the direction of the relationship.
### TABLE 2
CONTINUED

<table>
<thead>
<tr>
<th></th>
<th>Daily weight gain in relation to</th>
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<th>Rate of daily weight gain in relation to</th>
<th>Rate of nightly weight loss in relation to</th>
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<td>Willow Tit</td>
<td></td>
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<td>juv ♂</td>
<td>0.47*</td>
<td>-0.04</td>
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<td>0.08</td>
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<td>0.37**</td>
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<td>(22)</td>
<td>(22)</td>
<td></td>
<td>(23)</td>
<td>(24)</td>
</tr>
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<td>-0.14</td>
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<td>juv ♀</td>
<td>0.81**</td>
<td>0.43</td>
<td>0.05</td>
<td>-0.37</td>
<td>0.21</td>
</tr>
</tbody>
</table>

* Number of records is in parentheses.

* *P < 0.05; **P < 0.01; ***P < 0.001.
at the same time as the air temperature falls, the birds theoretically need more energy to survive the night. The present data clearly confirm such a trend. Thus, the daily weight gain tends to increase as the winter proceeds and is, on the whole, greatest in midwinter, coincident with the shortest days and longest nights (Fig. 7). All the significant correlation coefficients for the relationship between daily weight gain and day length were negative in the present study, regardless of species (Table 2). Consistent with this trend, the correlation between the nightly weight loss and night length were positive (Table 2).

For those birds that survived the winter, there must have been a close relationship between weight gain during the day and the weight loss during night. This is confirmed by the data shown in Fig. 7 and Table 2.

An increase in the food requirement at the same time as the days are becoming gradually shorter must necessarily influence the feeding rate to a great extent. In fact, the feeding rate, expressed as the weight gain per hour, was about twice as high in the middle of the winter with the day length at its shortest, as it was in the autumn and the spring (Fig. 8, see also Table 2).

The rate of nightly weight loss, on the other hand, turned out to be fairly stable throughout the winter (Fig. 8). A closer look, however, does show a significant tendency in many birds for the rate of weight loss to vary inversely with night length (Table 2). This means that the birds used less energy per hour during the long nights in the middle of the winter than either before or after the solstice. How the birds managed to do that is unknown, but at least in the Willow Tit nocturnal hypothermia may play an important role (Reinertsen and Haftorn 1983). All the species in the present study showed this inverse relationship except the Coal Tit, but the data for this species were too few to be conclusive.

Factors regulating the body weight.—Winter fattening in titmice and other passerines is considered to be regulated by changes in air temperature and photoperiod (e.g., Evans 1969, Newton 1969, O’Connor 1973, King 1972, Haftorn 1976, Lehikoinen 1987). For tits at least, the photoperiod would seem to be the prime proximate factor, whereas the air temperature has only a moderate effect. Typically the birds gain in weight until the winter solstice. Up to this time body weight is inversely correlated with both day length and air temperature. From December onwards, however, the winter weight usually declines despite the continued fall in mean temperature.

I have previously suggested that this trend might be due to starvation (Haftorn 1951, 1976). But even if the tits have unlimited access to food, as when being fed artificially, many birds nevertheless start losing weight
Fig. 8. Monthly means (+ 2 SE) of the rate of daily body weight gain and nightly loss, respectively, for the same individuals as in Fig. 7. Day length is the duration of the tits' activity period (monthly means).
### Table 3

**Stepwise Regression Analyses of Evening Body Weight in Relation to Photoperiod (in Terms of Duration of the Tits’ Daily Activity) and Air Temperature (Mean Daytime Temperature)**

<table>
<thead>
<tr>
<th>Independent factors</th>
<th>Photoperiod</th>
<th>Air temp.</th>
<th>Multiple R</th>
<th>Standardized R²</th>
<th>N</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great Tit juv ♂</td>
<td>-0.48</td>
<td>0.39</td>
<td>0.50***</td>
<td>0.22</td>
<td>63</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Great Tit ♂</td>
<td>-0.37</td>
<td>ns</td>
<td>0.37*</td>
<td>0.12</td>
<td>47</td>
<td>Klaebu</td>
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<tr>
<td>Great Tit ad ♀</td>
<td>-0.62</td>
<td>ns</td>
<td>0.62***</td>
<td>0.36</td>
<td>29</td>
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<tr>
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<td>ns</td>
<td>0.42**</td>
<td>0.16</td>
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</tr>
<tr>
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<td>-0.68</td>
<td>ns</td>
<td>0.68***</td>
<td>0.45</td>
<td>39</td>
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<td>-0.47</td>
<td>-0.41</td>
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</tr>
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<td>Coal Tit ad ♂</td>
<td>-0.60</td>
<td>ns</td>
<td>0.60***</td>
<td>0.34</td>
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</tr>
<tr>
<td>Marhs Tit ♂</td>
<td>-0.68</td>
<td>ns</td>
<td>0.68***</td>
<td>0.45</td>
<td>75</td>
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</tr>
<tr>
<td>Marhs Tit ♀</td>
<td>-0.83</td>
<td>ns</td>
<td>0.83***</td>
<td>0.67</td>
<td>28</td>
<td>Klaebu</td>
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<tr>
<td>Marhs Tit ♀</td>
<td>-0.64</td>
<td>ns</td>
<td>0.64***</td>
<td>0.40</td>
<td>56</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Willow Tit juv ♂</td>
<td>-0.53</td>
<td>ns</td>
<td>0.53**</td>
<td>0.26</td>
<td>29</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Willow Tit ♀</td>
<td>-0.71</td>
<td>ns</td>
<td>0.71***</td>
<td>0.48</td>
<td>20</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Willow Tit ♀</td>
<td>-0.53</td>
<td>ns</td>
<td>0.53***</td>
<td>0.26</td>
<td>41</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Willow Tit ♀</td>
<td>-0.78</td>
<td>ns</td>
<td>0.78***</td>
<td>0.60</td>
<td>67</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Willow Tit ♀</td>
<td>-0.55</td>
<td>ns</td>
<td>0.55***</td>
<td>0.29</td>
<td>38</td>
<td>Klaebu</td>
</tr>
<tr>
<td>Willow Tit ad ♀</td>
<td>-0.71</td>
<td>0.35</td>
<td>0.75***</td>
<td>0.52</td>
<td>23</td>
<td>Venabu</td>
</tr>
<tr>
<td>Willow Tit juv ♀</td>
<td>ns</td>
<td>0.54</td>
<td>0.54**</td>
<td>0.26</td>
<td>24</td>
<td>Venabu</td>
</tr>
<tr>
<td>Willow Tit ♂</td>
<td>-0.57</td>
<td>ns</td>
<td>0.57**</td>
<td>0.29</td>
<td>21</td>
<td>Venabu</td>
</tr>
</tbody>
</table>

* *P < 0.05.
** *P < 0.01.
*** *P < 0.001.
ns = not significant.

from December onwards. Such a development indicates that the regulatory effect of the photoperiod is relatively stronger than that of air temperature. This view is supported by the results of stepwise regression analyses on body weight with photoperiod and air temperature as independent factors. In only four out of 18 individuals studied did the air temperature enter the equation as a significant factor, whereas the photoperiod was included in all cases but one (Table 3). This finding is consistent with the results of previous analyses of the influence of air temperature on the body weight of the Great Tit (Haftom 1976).

In December, the tits in central Norway utilize the short days effectively by foraging intensively from before sunrise to after sunset. As the days become longer from January onwards, the birds do not follow up by extending their daily activity correspondingly, as would be expected if they were underfed. Instead they cease foraging and go to roost progressively earlier in relation to the time of sunset. Already during the latter
part of February, they cease their daily activity before sunset (Fig. 9). In other words, despite the fact that January–February represents the coldest period of the year, they do not seize the chance to build up as great a fat store as they had before, even when there is a food surplus. Apparently they need less energy during the latter part of the winter, possibly because the nights are shorter.

The above statement does not mean, however, that the influence of temperature on body weight is considered to be unimportant. In previous
studies of two different Norwegian populations of Great Tits, at Oslo and Drammen, respectively, I found that the mean winter weight varied inversely with the mean winter temperature (Haftorn 1951, 1976). Other workers, too, have found clear effects of temperature on the body weight of Great Tits (van Balen 1967, Lehikoinen 1987).

The relationship between body weight and temperature is not a straight-forward one, however. Although the winter temperature was lower at Venabu than at Klaebu, the Willow Tits at Venabu did not show a higher degree of winter fattening, at least not one that was detectable at the individual level.

Concluding remarks.—To sum up, regardless of species, most individuals in the present study, although not all, gained in weight during the winter, and this applied to both the morning and the evening weights. In other words, they followed the “winter fattening strategy.” Although the morning weight of a few birds tended to be relatively stable (Figs. 2D and 4A, C), no convincing examples of the “constant morning weight strategy” were found. The usual pattern was that the changes in morning weight paralleled those in evening weight, whether or not the particular bird actually gained or lost weight. It should be added that the noon weights followed exactly the same trend (Fig. 2A–C). At noon, birds had gained about half the daily weight increase.

No clear interspecific differences in the winter fattening patterns were observed. On the whole, the gain in weight from September to the winter peak was moderate in both study areas, usually being between 2 and 8%, for both the morning and the evening weights. The diurnal variation in weight observed in the present study was considerably greater than the degree of winter fattening, namely about 7–12%. Furthermore, it is noteworthy that the most sedentary of the titmice, the Marsh Tit and the Willow Tit, showed significantly less diurnal variation in weight than the other three species.

The winter weight of one male Great Tit did not increase at all, but declined from October onwards, apparently for some reasons other than starvation or competition with other birds. This trend may be related to its high-ranking status in the social hierarchy, a hypothesis which should be tested by further observations.

ACKNOWLEDGMENTS

I thank Toril Berg and Ingeborg Harder for technical assistance, and P. A. Tallantire for improving the English.

LITERATURE CITED


LAYING DATES AND CLUTCH SIZE IN THE GREAT TIT

C. M. PERRINS and R. H. McCLEERY

ABSTRACT.—During the course of 40 years of observations, we found that the mean date at which a population of Great Tits (Parus major) starts to lay varies from 10 April to 10 May. Clutch size is shown to decline with laying date and such an effect is apparent between as well as within seasons, with birds laying larger clutches in early seasons than they do in late ones. Clutch size also declines with increasing density of both Great Tits and Blue Tits (P. caeruleus). Breeding success decreases seasonally and the decline can be very marked in some years. The laying bird, therefore, has the “choice” of whether to lay more eggs, and suffer the reduced success of having them hatch later, or of stopping laying sooner and hence having a smaller brood but gaining the advantages of having them hatch earlier. The relative advantages of these two options are discussed, and it shown that the seasonal decline in nesting success is insufficient to explain why birds lay the smaller clutches observed; differences in individual bird quality are also involved.

The aim of this paper is to examine factors affecting the timing of breeding and clutch size of the Great Tit (Parus major). A number of factors have been shown to affect these aspects of breeding, and these are re-examined here with a larger set of data. Some comparisons are made with data for the Blue Tit (P. caeruleus). The breeding biology of the Great Tit is probably better known than that of any other wild bird. It is convenient for study purposes for a number of reasons. It is common and usually nests in broad-leaved deciduous woods at densities of approximately one pair per ha or more. It largely is sedentary, thus studies can be continued through the winter. Also, many of the nestlings raised in a study area breed there in later years. Above all, it is a hole nester, accepting nest boxes readily. Normally, virtually all Great Tits nesting in a woods will use nest boxes if these are available. Furthermore, over much of Europe, it is one of only two abundant hole nesters, the other being the Blue Tit; since the latter species is much smaller (10–12 g as opposed to 18–20 g), the Great Tit normally wins disputes for nest boxes. Therefore, the numbers nesting in boxes closely reflect the number of breeding pairs present.

Long-term studies have provided much of the basic data. The first, started in the Netherlands in 1912 by H. Wolda, subsequently was made famous by the works of H. N. Kluijver (Kluyver 1951). The present paper is based on some analyses from the long-term British study begun in 1947.

by Lack and Gibb in Wytham Wood, a wood owned by the University of Oxford (e.g., Lack 1966). We now have data for 42 consecutive years. The original work was carried out in a 26.7-ha subsection of Wytham Wood called Marley Wood, and it was not until 1958–64 that the study was expanded to cover the whole woods, an area of some 230 ha (e.g., Perrins 1979, Minot and Perrins 1986). The data for Marley Wood are less extensive but cover more years, whereas those for the whole wood are more extensive but only cover a period of a little over 20 years. Further, many of the areas outside Marley Wood contain a lower density of nest boxes, and at least at times of high breeding numbers, not all the Blue Tits are able to obtain a box. In this paper, we use mainly the data for Marley Wood, but for some analyses we have used the more extensive data for the whole forest of Wytham.

Definitions

The following conventions are used in this paper: (1) Laying date. The annual laying dates given are the means of the dates on which each pair in the population laid their first egg. Since Great Tits usually lay one egg per day throughout their laying period, the date on which the first egg in a clutch was laid can be extrapolated from weekly visits to the nesting boxes. There are, however, some potential sources of error in calculating mean laying dates. Because some nests fail during the laying period, usually due to predation, and because the parent birds lay a replacement clutch, more clutches are started than there are breeding pairs in the wood. A replacement clutch of an early pair may be laid before the first clutches of later pairs. Since the identities of the birds are not known at this time, we do not know the status of all nests, with the result that the decision as to which are first clutches and which are replacements (second broods are rare and come much later) is inevitably somewhat subjective. However, the status of only a small number of nests is in doubt, and their inclusion or exclusion rarely affects the mean date of laying by more than a day. (2) Clutch size. Certain nests in which eggs were laid were excluded from the calculations; these included those where the female never got as far as incubating. They were mostly incomplete or late nests (i.e., those excluded on the basis of their date of laying). All nests of four or fewer eggs were also excluded, even though they may have been incubated; such small clutches are rare and probably usually incomplete. (3) Recruits. We have used as our measure of breeding success the number of young which survive long enough to breed in the nest boxes. The number of such recruits does not fully reflect the total number of young which survive to breed, since some emigrate from the study area and breed elsewhere (McCleery and Perrins 1985). There is, however, no reason to suppose
that the number of recruits is not an accurate indication of the relative success of the different classes of nests.

Variations in Laying Date

Both the clutch size and the laying date of the Great Tit are very variable. In our study area, the mean date of laying has varied from 10 April to 10 May, while the annual mean clutch size has varied from 7.7 to 12.1. These year-to-year changes are the result of all birds in the population “tracking” the annual changes. This was clearly shown in 1986 and 1987, respectively, a very late year and a fairly early one. Ninety-four Great Tits bred in both these seasons, and their laying dates and clutches in both seasons are shown alongside those for the population as a whole (Table 1).

Many birds breed earlier in warm springs than in cool ones. This holds true for the tits. Previous studies of the Great Tit, (Kluijver 1951 [with some modifications 1952], Dhondt 1970, van Balen 1973) have shown that the laying date markedly is affected by spring temperature. This correlation has been demonstrated in a variety of ways; in particular, Kluijver (1951) and van Balen (1973) showed that the spring temperatures (as measured by the sum of the mean of the maximum and minimum temperatures for each day = the “Warmth-Sum”) have a major effect on the date at which laying starts. Although Kluijver (1951) thought that temperatures as early as January might affect the date of laying, he later decided that the period from mid-March onward was the most important (Kluijver 1952). van Balen (1973) showed that the period with which, statistically, the date of laying is most closely correlated is 1 March to 20 April. He thought that temperatures before 1 March did not contribute to the timing of laying. This analysis of the Wytham Wood data supports this conclusion in that mean laying dates of the Great Tit are not correlated significantly with the sum of the maximum and minimum temperatures for February. In the case of the Blue Tit (which lays a few days earlier than the Great Tit), February temperature has a small but statistically significant effect on the laying date:

Blue Tit laying date = 53.1 - 0.0239 Feb-Warmth-Sum,  \( P < 0.01 \)

The March/April Warmth-Sums explain almost 70% of the variation in laying date in both species, showing spring temperature to have a very strong effect on the timing of breeding in the tits. Indeed, it is probably stronger than these analyses suggest, because there are a number of ways in which such analyses are not entirely satisfactory. The most important of these is that, since the laying date varies by a month between years, any fixed period of time will not coincide closely with the onset of laying
TABLE 1
CHANGES IN LAYING DATE (L-d) AND CLUTCH SIZE (C-s) OF THE SAME BIRDS IN SUCCESSIVE YEARS, 1986 AND 1987

<table>
<thead>
<tr>
<th></th>
<th>1986</th>
<th>1987</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>L-d</td>
</tr>
<tr>
<td>Total population*</td>
<td>193</td>
<td>38.4</td>
</tr>
<tr>
<td>Known to breed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td>188</td>
<td>38.4</td>
</tr>
<tr>
<td>in both years</td>
<td>61</td>
<td>39.0</td>
</tr>
<tr>
<td>1984</td>
<td>33</td>
<td>38.1</td>
</tr>
<tr>
<td>Combined</td>
<td>94</td>
<td>38.7</td>
</tr>
<tr>
<td>Shift (in total)</td>
<td></td>
<td>L-d</td>
</tr>
<tr>
<td>Shift (in 94 birds)</td>
<td>L-d</td>
<td>16.9</td>
</tr>
</tbody>
</table>

The first two rows show laying date and clutch size for all birds in both years. In rows 3 and 4 the 94 birds are divided by whether they were breeding for the first time in 1986 (1985 = born in 1985, 1984 = born in 1984 or earlier), since the laying dates and clutch size of first-year birds are usually later and smaller (respectively) than those of older birds. In this case, none of the differences between the two age groups is significant, though clutch size in 1986 approaches significance (P = 0.08). Also note that the total population in 1987 will have contained many young birds, while all the 94 were at least two years of age by then; hence the latter group would be expected to have a slightly larger clutch size than the whole population.

in all springs; for example, in one year (1948) the mean date of laying occurred ten days before the end of the period over which the Warmth-Sums are measured, while in others (1979, 1986) a full 20 days elapsed between the end of this period and the mean laying date.

Second, as pointed out by both Kluijver (1951) and Dhondt (1970), the relationship between laying date and spring temperature is not a simple one; more than a single factor is involved. Dhondt suggested that the daily mean temperature had to reach at least 10°C before the birds would start to breed. Kluijver suggested that the birds were affected by two factors. First the Warmth-Sum had to reach a threshold (of about 32°F) by the beginning of April if breeding was to start early, but if the birds were delayed from starting then, the Warmth-Sum required for breeding to commence falls as the spring progresses. In other words, breeding would start relatively earlier with regard to any given Warmth-Sum, the later the date. Kluijver suggested that some other factor such as day length held the birds in check earlier in the season, but that after the temperature threshold had been reached, this second factor ceased to act. Clearly temperature is not the only factor affecting the birds at this time; among other things, the days become progressively longer. Comparing the two extremes of the starting dates in Wytham Wood (10 April and 10 May), there is an increase in daylight of almost two hours between them (a 12.6% increase in feeding time or a 19% reduction in fasting time). Hence, even if all other environmental conditions (especially food and temper-
Fig. 1. The effect of cold weather during the laying season on the number of nests started each day. Upper graph shows minimum daily temperatures (vertical axis = °F), horizontal line freezing point, and the histogram shows the number of nests started each day. Laying normally starts four days after an increase in temperature. In this year (1981) a cold snap discouraged many birds from laying and they did not start until four days after the weather improved again.

ature) were identical, birds should find it easier to start breeding in cold conditions in May than in April—they then would have longer in which to gather food.

Third, temperature also has short-term effects. A sudden period of warm weather may stimulate laying, or a sudden cold snap may deter it. This means that the weather of the moment may override more general trends of the Warmth-Sum. This may even happen after the first birds have laid; a cold snap may deter the rest from starting (Fig. 1). As a result, the spread of laying can be quite variable between years. Not surprisingly under these conditions, the laying date of the first quarter of the population is more closely correlated with the Warmth-Sum than is that of the population as a whole.
Fourth, taking the mean of the maximum and minimum temperatures may not be the best way of measuring what is happening in the environment. Kluijver first made this point, in fact his Warmth-Sum discounts temperatures below freezing, counting all such temperatures as 32°F. The Wytham data also show a closer correlation between laying date and temperature if this is done. There is, of course, no reason why freezing point should be the critical temperature above which the Warmth-Sum should be calculated. It may be that it is the accumulated warmth above some other level that is important. Some analyses of the timing of bud-burst in forest trees have shown a complex relationship with low temperatures in winter and temperatures above 5°C (41°F) in spring (Cannell and Smith 1983). However, using 41°F as the lower threshold for the Warmth-Sum gives a much lower correlation with laying date than does the Warmth-Sum with a 32°F threshold. Similarly, using a more recent model for bud-burst of oak trees (Nizinsky and Sangier 1988) does not improve the correlation between laying date and temperature. Nevertheless, some effect of the warmest weather seems likely to be important in the tits, since an analysis of the Wytham data against only the sum of the maximum temperatures gives an even higher correlation than that between the laying date and Warmth-Sum in both Great and Blue tits; these are shown in Fig. 2. Not surprisingly, the laying dates of the two species are closely correlated with each other ($r = 0.880, P < 0.001$).

The timing of laying in the tits is also correlated closely with the shifts in abundance of their main prey, the caterpillars which feed on the leaves of oaks (Quercus). The most common species of prey, the winter moth (Operophtera brumata) was studied intensively in Wytham Wood for a number of years (Varley et al. 1973). When it is fully grown, the winter moth larva drops from the tree and pupates in the ground after which it is no longer available to the tits. In Wytham Wood, the mean date of pupation of the winter moth caterpillars has varied from 14 May in 1948 to 8 June in 1951 and 1962. Like the tits' breeding season, the caterpillars' season is closely correlated with the Warmth-Sum. The date at which half the caterpillars have fallen is well correlated with the laying date of the tits (Fig. 3). The tits' laying date does not seem to be correlated with the numbers of caterpillars present (Fig. 4). Although there is a statistically significant correlation, this is heavily dependent on the one outlying point, and its removal makes the correlation non-significant. What is not immediately apparent from the between-species correlations is that there is considerable variation in the timing of one species compared with the other (Fig. 5). Although, on average, the Blue Tits tend to lay 2–3 days before the Great Tits, they have laid as much as 10 days earlier and as
much as four days later than the Great Tits. This variation does not seem to be associated with breeding densities or earliness or lateness of season although it is correlated significantly with February temperatures. The higher the February temperatures, the more the Blue Tits lay in advance of the Great Tits. For the present, in spite of the problems in such analyses, one can safely conclude that laying date is very strongly influenced by spring temperatures, specifically those in March and April.
Variations in Clutch Size

It has long been known that the Great Tit's clutch size is affected by the laying date and also by the density of the breeding pairs (Kluijver 1951, Lack 1958). This is likewise true of the data examined here, but other factors also seem to be involved. The factors with which clutch size is correlated significantly are shown, for both Great and Blue tits, in Table 2.

Laying date and food supply. — As in previous analyses, clutches are smaller in years when the breeding season is late (Table 2). This is borne out in the present analysis which shows clutch size declining by almost 0.07 eggs for each day's delay in the mean laying date (where April 1 = 1):

\[ \text{Clutch size} = 11.0 - 0.0675 \times \text{Laying date} \pm 0.02243, \quad P < 0.01 \]

We have data for the years 1947–71 on the densities of the winter moth, and there is a significant correlation between clutch size and caterpillar density (Fig. 6), which is still present if the one year of very high caterpillar density is removed. There is also a significant tendency for there to be more caterpillars in early springs than late ones, although again, as with the correlation between laying date and caterpillar numbers, this correlation is heavily dependent on the one year. Hence, the correlation between clutch size and laying date seems likely to be one of food supply rather than laying date per se. Nonetheless, the relationship between clutch
size and the food supply is more complex when the two species are considered together, since as is shown in Fig. 5, their clutches vary considerably in relation to each other between years. Therefore, either clutch size is not closely related to the food supply or the two species must be taking different prey.

**Breeding density of Great Tits.**—Overall, there is a strong correlation between breeding density and clutch size (Table 2). Clutch size decreases by 0.026 of an egg for each extra pair of Great Tits breeding in the wood.

**Breeding density of Blue Tits.**—If the presence of other Great Tits leads to a reduction in clutch size, is such an effect purely intraspecific or do other species have an influence? The most abundant species, for which we have similar data, is the Blue Tit; breeding numbers of Blue Tits also have a significant effect on the clutch size of the Great Tit, which decreases by 0.016 of an egg for each extra pair of Blue Tits in the woods. The clutch size of the Blue Tit is similarly affected by the densities of both species (Table 2).

**Between year effects.**—We have found one further factor with which the clutch size seems to be correlated and that is the clutch size in the previous year (Table 2). There is no significant autocorrelation over periods longer than one year. Since clutch size is negatively correlated with population size, one possibility could be that this correlation results from
Fig. 5. Relationship between the mean laying dates and the mean clutch sizes of the Great and Blue tits. Both axes show the annual mean for the Blue Tit minus the annual mean for the Great Tit. The earlier the Blue Tit breeds in relation to the Great Tit, the larger is the difference between their mean clutch sizes.

Table 2
Regression of Density of Great Tits and Blue Tits, of Mean Laying Date and of Clutch Size the Previous Year on Clutch Size of Great Tit and Blue Tit

<table>
<thead>
<tr>
<th></th>
<th>Correlation coefficient</th>
<th>SD</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Great Tit</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>9.780</td>
<td>1.257</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Density of Great Tit</td>
<td>-0.027</td>
<td>0.008</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Density of Blue Tit</td>
<td>-0.016</td>
<td>0.006</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mean date of laying</td>
<td>-0.059</td>
<td>0.0159</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Previous year’s clutch</td>
<td>0.276</td>
<td>0.105</td>
<td>r² 59.2%</td>
</tr>
<tr>
<td><strong>Blue Tit</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>10.519</td>
<td>1.570</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Density of Great Tit</td>
<td>-0.029</td>
<td>0.009</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Density of Blue Tit</td>
<td>-0.016</td>
<td>0.006</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Mean date of laying</td>
<td>-0.052</td>
<td>0.019</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Previous year’s clutch</td>
<td>0.255</td>
<td>0.011</td>
<td>r² 51.5%</td>
</tr>
</tbody>
</table>
between-year correlations in population size. However, these are very weak and do not appear to be the explanation.

One way in which such a correlation might arise would be if individual cohorts laid, on average, slightly different clutch sizes. This is possible since clutch size is an inherited characteristic (Perrins and Jones 1974), and there are shifts in selection from year to year (van Noordwijk et al. 1981). On average, in any year about 50% of the breeding population is made up of one-year-old birds which, since they have a survival rate of about 50%, make up roughly 25% of the birds of the following year. Thus, the presence of the same cohort in their first and second years of life provides a common component between years. However, we do not have sufficient data for Marley Wood alone from the early years to analyze for this. Using the much larger data set for the whole of Wytham Wood (but for a shorter run of years), we were not able to find either a between-year correlation or significant differences between the clutch sizes of different cohorts. Hence, we cannot explain why this between-year correlation occurs. It is, however, also apparent in Blue Tits.

Overall, these four factors, i.e., food supply, numbers of breeding pairs of Great Tits and of Blue Tits, and the between-year correlation, are all significant, and in combination they explain 51.5% of the variation in Blue Tit clutch size and 59.2% of the variation in Great Tit clutch size.

There is, however, a problem with these analyses. As reported elsewhere for the effect of density on clutch size (McCleery and Perrins 1985), the
strength of the effect of all four of these factors on clutch size has varied with time. Clutch size was strongly correlated with all four variables in the first part of the study, barely at all with any of them in the middle period, and strongly again in the most recent period. The combined $r^2$ for each of the four periods (1947–57, 1958–67, 1968–77, and 1978–88) were 90%, 9%, 21%, and 82%, respectively (the comparable figures for Blue Tits are 41%, 13%, 65%, and 91%). We have no explanation for this.

**Within season variation in clutch size.**—Clutch size is also correlated with laying date within breeding seasons. Although the slope differs greatly between years, a seasonal decline in clutch size is apparent in almost all years (Fig. 7). The reason for this decline is almost certainly associated with the fact that late nests are less successful than early ones. Fig. 8 shows the number of young per nest which survived to breed in later years as a function of the date on which laying started in each nest. Again there is great variation, but overall the penalty for being late is very severe; for each day’s delay in starting (and hence in hatching the young) the number of survivors produced decreases by an average of 3.7% (range 0.5%–10.6%).

The pattern is more complex than this, as can be seen from Fig. 9 which shows the data for all years combined (but thereby loses the variation between years). There are four points to note. First, there is an inverse relationship between clutch size and the proportion of the season over which that size of clutch is laid. Very large clutches are laid only during the first third of the season. Second, the seasonal decline in success is not linear, the very first clutches laid are less successful than those started a few days later (this is certainly very variable between years, with the very first clutches faring well in some years and quite poorly in others). Third, the success of large clutches decreases more sharply with season than does that of small clutches. Fourth, although not clearly visible in this projection of the data, there is a slight, but statistically significant, decrease in survival rate per young with increasing brood size, such that the number of survivors does not increase proportionately with increasing brood size.

**DISCUSSION**

Why should these birds show such marked variations in laying date and clutch size? The general answer to this is probably fairly easy, although the details are elusive. Tits have very large broods; indeed, as far as is known, the Blue Tit lays the largest clutch of any nidicolous bird in the world. Tits feed their young primarily on caterpillars, which in our study area were mainly ones collected from oaks. The birds are dependent on being able to get very large numbers of caterpillars for their large broods. When feeding large young, both Great and Blue tits may bring caterpillars
Fig. 7. The mean clutch size in relation to the date of laying within years. The thick line shows the average for all years; the thin lines a range of individual years. Based on data for the whole wood for the years 1960-87.

to the nest at the rate of one per minute throughout the whole of a 16-h day, almost 1000 caterpillars per day. However, the caterpillars vary markedly in the time of year when they are present and in their numbers; in particular, they develop very rapidly, and they may only be present in any numbers for 2-3 weeks (Gibb 1950).

Ideally, tits should benefit from being able to respond to these changes. Theoretically, they need to be able to cope with two rather different problems. First, they might benefit from knowing how many caterpillars there will be. Second, and perhaps more crucial, they need to have their young in the nest as early as possible in relation to the short period of caterpillar abundance; as we have shown, later nesting birds do much less well.

We suggest that the variations in laying date are made so that the birds can match these shifts in the food supply and that the variations in clutch size are made so as to take into account variations in the quantity of food available. If this is indeed the case, how well can they do this? The answer seems to be only moderately well. There are some things that they simply cannot do. First, we have emphasized that it is crucial for them to get their timing right. However, they cannot do this precisely since the time taken by the caterpillars to develop (from hatching to pupation) varies by more than two weeks between years as a result of temperatures after the birds have laid (Perrins 1973).

Laying date.—Laying date is clearly and markedly related to the spring
temperature, and these mirror the progress of spring. Plainly, plentiful food is available to the tits earlier in a warm spring than in a cold one. In their turn, the caterpillars must be able to move their season to match that of the bud-break of the oaks, since they grow much better on a diet of newly emerging leaves; these also develop earlier in warm springs than in cool ones.

One could, therefore, argue that in every year the birds are merely breeding as early as they can and that their laying date is just a reflection of the time when the food becomes abundant enough for them to be able to start breeding. However, the situation is probably not as simple as that since the laying dates of the two species vary so much in relation to each other.

It is interesting to speculate about how the birds are able to respond. Kluijver (1952) suggested that the birds laid earlier in warm springs, compared with cool ones, because females preparing to breed in warm weather would need less food to maintain themselves and could therefore get into breeding condition more quickly. However, while it is doubtless true that warm weather has such a proximate effect on a bird, we suspect that the weather has an even more important effect on the timing of the food supply.

One reason for thinking that it is the food supply to which the tits are responding, rather than the direct effect of the temperatures on themselves, is that other birds show similar changes in the timing of their breeding

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**Fig. 8.** The number of survivors per brood (=recruits) in relation to date of laying. The thick line shows the average for all years, the thin lines a range of individual years. Based on data for the whole wood for the years 1960–87.
Fig. 9. The number of survivors per brood (=recruits) in relation to date of laying and clutch size. The distribution is based on a Poisson model with square terms for both clutch size and laying date and cubic terms for laying date, all of which significantly affect the model.

season in relation to spring temperature. One of these is the Pied Flycatcher (*Ficedula hypoleuca*) (Löhrl 1957). However, unlike the tits, this species is migratory and is not in Europe during March, so it cannot experience the actual temperatures which might affect its laying date. In this species, the temperatures can only affect the birds indirectly, presumably through effects on other environmental factors such as their food supply.

More direct evidence that laying date is influenced by food availability comes from experiments where artificial food has been supplied to some birds but not to others (Källander 1974, von Bromssen and Jansson 1980). In these experiments on Great Tits and other tit species, the fed birds laid earlier than the controls, though the differences were only a matter of a few days rather than a month as observed here. These feeding experiments indicate that the birds will lay earlier when given extra food at the time of laying. However, there is no convincing correlation between laying date and caterpillar numbers. Further, one might expect that, when they were preparing to lay, the birds would find natural food supplies more difficult to come by, and so breed later in years of high than years of low density. There is no sign that laying date is affected by breeding density in either species. Hence, under natural conditions, the laying date
of the birds does not seem to be affected by the size of the natural food supply.

Clearly, spring temperatures affect date of laying. We suggest that this is largely via its effect on the food supply. This is in contrast to Kluijver (1952) who thought that it was mainly due to direct effects on the birds but in agreement with Tollenaar (1922) who thought that the effects were indirect.

**Clutch size.**—In contrast to laying date, clutch size is affected by a number of different factors. We suggest that all these responses are best seen as attempts by the tits to maximize the number of fledglings that they produce.

Clutch size is correlated with caterpillar numbers over the smaller run of years from which we have data. Since there is also a significant tendency for there to be more caterpillars in an early season than a late one, this may explain why there is a correlation between clutch size and laying date. However, there may be a separate advantage of breeding in an early spring, which is independent of caterpillar numbers. Since, on average, the weather gets warmer as the spring progresses, the caterpillars tend to encounter cooler weather in early seasons than in late ones. As a result, they develop more slowly in early than in late seasons; their prolonged presence should be of considerable advantage to the tits (Perrins 1973). What is perhaps surprising is that feeding experiments show that providing extra food results in a marked shift of laying date but not of clutch size. This could be because the birds are monitoring the natural foods in order to determine their clutch size and are only taking advantage of the extra food provided by man in order to be able to breed earlier.

For a long time it was thought that the caterpillars were so abundant that competition for them by tits raising broods was negligible. The observations of Minot (1981) show that this may not be the case. By removing nestling Blue Tits from an area of woodland, Minot was able to show that the Great Tits were able to feed their young better and fledge them at higher weight than those Great Tits breeding in other areas nearby where Blue Tits were also busily collecting caterpillars for their young. The presence of large numbers of both species depresses clutch size, perhaps for the same reason: the more pairs there are present, the more difficult it is for the parents to raise their young so the better it is to start with smaller broods. If this is indeed the case, it is not surprising that the clutch sizes of both species are affected by the breeding densities of both species. As far as we know, this is the first time that it has been suggested that there may be interspecific effects of density on clutch size. One would like to know how general a phenomenon this is and whether the clutch size of the tits is affected by the density of other species in the same guild and vice-versa.
Early pairs raise more young than later ones; these chicks are heavier and survive better. Fig. 9 shows how survival goes down the later the birds breed and that this decrease in survival rate is more marked the larger the brood size.

There is, however, a problem here. Although Fig. 9 shows qualitatively that the number of recruits produced decreases markedly with season, this model is not, by itself, sufficient to explain quantitatively why clutch size decreases with season. Suppose a bird has the option of stopping laying today or laying one further egg tomorrow. In the first case, its reproductive output will suffer by having one chick fewer but gain by being able to raise the whole brood one day earlier. In the second, the reverse will be the case; it will gain by having one more chick, but lose by having to rear its brood one day later. Since the average reduction in success is about 3.6% per day, this loss is almost always outweighed by the advantage of an additional chick which is much bigger in percentage terms than 3%; in only the one year when the daily reduction in success reached 10%, was this high enough to counterbalance the advantage of increasing clutch size (for a bird laying ten eggs). Hence, by delaying one day and having the extra chick, the parent birds would almost always raise more young. Of course, this is not true without limit, since increasing brood size also has a deleterious effect on chick survival. At some point, fewer young are raised by having another egg than would be raised by having one fewer. This trend can be seen in Fig. 9, but it has only a small effect.

The reason why the model is insufficient to explain why a bird should stop rather than go on to have a larger clutch is that it is incomplete in one respect. It compares the success of a bird’s laying a clutch of nine eggs with that of a bird laying a clutch of ten, and it assumes that if the bird which laid nine eggs had laid ten it would have been just as successful as the bird which actually laid ten. This is not the case. The clutch size of an individual bird is linked closely to the number of chicks which that particular bird can raise (Pettifor et al. 1988). Hence, the slope showing survival in relation to brood size (which is based on information from different individuals) would be much more sharply curved downwards for any one individual.

In conclusion, we emphasize that tits vary their breeding season and their clutch size in ways related to their food supplies. They breed earlier when the caterpillars are early and adjust their clutch size so as to lay larger clutches under those conditions when food is either actually more plentiful or relatively more plentiful because there are fewer birds taking it. They lay smaller clutches when the reverse is the case.
ACKNOWLEDGMENTS

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SOCIAL ORGANIZATION AND DOMINANCE BEHAVIOR IN SOME PARUS SPECIES

OLAV HOGSTAD

Abstract.—Several Parus species live in small, coherent, winter flocks with a dominance hierarchy in which males usually dominate females and adults dominate juveniles. By allocating time to aggression, dominant adults secure the best resources, such as feeding sites and cover against predator, while subordinate juveniles are prevented from using preferred microhabitats. Juveniles, therefore, have higher predation risks than adults. Accordingly, winter survival of adults is higher than that of juveniles. Social dominance entails an increased metabolic rate during the daylight period, but not during night. Subordinates presumably accept their submissive roles while waiting for a chance to improve their social rank positions by replacing dead, high-ranking adults.

Parids remaining at higher latitudes throughout the year are confronted by low ambient temperature, snow cover, periods of food shortage, and short days. Air temperature affects the birds directly, by increasing energy demand, and small birds have relatively high energy requirements (Calder 1974, Calder and King 1974, Kendeigh et al. 1977). Therefore, during cold winter days, parids spend most of the day foraging (Gibb 1954, Ulfstrand 1962, Hogstad 1988a). The winter survival of tits is clearly affected by the severity of the winter (e.g., Ticehurst and Hartley 1948, Kluijver 1951, Gibb 1960) but seems modified by the food supply (Gibb 1960, Perrins 1965, von Haartman 1973). Improved survival of Great Tits (Parus major) (von Haartman 1973), Willow Tits (P. montanus) (Jansson et al. 1981, Hogstad 1988d) and Crested Tits (P. cristatus) (Jansson et al. 1981) when provided with extra food reveals that food availability is crucial to survival. Nighttime is probably the most difficult period for survival. The short period of daylight in mid-winter restricts the available foraging time and necessitates a nocturnal fasting period of up to 18–19 h. Although several species use protected roosting-sites, such as dense foliage, or holes in snow or trees (Kendeigh 1961, Sulkava 1969, Andreev 1980, Korhonen 1981), or utilize nocturnal hypothermia to limit their energy expenditure (Reinertsen and Haftorn 1983), they have to maintain a high rate of energy intake during the few available hours of daylight. However, foraging time may be restricted because of vigilance for predators. To enhance feeding efficiency and reduce the individual risks of predation, tits may congregate in flocks. Individuals in flocks often are able to detect an approaching predator sooner than solitary individuals.
(Pulliam 1973, Powell 1974, Bertram 1978, Lazarus 1979), and each member of the flock can therefore allocate more time to other activities such as foraging (Caraco 1979, Caraco et al. 1980, Studd et al. 1983).

Energy stress and predation are probably main factors responsible for winter mortality of parids. Since juveniles seem to suffer more from cold and predation than do adults (e.g., Ekman et al. 1981, Ekman 1984, Hogstad 1988d), it might be suggested that this difference in winter mortality is determined more by social interactions than by environmental factors. The present paper gives some examples of the effect of social factors on the behavior of parids living in stable winter flocks.

Social organization.—All Parus species live in social units in winter, either in temporary aggregations or in stable flocks, the “nucleus” of which often consists of a former breeding pair. Species known to live in such stable flocks are Black-capped (P. atricapillus), Carolina (P. carolinensis), and Mountain chickadees (P. gambeli), Tufted Titmice (P. bicolor), and Crested, Willow, and Marsh tits (P. palustris). Such flocks form during late summer and early autumn as juvenile tits, after family breakup and a dispersal period, become sedentary and join a mated pair. These social flocks usually contain a small number of non-kin members that defend their territory against flocks of conspecifics during autumn and winter (Löhrl 1950, Dixon 1965, Glase 1973, Smith 1976, Ekman 1979a, Weise and Meyer 1979, Brawn and Samson 1983, Hogstad 1987a, Rost 1987, Nilsson 1988, T. C. Grubb Jr., pers. comm.).

Within such conspecific flocks a linear dominance hierarchy is established in which males dominate females and adults dominate juveniles (Glase 1973, Smith 1976, Ficken et al. 1981, Hogstad 1987a). The hierarchical order is established during flock formation in late summer and autumn, and, unless some members disappear, the hierarchy remains stable throughout the winter. Factors affecting dominance are age, sex, seniority in the flock, body size, and plumage coloration (Glase 1973, Saitou 1979, Brawn and Samson 1983, Järvi and Bakken 1984, Nilsson and Smith 1985, Hogstad 1987a, Nilsson 1988).

The number of conspecifics per flock varies, but usually consists of one adult mated pair and 2–4 juveniles (Glase 1973, Ekman 1979a, Hogstad 1987a, Rost 1987). The juveniles also probably establish pairbonds, in which females have dominance ranks parallel to that of their mates (Dixon 1963, Smith 1984, Hogstad 1987a). In the Great Tit, however, the juveniles do not seem to establish pairbonds as long as they are associated with adults in stable winter flocks (Saitou 1978). Since adult and juvenile Willow Tits chase their mates less frequently than other female flock members, and since females are less vigilant when accompanied by their mates, mate protection is suggested (Hogstad 1988c, d).
Flock size seems dependent on the absence or presence of congeneric species in the area (Hogstad 1988b). Because vigilance level, aggression, and intraspecific competition usually increase with flock size (Fretwell 1972, Caraco 1979), fewer birds of more than one species can form mixed-species flocks. The number of individuals that form single-species flocks is often larger than the number of conspecific individuals in mixed-species flocks (Buskirk 1976, Hogstad 1988b). This may be explained as optimization between predator evasion and reduction of food competition (e.g., Alatalo et al. 1986). Thus, the individual vigilance time in Willow Tits was found to be affected more by the total flock size of Willow Tits and Coal Tits (P. ater) than by the number of Willow Tits alone (Hogstad 1988b). Most parids, therefore, participate in mixed-species winter flocks, and the individuals benefit from the presence of the other species (cf. Krebs 1973, Morse 1977, Sullivan 1984, Pöysä 1985).

Although flocks of several species consist of permanent members that only occasionally leave their territory, the flocks often split up into subflocks for minutes or as long as several hours. The degree of flock coherence increases with temperature stress and energy requirement, which indicates that energetic considerations are important for flock behavior. Increased flock sizes in cold weather have been observed for Tufted Titmice (Morse 1970), Carolina Chickadees (Morse 1970), Great Tits (Hinde 1952; Morse 1970, 1978; Saitou 1978), Blue Tits (P. caeruleus) (Morse 1970, 1978), Marsh Tits (Lüdescher 1973), and Willow Tits (Lüdescher 1973, Hogstad 1984, 1988b, d).

An unknown, but probably substantial proportion of juvenile parids does not succeed in achieving permanent flock membership. The existence of such non-territorial juvenile birds, or floaters, that do not settle as resident flock members in autumn has been observed among Tufted Titmice (Samson and Lewis 1979), Great Tits (Drent 1983), Blue Tits, (Colquhoun 1942), Marsh Tits (Morley 1950, Nilsson and Smith, 1988), Black-capped Chickadees (Smith 1976, 1984, 1987; Samson and Lewis 1979; Weise and Meyer 1979) and Willow and Crested tits (Ekman 1979a, b; Ekman et al. 1981). When such non-territorial Willow Tits visited flocks of conspecifics in a Norwegian subalpine forest during September, they were accepted as members of flocks of four or five, but they were prevented by the resident birds from joining flocks consisting of six members, probably the optimal flock size of Willow Tits in that area (Hogstad, in press). The juvenile resident males were especially aggressive and chased the newcomers away (see also Nilsson 1988 for Marsh Tits). The greater aggression of juveniles compared to that of adults may be explained in terms of fitness. A further increase in flock size would probably affect the fitness of the subdominant juveniles more negatively than that of the
dominant adults which have priority of access to contested resources. Since these non-territorial juveniles lower their fitness by staying outside social territorial flocks (cf. Rubenstein 1976, Rubenstein et al. 1977), their chances of surviving the winter seem poor (Ekman 1979a, b; Ekman et al. 1981, Nilsson 1986).

**Dominance behavior.**—The costs and benefits among flock members differ, and a skewed access in favor of the dominants to resources such as feeding sites and cover against predators has been verified for Blue Tits (de Laet 1985), Black-capped Chickadees (Glase 1973), and Willow Tits (Ekman and Askenmo 1984; Hogstad 1988a, c). Among Willow Tits, the subordinate juveniles are apparently prevented by the adults from using the preferred upper half of coniferous trees, a region that probably provides greater protection from predation than the lower half (Ekman and Askenmo 1984, Ekman 1986, Hogstad 1988c). Tits prefer to feed close to protected cover, and because of their social dominance, higher-ranked Willow Tits use feeding sites close to cover more frequently than lower-ranked flock members. They even prevent subordinates from using such feeding sites (Ekman 1987, Hogstad 1988a). As a consequence, juveniles have to increase their vigilance time (Ekman 1987). Subordinate Willow Tits that foraged in close presence of adults also increased their vigilance time to keep dominants under surveillance so as to reduce the chance of their being attacked or kleptoparasitized (Hogstad 1988a, d). Because they spend time watching dominants in addition to predator vigilance, the energy budget of subordinates is likely more strained than that of adults. The sequence of return of Willow Tits to a feeding site after a life-like, stuffed predator placed close to the site was removed was correlated with dominance rank of Willow Tits, showing that it was the subordinates that took the greatest risks of predation (Hogstad 1988a). The adults apparently behaved more cautiously than the juveniles, and they reduced their potential rate of food intake in order to reduce the risk of predation to a greater degree than the juveniles. By being subject to less stress (Silverin et al. 1984) and probably being in better physiological condition than subordinates, dominants can afford to take less risks (cf. de Laet 1985, Hegner 1985).

In Willow Tits, it is usually the top-ranked bird among the juvenile flock members that replaces dead dominant adults of its own sex (Hogstad 1987b, unpubl. data). A high rank is therefore essential for improving winter survival chances of juveniles.

The dominance asymmetry within flocks obviously forces juveniles to pay for their membership. Despite having fewer benefits than dominant flock members, subordinates benefit from improved predator vigilance by being in a flock, especially during severe weather conditions (Ekman
1987, Hogstad 1988b). When the energy stress is lessened, e.g., in mild weather or when the birds are provided with extra food, the total vigilance level can be maintained even in small flocks (Jansson et al. 1981, Berner and Grubb 1985, Ekman 1987). Under such conditions, it seems more profitable for juvenile Willow Tits to avoid company with dominant adults and to forage in less predator-risky habitats such as in the upper half of conifers (Hogstad 1988d).

However, social dominance also entails an extra energetic cost. The metabolic rate, or oxygen consumption rate of Willow Tits, increases with the social dominance status. The alpha male in a flock may have up to 25% higher oxygen consumption than the lowest-ranking bird in the same flock (Hogstad 1987b). After removal of the alpha male from a flock, the beta male became the top-ranked member of the flock. Concomitantly, his oxygen consumption rate increased significantly more than that of the other members in the flock. After removal of one of the subordinates, only minor changes were recorded in the oxygen consumption of the remaining flock members. Thus, the metabolic rate of a flock member is not stable but is conditional upon its dominance rank (Hogstad 1987b). During nighttime, however, no such relationship between dominance rank and nocturnal metabolic rate was found (Reinertsen and Hogstad, unpubl. data). The oxygen consumption rates of dominant males and subordinate females decreased to the same level during the nighttime period. This strongly indicates that the relation between social rank and metabolic rate is primarily due to the difference in activity linked to social role. Since the alpha male is the most aggressive in defending the flock territory against conspecific flocks (Hogstad 1987a), this activity also is likely to be reflected in its metabolic rate. Although dominant individuals have higher energy requirements during daytime, they gain the best access to the available food resources and therefore probably have no difficulty in compensating for this extra cost. During nighttime, however, both dominants and subordinates depend on the energy reserves built up during the daylight period, a reserve that must last throughout the night because it is impossible to replace until the next day.

Instead of devoting relatively large proportions of their energy budgets to aggressive behavior, subordinates presumably accept their submissive roles and do not fight higher-ranking individuals. This acceptance by subordinates is the intrinsic value of dominance. Subordinates probably make the best of their actual situation while waiting for a higher social status with maturity. Although the majority of the juveniles die during their first winter, some are able to improve their social rank by replacing dominant adults that die during winter. For tits in hierarchical flocks, subordination may therefore be viewed as a conditional strategy.
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ECOLOGY OF NON-BREEDING SOCIAL SYSTEMS OF *PARUS*

**Jan Ekman**

**Abstract.**—Most parids of temperate regions during the non-breeding season associate in small, generally non-kin, flocks. The typical pattern is discrete social units, often with stable composition and high coherence among the members. Exceptions are the Great Tit (*Parus major*) and the Blue Tit (*P. caeruleus*) with a more loosely organized system of "basic flocks" which may intermingle, and where space is divided into overlapping ranges rather than territories. This dichotomy in social organization may be linked to food hoarding where low tolerance toward conspecifics is associated with the value of protecting hoarded food. Discrete social units in territories are known only among hoarding species. The selective advantages for conspecific flocking are unclear. Benefits of flocking involving lower vigilance time have been verified, but predator protection can also be obtained from flocking with heterospecifics as well as conspecifics. Further, costs of being of low rank suggest that joining a flock with dominants may be a poor option for subordinates. Flocking in parids may be associated with steep gradients in quality of the habitat, causing a sharp reduction of options that are alternatives to settling as a low-ranking flock member. Habitat constraints should then be a main ecological factor affecting flocking among parids, and flock size may vary with habitat structure.

Over the years descriptions of social patterns of many different *Parus* species have accumulated. The social organization in individually marked populations has been studied for more than a dozen species. My intention is to do a synthesis of this information to identify general patterns. Parids of temperate regions may be a suitable group in which to study ecological factors relating to the evolution of sociality. Few species live in kin groups (Ekman, in press), hence the evolutionary approach will not be plagued by difficulties in separating direct from indirect fitness components operating through relatives.

Most parid studies describe general social patterns, and objectives have differed considerably as social organization is such a broad concept. Pioneering studies of social dominance outside the laboratory were done with parids (Hamerstrom 1942, Odum 1942). Recent studies have involved more systematic approaches to testing ecological theories (e.g., Saitou 1978, Drent 1983, Smith 1984, Ekman 1987, Hogstad 1988).

**Patterns**

The Dichotomy

All *Parus* species studied so far are social to a varying extent during the non-breeding season (Table 1). Among species studied, there is a strong
<table>
<thead>
<tr>
<th>Species</th>
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<th>Location</th>
<th>Season</th>
<th>Reference</th>
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<tr>
<td><strong>Black Tit (Parus niger)</strong></td>
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<td>2.7–3.9 (19)</td>
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<td>Pre and post-breed.</td>
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<td>Tarboton 1979, 1981</td>
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<td>Winter</td>
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<td>S. Sweden</td>
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<td>4.1–6.7 (?)</td>
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* = Data from Studies with Individually Color-banded Birds. N = Number of Units Studied.
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<td>Saitou 1978</td>
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<td>Hinde 1952</td>
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<td></td>
<td>* 8 (1)</td>
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<td>Nice 1930</td>
</tr>
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<td>* 3 (1)</td>
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<td>Winter</td>
<td>Laskey 1957</td>
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<td>Condee 1970</td>
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<tr>
<td></td>
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<td>Pennsylvania, USA</td>
<td>Winter</td>
<td>Samson &amp; Lewis 1979</td>
</tr>
<tr>
<td></td>
<td>* 2.9 (14)</td>
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<td>October</td>
<td>Brawn &amp; Samson 1983</td>
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<tr>
<td>Varied Tit (P. varius)</td>
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<td>Japan</td>
<td>Oct–Nov</td>
<td>Higuchi 1976</td>
</tr>
<tr>
<td></td>
<td>* 1.9 (10)</td>
<td>Japan</td>
<td>Nov</td>
<td>Higuchi 1976</td>
</tr>
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<td>Willow Tit (P. montanus)</td>
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<td>* 2-4 (?)</td>
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<td>Winter</td>
<td>Ludescher 1973</td>
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</tr>
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* Median values.
* Deciduous habitat.
* Coniferous habitat.
bias towards the temperate zones of Europe and North America. Two main patterns emerge among these species studied in individually marked populations, where detailed information is available on associations among individuals and their use of space. One characteristic of most temperate zone parids is discrete units with high coherence among members which reside within non-overlapping territories. The other, represented by the Great Tit, and probably also the Blue Tit, has a looser organization (Saitou 1978) characterized by semi-stable flocks which often intermingle and live in overlapping home ranges (Table 2). These differences pertain to the established population cohort where individuals are resident within defined areas. Both systems have in common floaters which move between flocks.

For some species listed in Table 1, such as the Boreal Chickadee (Parus hudsonicus), the Bridled Titmouse (P. wollweberi), the Siberian Tit (P. cinctus), and the Sombre Tit (P. lugubris), the information is still too meager to allow any conclusions concerning where they fit in this system.

Discrete Units and Territories

*Group cohesion and space use.*—The majority of temperate zone Parus species live in tightly knit social units using a common exclusive area ("discrete units, territories"; Table 3). The coherence is high among permanent members of a social unit. This pattern is shown in the social organization of the Black-capped Chickadee (P. atricapillus), the Carolina Chickadee (P. carolinensis), the Coal Tit (P. ater), the Crested Tit (P. cristatus), the Marsh Tit (P. palustris), the Mountain Chickadee (P. gambelii), the Plain Titmouse (P. inornatus), the Varied Tit (P. varius), and the Willow Tit (P. montanus) (Table 3).

The social organization of the Tufted Titmouse (P. bicolor) fits the description above, but this species probably should be considered separately as there is evidence for kin associations during winter (Tarbell

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**Table 2**

**Characteristics of Winter Social Systems Among Parids**

<table>
<thead>
<tr>
<th>“Basic flock” system</th>
<th>Discrete flocks</th>
</tr>
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<td>Social units mingle</td>
<td>Non-mixing flocks</td>
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<tr>
<td>Non-exclusive ranges</td>
<td>Flock areas exclusive</td>
</tr>
<tr>
<td>Exchange of individuals</td>
<td>Stable group composition</td>
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<tr>
<td>Site-related dominance</td>
<td>Linear hierarchies</td>
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<td>Small–large (−50) units</td>
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<td>----------------------</td>
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<td></td>
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</tr>
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<td></td>
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</tr>
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<td>Willow Tit</td>
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1983). The Tufted Titmouse appears to differ in other respects as well. Flock territories are exclusive, but individual members seem to prefer different subareas (Samson and Lewis 1979, Brawn and Samson 1983). As a corollary, coherence within Tufted Titmouse groups appears lower (Brawn and Samson 1983) relative to other group-territorial parids.

Age and sex.—Sex ratios have generally proved to be equal in these discrete social units (Dixon 1963, Glase 1973, Ekman 1979, Brawn and Samson 1983, Smith 1984) suggesting that pairs form before winter. Winter groups are sometimes formed around the nucleus of a former breeding pair remaining in their territory (Dixon 1963, Glase 1973, Ekman 1979, Brawn and Samson 1983), but winter groups in which several adult pairs occur in the same unit have been reported (Glase 1973). Still, pure juvenile groups may also form in territories without survivors from the previous winter (e.g., Nilsson and Smith 1988).

Winter groups are dominance-structured. Several workers have reported what appears to be a general pattern where males dominate females, and within sexes adults generally dominate juveniles (Dixon 1963, 1965; Glase 1973; Brawn and Samson 1983; Hogstad 1987a), although there may be exceptions to such a clearcut dominance structure. There is at least one example where linear and stable dominance relationships did not develop in a Carolina Chickadee population (Mostrom pers. comm.).

Juvenile dispersal takes place shortly after fledging (e.g., Nilsson and Smith 1985), and most recoveries of juveniles which have become permanent winter group members are made at a distance of just a few territories from their natal territory (Weise and Meyer 1979, Ekman and Askenmo 1984, Nilsson 1988). Further, the overwhelming majority of permanent members in coherent and discrete winter groups become established within a month after independence (Weise and Meyer 1979, Ekman, in press, Nilsson and Smith 1988). Longer movements may occur, but the general rule appears to be early establishment. Early establishment as a permanent member of a winter group may have survival value as new members are recruited from the bottom of the rank order (Nilsson and Smith 1988), suggesting strong competition for positions in hierarchies. Still early establishment and prior occupancy may not always bring benefits through high rank, as there are populations of Carolina Chickadees where early settlers have no advantage (Mostrom pers. comm.).

Although a large fraction of juveniles rapidly become permanent members of a winter group some juveniles do not become permanent members of a specific group but remain "floaters" (Ekman et al. 1981, Smith 1984, Nilsson and Smith 1988). Apparently some floaters finally find a vacant position and become a permanent member of a flock (Smith 1984, Ekman,
in press, Nilsson and Smith 1988). In the Crested Tit, the Marsh Tit, and the Willow Tit, the cohort of floaters finally disappears during the autumn (Ekman et al. 1981, Nilsson and Smith 1988), while they are present throughout the winter in Black-capped Chickadees (Smith 1984).

Although patterns appear remarkably constant among species with this social organization, some studies of the Black-capped Chickadee (Brittingham pers. comm., Howitz pers. comm.) and the Carolina Chickadee (Mostrom pers. comm.) suggest substantial intraspecific plasticity. One problem in interpreting this variability is to sort out the effect of supplemental food which has been used in many North American studies. Food provisioning can profoundly affect social organization (Ekman 1987) and introduce intraspecific variability.

The Loose “Basic Flock” System

In winter the Great Tit and the Blue Tit are organized in a looser system than the majority of temperate parids. A description of the main characteristics of the social organization of the Blue Tit is provided by Colquhoun (1942) and for the Great Tit by Saitou (1978, in press) and Drent (1983). Great Tits belong to “basic flocks” (Saitou 1978) composed of either several birds or just a pair (Drent 1983). The area used by “basic flocks” appears more like a home range than an exclusive territory. “Basic flocks” readily intermingle when they meet and utilize a communal area. A similar pattern seems likely among Blue Tits as well, or quoting Colquhoun, “... when breeding is over flocking occurs, territories are invaded and, superficially, have ceased to exist” (1942:239). Space thus appears not to be as rigidly partitioned into exclusive areas among Great Tits and Blue Tits as in parids with discrete social units.

Great Tits do not adhere strictly to their late summer range and may abandon it for long periods in the winter (Perrins 1971, Drent 1983). In this respect, they differ from parids organized in discrete units within exclusive territories. The latter species are sedentary and stay within their winter ranges even during adverse conditions. Linked to the organization in a “basic flock” system is site-dependent social dominance (Brian 1949, de Laet 1984), so that the outcome of interactions shifts in favor of the bird on home ground. It is not clear whether Blue Tits also have this site-dependent dominance. Low-ranked individuals bred farther away from the feeders (Colquhoun 1942), but they may just as well have been subordinates that were evicted. Aggressive behavior by Great Tits and Blue Tits during the non-breeding season may serve primarily the purpose of securing priority to resources within a bird’s home range rather than excluding intruders (Drent 1983). Due to lack of defense of an area, Great
Tit and Blue Tit flocks have a potential of becoming much larger than those of most parids and flocks of about 50 conspecifics (Great Tits) have been reported (Hinde 1952).

Juveniles of Great Tits or Blue Tits also disperse shortly after fledging (Goodbody 1952), but they often spend their first winter without becoming a regular member of a "basic flock" and only settle permanently their first breeding season (e.g., Dhondt and Schillemans 1983).

**CAUSATION—A TENTATIVE SKETCH**

The route to sociality among parids consists of several steps. I will consider the following ones: (1) whether to become sedentary, (2) to share a range with conspecifics, or (3) to be gregarious. Several questions may thus be asked in order to understand the evolution of sociality; these questions may be relevant to the diversity of social organizations on different levels. They may refer to differences between species, populations of a species or individuals within a population. The prime goal will be to identify the factor(s) generating the main dichotomy of discrete and non-discrete social units within the genus *Parus*. To understand each system further, we have to identify the options open to individuals and the factors determining their value.

**Exclusive Ranges—the Impact of Hoarding**

The main dichotomy between a discrete and a loose "basic flock" system among parids is a matter of exclusive ranges. Non-overlapping ranges will necessarily entail that units do not intermingle. Exclusive access to resources usually has been interpreted in terms of economic defendability (Brown 1964). In parids, there is no apparent difference in the distribution of resources for species using exclusive and those having overlapping ranges. This pattern does not suggest large differences in economic defendability. Species with territories and discrete flocks are dependent largely on sparse and widely scattered insect food (Palmgren 1932; Haftorn 1954, 1956a, b; Betts 1955; Gibb 1960; Jansson 1982). In such cases the costs of defense are low relative to the value of the resource.

Economic defendability generally is assumed to vary mainly with costs of defense (Brown 1964), but many parids improve the value of their resource by hoarding large amounts of food in summer and autumn (Butts 1931; Bent 1946; Löhrl 1950; Haftorn 1953, 1954, 1956a, b, 1974; Laskey 1957; Lawrence 1958; Löhrl 1966; Davis et al. 1973; Higuchi 1977; Alatalo and Carlsson 1987). The value of resources then largely depends on the time and energy invested in accumulating supplies. Efforts devoted to hoarding are only rewarded if the hoarder retrieves its supplies, and exclusion of potential scroungers should be strongly favored (Andersson...
and Krebs 1978). There is also a link to sociality, as parids that hoard are organized in discrete territorial units (Table 4). Territoriality could conceivably be an evolutionary response to the risk of scrounging. This inference is based on a correlation, and as such does not prove any causal relationship. Further, it is not clear whether hoarding has evolved separately for each Parus species or if its occurrence represents a single evolutionary event. However, territoriality in an unrelated hoarding species, such as the Eurasian Nuthatch (Sitta europea) (Enoksson 1988, Matthysen, in press), strongly suggests that the relationship between hoarding and sociality is a real one. The hypothesis of relationship between hoarding and a social system suggested in Table 4 needs further testing. The prediction is that the social organization of hoarding species such as the Boreal Chickadee, the Siberian Tit, and the Sombre Tit should conform to a pattern with discrete units within exclusive territories.

It should be noted that hoarding is only a behavioral response for efficient resource use, and conditions generating hoarding are the factors fundamentally driving the social system. Temporary abundance of a rich food resource can be one factor favoring hoarding (Sherry et al. 1982), but little is presently known about all factors which generate hoarding, especially the long-term hoarding reported for other parids (Haftorn 1956c).

It is important to note that hoarding can account only for exclusive ranges, but not for the formation of groups. Additional individuals will

<table>
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<th>Hoarding</th>
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<td>*</td>
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<tr>
<td>Discrete flocks</td>
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<td>Butts 1931, Lawrence 1958</td>
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<td>Haftorn 1956a</td>
</tr>
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<td>Haftorn 1974</td>
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<td>Bent 1946, Laskey 1957</td>
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<td>Varied Tit</td>
<td>*</td>
<td>Higuchi 1977</td>
</tr>
<tr>
<td></td>
<td>Willow Tit</td>
<td>*</td>
<td>Haftorn 1956b</td>
</tr>
</tbody>
</table>

Σ 9 2a

* Significant difference in social organization between hoarders and non-hoarders (P < 0.02, Fishers exact probability test).
merely increase the risk for scrounging. One of the unsolved riddles of parid biology is how hoarding can be reconciled with sociality. The memory capacity demonstrated for Marsh Tits and Black-capped Chickadees, allowing individuals to remember their own specific hoarding sites (Shettleworth 1983, Sherry 1984), is a possible mechanism making hoarding within groups possible. Individually specific foraging sites as in Black-capped Chickadees (Glase 1973) and Willow Tits (Ekman and Askenmo 1984) are another possibility, although the evolutionary consequences of such foraging have not been evaluated.

Gregariousness

All parids are social despite some differences in social organization. Formation of kin groups is confined to a few species, and sociality for most parids must therefore be associated with factors other than kin selection.

Kin groups. — Prolonged juvenile association with the parents is known only for the Black Tit (P. niger) (Tarboton 1981), Tufted Titmouse (van Tyne 1948, Laskey 1957, Tarbell 1983), and the Varied Tit (Higuchi and Momose 1981), and this association is only known to lead to cooperatively breeding units in the Black Tit (Tarboton 1981) and the Tufted Titmouse (Tarbell 1983). The frequency of juvenile retention and cooperative breeding in these species is not known. It might be relatively common in the Tufted Titmouse, while it seems clear that not all Black Tit groups consist of relatives.

The ecology of flocking. — Ecological benefits of gregariousness have generally been coined in terms of either improved predator protection like the "many eyes" hypothesis (Pulliam 1973) or improved efficiency at locating food such as local enhancement (Thorpe 1963). Direct measurements of the value of gregariousness in parids are still in their infancy and there are hardly any actual field data. From aviary experiments, it is known that Great Tits do find clumped food faster through the information conveyed during social foraging (Krebs et al. 1972). Further, free-ranging Willow Tits allocated less time to scanning for predators per capita the more conspecifics in the group (Ekman 1987), as is found in a number of other studies (e.g., Powell 1974, Caraco 1979).

Predator protection. — Sociality allows savings in vigilance time without suffering increments in risk of predation (Caraco 1979). Still, there must be a substantial risk of predation in the first place for increased protection to have any value. Further, the forager must be stressed for time in order to benefit from reduced vigilance time. These conditions may well both be met during the non-breeding season. The information available on predation by Sparrowhawks (Accipiter nisus) on Great Tits in Britain
and but and as available protection shaping substantial congener (Alerstam in two specific flocks in Germany) in the West are potential winter predators on small passerines. Conceivably there is a shortage of foraging time for temperate parids in winter. Great Tits and Black-capped Chickadees start foraging earlier relative to sunrise and cease foraging later relative to sunset in winter as compared to summer (Kluijver 1950, Dunnet and Hinde 1953, Kessel 1976). Additional food also roughly doubled winter survival for Willow and Crested tits (Jansson et al. 1981) by mitigating their time stress in balancing foraging against predator vigilance (Ekman 1987). Extra food allowed Willow Tits to abandon exposed foraging sites requiring high vigilance levels, and to reallocate time from vigilance to searching (Ekman 1987), thus providing the mechanism linking starvation and predation risks, and demonstrating the value of savings in vigilance time through gregariousness. Conceivably other tit species make the same time profit, although it has not been studied in detail. It is known only that predation risk will influence access to feeders for Great and Blue tits (de Laet 1985, Hegner 1985). Predation may be more substantial among parids than recognized, and it may be an important factor shaping their social behavior.

Willow Tits save vigilance time not only from flocking with conspecifics but also by associating with other tit species, Goldcrests (Regulus regulus) and Treecreepers (Certhia familiaris). Heterospecifics in such mixed-species flocks are generally considered to substitute for conspecifics as predator protection at low competition cost. The number of coexisting Parus species available for predator protection could thus be one determinant of conspecific flock size. The data available to test this possibility are limited and not very conclusive. Group size increases for the Willow Tit from two in Germany and Britain, through four in Sweden to six in Norway, as the number of congeners decreases (Fig. 1). The substantial increase in Coal Tit group size from the Swedish mainland to the island of Gotland (Alerstam et al. 1974) also parallels a decline in the number of coexisting congeners from two to none.

There is a tendency for larger group size in North American parids. For instance, the number of conspecifics in a flock ranges from six to eight in the Black-capped Chickadee and the Tufted Titmouse (Fig. 2). Larger conspecific groups may be interpreted as a compensation for the fewer coexisting Parus species in North America (Lack 1971) to uphold the
Fig. 1. Regional trends in the group size of the Willow Tit in northern Europe in relation to the number of coexisting congeners. Pa = Coal Tit, Pca = Blue Tit, Per = Crested Tit, Pm = Great Tit and Pp = Marsh Tit. Data from Foster and Godfrey (1950), Ludescher (1973), Ekman (1979), Hogstad (1987c).

joint vigilance to predators. Still, other factors such as habitat complexity and predator skill should contribute to variations in group size as an anti-predator device. More data are badly needed for a more rigid test of whether the set of coexisting congeners influences sociality. The only data available actually trying to quantify the influence of conspecific and heterospecific company for the value of sociality do not show any decisive advantage of heterospecific company (Hogstad 1988), and the higher cost of conspecific company further remains to be shown.

Social foraging. —Social foraging may reduce the risk of energetic shortfall (Caraco 1981; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Ekman and Rosander 1987) which could be another reason for parids to be social during the non-breeding season when survival is the main fitness component. Benefits of social foraging in reducing starvation risk require clumped food distribution where foraging individuals convey information about its location (Local enhancement—Thorpe 1963). It is, however, doubtful if food of parids in general is clumped sufficiently for social searching to bring benefits. A diet which is largely insectivorous (Palmgren 1932; Haftorn 1954, 1956a, b) consists of food items which cannot be shared and which often occur sparsely and spaced out (Jansson and von Brömssen 1981). Information about the location of food should then be of little value. Response to information about the location of food has been verified in the Great Tit (Krebs et al. 1972) which is largely...
granivorous in winter, a diet where information transfer can be used. The beech mast that Great Tits largely feed on in winter occurs in local clumps that are sufficiently rich to be shared. Yet, it has only been verified that Great Tits respond to information conveyed by flock mates about the location of food. If social foraging is to be considered a selective advantage of sociality, adjustments of flock size are required as the social strategy minimizing starvation risk changes with food abundance (Caraco 1981; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Ekman and Rosander 1987). Some empirical evidence suggest that such diverse animals as finches and spiders actually are able to make these adjustments (Ekman and Hake 1988, Uetz 1988).

OPEN OR CLOSED SYSTEM?

Characteristics.—Enhanced predator protection and food-finding efficiency are factors making sociality beneficial but whether individuals will coalesce into social units also depends upon the options available. The decision animals face then differs according to whether there is a limit on the number of social units or not, corresponding to closed and open
systems in the terminology of Cohen (1971). In closed systems there is a limit to the number of social units an area can accommodate, while there is no such limit in open systems. Once all social units have been established in a closed system, the only alternative option to leaving the habitat for unestablished individuals will be to settle within already existing units. Formation of social units in an open system is a matter of whether it brings any additional benefits, as the individual still has access to the habitat, while membership in a social unit within a closed system may serve as a “ticket” to enter the habitat.

Implicit in the concept of a closed system is that dominants can enforce its priority of access to resources on subordinates. Individuals of low social rank may then be forced to accept a fitness loss relative to being the solitary owner of an area, if their only option is to leave for a habitat of inferior quality. The free access to habitat in open systems does not necessarily exclude aggressive interaction over resources, but they must not result in exclusion of individuals or unequal access to resources. In open systems solitary individuals are able to impose themselves upon existing flocks, and the evolutionary stable size will therefore be larger than optimal (Sibly 1983, Pulliam and Caraco 1984).

Field data.—Members of Great Tit and Blue Tit flocks with their looser organization, appear to have access to their habitat as assumed for open systems (Colquhoun 1942, Saitou 1978, Drent 1983). Site-dependent dominance (Brian 1949, de Laet 1984) also reconciles aggressive behavior with equal access to resources if each member has its own area of dominance. Individuals then do not fight over exclusive right to an area but merely priority to resources within it (Drent 1983).

Discrete and coherent groups residing within territories, which appears to be the prevalent pattern among temperate zone parids, match the requirements of a closed system. Removal experiments have confirmed that established groups within such systems prevent new groups from being formed and new members from joining in at least the Crested Tit, the Tufted Titmouse, and the Willow Tit (Samson and Lewis 1979, Ekman et al. 1981). The lack of replacements in the Black-capped Chickadee, as reported by Samson and Lewis (1979), does not exclude a closed system. The lack of replacements, except by local birds, only shows that there are no floaters around to fill vacancies within flocks. Still, not only floaters but also flock subordinates could be prevented from taking up territories of their own in a closed system. This was the case in a Crested Tit population where removal of flocks resulted in splitting of neighboring groups with subsequent emigration to the vacated area by subordinates (Fig. 3). A similar experiment with Willow Tits confirms that it is subordinates which depart (Ekman, in press). Such replacement not only
Fig. 3. Redistribution of group members in a Crested Tit population after an autumn removal (Ekman et al. 1981). Bold lines = borders of vacated territories, stippled bold lines = borders after replacement, arrows = the origin of immigrant birds, shaded = lake, figures give group size before removal and after replacement. Territory size around 20 ha.

shows a limit to the number of groups but also that group membership could be a second-rate choice to subordinates. Subordinate Willow Tits not only choose to depart, but their survival also improved after the break-up of groups (Ekman et al. 1981). Hence, the long-term costs of increased local competition within groups obviously outweighs short-term benefits of gregariousness, for instance predator vigilance (Ekman 1987).

Subordinate options.—Parid societies organized in discrete flocks living within territories are dominance-structured, and hierarchies are as a rule linear and stable. The ecological and evolutionary consequences of this dominance structure are poorly known. Survival is better for high-ranked flock members among Black-capped Chickadees (Smith 1984) and Willow Tits (Ekman and Askenmo 1984, Koivula and Orell 1988), the only parids with data available for individuals of known rank. A problem plaguing attempts to relate social rank to survival is that individuals rise within the dominance hierarchy as they come of age, and rank will, therefore, be correlated with age and experience. A comparison of the recruitment probability of juvenile Willow Tits shows that the probability of being recruited as a breeder is higher for more dominant individuals (Ekman, in press). Such age-specific comparisons avoid the risk that survival effects are due to differences in age or experience. The rank effect on survival is at least partly the effect of rank-related differences in tree use (Ekman and Askenmo 1984, Hogstad 1987c) where dominants have priority to more protected sites (Ekman 1987). Individual differences in habitat use are
known also among Black-capped Chickadees (Glase 1973), although their ecological consequences have not been studied.

The information is too meager for generalizations, but available data suggest that subordinates do less well than dominants within the parid group system. Data for more species are needed to determine whether this is a general pattern. Metabolic costs of maintaining a high rank (Røskaft et al. 1986, Hogstad 1987b) are apparently not sufficient to outweigh benefits of resource priority for dominant Willow Tits, and rank does not appear to be maintained in a frequency-dependent balance as a mixed ESS. As subordinates within parid groups consistently appear to be younger individuals (Dixon 1963, 1965; Glase 1973; Brawn and Samson 1983; Hogstad 1987a), all present evidence suggests that they are "hopeful dominants" (West Eberhard 1975) suffering a transient fitness loss. As subordinates rise in rank with age, it is perfectly conceivable that in a long-term perspective the expected lifetime fitness is equal for all members in a group, although at present the possibility cannot be excluded that among those which die as subordinate juveniles, there are poorer phenotypes that had a reduced probability of ever becoming dominants.

*When to settle.* — The rapid establishment of groups after independence (Nilsson and Smith 1988, Ekman, in press) is one characteristic of the parid group system. How long do dispersing juveniles wait until they finally settle? One good reason for them to settle as early as possible might be the benefit of being able to hoard for a long time. There is no point in hoarding other than in areas the individual expects to use later on. Still, the benefit of becoming a permanent member of a group early leaves us with the problem of explaining individual differences in the time of establishment in a group as some juveniles apparently defer to become members. Are such individuals precluded from groups or do they refrain from settling? Early establishment may also have its cost in a dominance-structured society, as the individual then runs a risk of forgoing the opportunity of finding an even better position. As higher rank positions fill up, the value of becoming established declines, as high-rank positions will then only become available as group members die. Assume that the probability for a flock member of rank i to survive is P. The probability for a vacancy of rank i is then 1 − P, which also represents the probability for an established individual of rank i + 1 to take this rank position. Now assume that juveniles have the option of remaining as floaters rather than settling with rank i + 1 (lower i means higher rank). If we assume that there are N groups available per floater, their corresponding probability of finding a vacancy becomes 1 − P^N. When will it pay to wait rather than to settle immediately? The survival probability, P(S), of a group member of rank i for time t is
assuming that the mortality rate, \( \Phi_i \), depends on social rank (f will be used for floaters) in line with the empirical evidence. In a continuous time model the probability for a vacancy of rank \( i \) to become available in time \( t \) (=waiting time) is:

\[
P_i(S(t)) = \exp(-\Phi_i t)
\]

(1)

where \( N = 1 \) for the special case of established group members. I assume that established subordinates can advance only within their own group.

We can see from this expression that the probability of finding a vacancy increases with time, \( N \) and mortality risk.

We can now compare survival of individuals which settle as permanent flock members with those that remain floaters. To do this, we first assume that there is a time horizon \( T \), in this case up to the next breeding season, available for settling. An individual gains from remaining a floater for time \( t \) only if

\[
P_i(S(t))P(\text{vacancy}(t))P_i(S(T - t)) > P_{i+1}(S(t))P(\text{vacancy}(t))P_i(S(T - t))
\]

(3)

After rearranging this expression and substituting equations 1 and 2 for the \( P_i \):s we obtain

\[
\frac{1 - \exp(-N\Phi_i t)}{1 - \exp(-\Phi_i t)} > \frac{\exp(-\Phi_{i+1} t)}{\exp(-\Phi_i t)}.
\]

(4)

Now assume there is a survival cost to being a floater. As the mortality risk in the lowest rank position available (\( \Phi_{i+1} \)) increases towards that of floaters, this inequality can be satisfied. The penalty of being a floater may then eventually become so small that it is outweighed by the enhanced survival value from better prospects of finding a vacancy of higher rank as a floater. If there is no survival cost of being a floater, it is trivial that floaters always do better because of their possibility of finding a better position of higher rank, and we would expect no subordinates to settle as permanent flock members.

From the left side of equation 4, we see that the compensation for costs of being a floater comes from being able to inspect more flocks to find out whether a vacancy of a dominant position has emerged. The more juveniles that settle, the more groups there will be available per floater with a higher probability of finding a vacancy of higher rank. The value of being a floater is, therefore, frequency-dependent. To compensate
for larger survival costs of being a floater, the probability of finding a high rank vacancy must increase, which requires a shift in the balance towards fewer floaters in the population. Notice that the actual value of the vacancy does not affect this decision. One consequence of this frequency-dependence is that group size may not be limited in the sense that floaters are actively precluded from becoming flock members. A rank-related access to resource as verified for Willow Tits (Ekman 1987) may be sufficient for the alternatives to benefit the bird.

The frequency-dependence in the payoff from being a floater does not necessarily imply a mixed ESS where group membership and being a floater are two routes of becoming recruited with equal success. A mixed ESS argument requires that floaters do not become recruited from the bottom of dominance hierarchies. Otherwise, floaters will never do better than existing subordinates, and will not be able to compensate later for their poor present survival by finding vacancies of high rank. Floaters recruited from the bottom will always be at a disadvantage compared to established members, as these have priority to higher rank positions that may become open. The evidence for this pattern is conflicting. Recruitment from the bottom of rank orders occurs in the Black-capped Chickadee (Hartzler 1970). A strong prior occupancy overriding both age and size has further been confirmed for the Marsh Tit (Nilsson and Smith 1988), and rank appears to be the effect of seniority in a number of parids (Dixon 1963, 1965; Glase 1973; Smith 1976; Brawn and Samson 1983). Prior occupancy implies that already established birds have priority for emerging vacancies and that floaters are recruited from the bottom of the rank order and that they can never expect the fitness of established subordinates. The generality of prior occupancy has been questioned by observations among Black-capped Chickadees (Smith 1984, 1987) and Carolina Chickadees (Mostrom pers. comm.), suggesting that floaters can be recruited to intermediate rank positions.

Presumably the parameters affecting the decision between taking a low-ranking position in a group and remaining a floater change during the season. Such seasonal dynamics could account for the eventual settling of floaters (Ekman et al. 1981, Nilsson and Smith 1988). For instance, the penalty for not having stored food is likely to increase as energy stress becomes more severe towards winter.

*Group size in a closed system.*—Subordination appears to entail a penalty in parids, judging by the limited data from the Black-capped Chickadee and especially from the Willow Tit. Then why do subordinates accept remaining as group members when they, like the Willow Tit, would do better in their own territories? One possibility is that the option for sub-
ordinates is not to be a dominant owner of a territory within a closed system, but to leave for a habitat of inferior quality. Flocking may be treated as a habitat selection game where crowding in the optimal habitat is traded against low competitor density in suboptimal habitat (Pulliam and Caraco 1984). Subordinates in dominance-structured population may then choose to stay for lack of good alternatives (Ekman 1989). Subordinates should be more willing to stay and accept the cost of low rank the steeper the gradient in habitat quality. Studies of performance in different habitats could thus be important to our understanding of the social system in parids. In the Plain Titmouse subordinates spend the winter in suboptimal habitat (Dixon 1949). Conceivably, the small social units (pairs) in the Plain Titmouse could be due to a gently sloping habitat gradient. In the Willow Tit, subordinates never venture into open farmland, which is the only alternative to coniferous forest (Ekman 1979). An abrupt habitat transition may then be a basic factor behind flock formation in this species (Ekman, in press).

The importance of social dominance was realized early in studies of parid sociality (Hamerstrom 1942, Odum 1942). Studies of the social organization of parids during the non-breeding season have shown that to understand sociality within dominance-structured populations it is not sufficient to focus on the evolutionary benefits of gregariousness. It is also crucial to understand the constraints imposed by the system itself and the options open to different individuals. The social system is part of the environment within which traits operate and are selected. Whether a Parus species is a hoarder or not generates different conditions affecting group size. The explanation of group formation among parids through habitat constraints has its counterpart for cooperative breeders (Koenig and Pi- telka 1981, Emlen 1982). Then why do more parid species not have king-groups? The habitat saturation leading to juvenile retention and group formation in many species depends on both demography and habitat structure. Juvenile dispersal should only be postponed under conditions of high adult survival when the probability of finding a vacancy is poor. Survival among temperate parids may, however, be low enough for sufficient numbers of vacancies to emerge for juvenile dispersal to be adaptive (Ekman, in press). Even if the habitat is not sufficiently saturated after breeding for juvenile retention to evolve, this fact is perfectly conceivable with a habitat saturated with winter territories as a consequence of juvenile dispersal. A shortage of space for territories in the optimal habitat may result in an overflow of unestablished individuals into alternative habitats, but a steep gradient in the quality of habitat at the habitat transition will increase the benefits of remaining in the saturated habitat. Such steep
habitat gradients, in combination with saturation of optimal habitats, could be a requirement for group formation in parid species when sub-ordination has a cost.

LITERATURE CITED


FOOD STORING IN THE PARIDAE

DAVID F. SHERRY

Abstract.—Food storing is widespread in the Paridae. Chickadees and tits store seeds, nuts, and invertebrate prey in a scattered distribution within their home range. They can establish hundreds to thousands of caches per day, and place only one, or a very few, food items at each cache site. Field experiments show that food is collected a few days after caching it, but there are also indications that stored food may remain available for longer periods. Behavioral and neurophysiological studies show that memory for the spatial locations of cache sites is the primary method used to retrieve stored food. The hippocampus plays an important role in the kinds of memory used to recover stored food, and is larger in size in families such as the Paridae in which food storing is common. The ecological and evolutionary relations between food storing and diet, body size, seasonality of the food supply, memory, and social organization are not well understood, but study of the Paridae can help to answer many of these questions.

The Paridae is one of several families of birds in which food storing is common. Food storing also occurs in many woodpeckers, nuthatches, and corvids, in a variety of raptors, shrikes, and bellmages (Cracticidae), in some muscicapid flycatchers (Powlesland 1980), and in bowerbirds (Pruett-Jones and Pruett-Jones 1985). Fourteen species of chickadees and tits are known to store food, and the behavior is known not to occur, or to occur very rarely, in two others (Table 1). That leaves thirty-one species for which there is no information on the occurrence of food storing. The behavior of many of these parids is not well known, and food storing may have been overlooked or not reported in others. This paper describes food storing as it occurs in chickadees and tits, emphasizing research on the role of memory in the recovery of caches of stored food.

One of the earliest descriptions of food storing by any bird is that of Johann Ferdinand Adam Pernau, Baron von Perney (1660–1731). His observations and methods were very sophisticated for their time but were practically unknown until their rediscovery by Stresemann (1947). In a book engagingly titled “Agreeable Country Pleasures (Angenehme Landlust),” Pernau writes: “He that searches for a proof of animals having some kind of reason, may allow a Marsh Tit (‘Hanfmeise,’ Parus palustris) to fly about in his room in which a tree was set where she can live. After she gets used to that room, one has to withhold food from her for half a day and then to strew uncrushed hemp on the table, or on the floor. Immediately the Marsh Tit will come and carry away in her bill three or

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TABLE 1

Food-Storing Parids

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Species</th>
<th>Status*</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marsh Tit</td>
<td>Parus palustris</td>
<td>S</td>
<td>Löhrl 1950</td>
</tr>
<tr>
<td>Sombre Tit</td>
<td>Parus lugubris</td>
<td>S</td>
<td>Löhrl 1966</td>
</tr>
<tr>
<td>Willow Tit</td>
<td>Parus montanus</td>
<td>S</td>
<td>Haftorn 1956b</td>
</tr>
<tr>
<td>Black-capped Chickadee</td>
<td>Parus atricapillus</td>
<td>S</td>
<td>Butts 1931</td>
</tr>
<tr>
<td>Carolina Chickadee</td>
<td>Parus carolinensis</td>
<td>S</td>
<td>Brewer 1963</td>
</tr>
<tr>
<td>Mountain Chickadee</td>
<td>Parus gambeli</td>
<td>S</td>
<td>Haftorn 1974</td>
</tr>
<tr>
<td>Siberian Tit</td>
<td>Parus cinctus</td>
<td>S</td>
<td>Haftorn 1973</td>
</tr>
<tr>
<td>Boreal Chickadee</td>
<td>Parus hudsonicus</td>
<td>S</td>
<td>Haftorn 1974</td>
</tr>
<tr>
<td>Chestnut-backed Chickadee</td>
<td>Parus rufescens</td>
<td>S</td>
<td>Varley 1974</td>
</tr>
<tr>
<td>Coal Tit</td>
<td>Parus ater</td>
<td>S</td>
<td>Haftorn 1956a</td>
</tr>
<tr>
<td>Crested Tit</td>
<td>Parus cristatus</td>
<td>S</td>
<td>Haftorn 1954</td>
</tr>
<tr>
<td>Great Tit</td>
<td>Parus major</td>
<td>NS</td>
<td>Haftorn 1956c</td>
</tr>
<tr>
<td>Blue Tit</td>
<td>Parus caeruleus</td>
<td>NS</td>
<td>Haftorn 1956c</td>
</tr>
<tr>
<td>Varied Tit</td>
<td>Parus varius</td>
<td>S</td>
<td>Higuchi 1977</td>
</tr>
<tr>
<td>Plain Titmouse</td>
<td>Parus inornatus</td>
<td>S</td>
<td>Davis Davis and Davis 1973</td>
</tr>
<tr>
<td>Tufted Titmouse</td>
<td>Parus bicolor</td>
<td>S</td>
<td>Bent 1946</td>
</tr>
</tbody>
</table>

* S = storing; NS = nonstoring.

four grains all at once. . . she will place all the others on a thick branch next to the stem, and then proceed to eat the first grain, frequently at quite another spot in the room. This done, she will fetch the rest of the hidden grains, one by one . . .” (translation by Stresemann 1947, p. 48).

Pernau provides a remarkably accurate description of the basic methods that are used today for observing food storing by chickadees and tits in captivity. Other early descriptions of food storing by parids can be found in Bechstein (1840) and Fatio and Studer (1889), along with a series of anecdotal observations in the journal British Birds (e.g., Astley 1923, Lewis 1923, Hibbert-Ware 1929). Research on food storing entered the modern era with an impressive series of studies of several European parids by Svein Haftorn (Haftorn 1944, 1953, 1954, 1956a, b, c). In addition to work on the Paridae, food storing has been extensively examined in the nutcrackers, Nucifraga caryocatactes and N. columbiana (Swanberg 1951, Balda 1980, Tomback 1980, Vander Wall 1982, Kamil and Balda 1985), and a variety of other birds and mammals (Smith and Reichman 1984, Sherry 1985).
THE NATURAL HISTORY OF FOOD STORING IN THE PARIDAE

Chickadees and tits store seeds, nuts, insects, and other invertebrate prey in a scattered distribution within their territory or home range. They may store hundreds to thousands of food items per day (Haftorn 1954, 1959, Sherry et al. 1982, Pravosudov 1985), placing only one or a very few items at each cache site. Pravosudov (1985) estimated that the Siberian Tit (P. cinctus) and Willow Tit (P. montanus) in the Murmansk area cache about twice as much food as they consume on the spot, about 15 kg of pine seeds and invertebrates per bird annually. Haftorn (1959) estimated that a typical food-storing tit in the Trondheim area stores between 50,000 and 80,000 spruce seeds each autumn.

Typical cache sites include tree bark, moss, lichen, conifer needles, hollow stems, and buds. Cache sites may be at any height above the ground from a few centimeters to many meters, and Marsh Tits sometimes push food into the ground to store it (Löhrl 1950, Gibb 1954, Cowie et al. 1981). Some species cover the cache with a piece of bark or lichen (Crested Tit [P. cristatus], Haftorn 1954, Varied Tit [P. varius], Higuchi 1977), and Haftorn (1974) reports Boreal Chickadees (P. hudsonicus) securing stored food in place with web and seed down. Most parids prepare insect material for storage by removing the head and sometimes other parts. The Crested Tit places such prepared insects at cache sites so that tissue fluids act as an adhesive with the substrate (Haftorn 1954). Cache sites are not re-used in the wild (Cowie et al. 1981, Sherry et al. 1982, Pravosudov 1985), and thus the number of different cache sites created roughly equals the number of items stored.

Food may be stored a few meters from where it was encountered (Pravosudov 1985) or carried distances of up to 100 meters (Richards 1958, Cowie et al. 1981, Moreno et al. 1981). The latter studies, reporting long carrying distances, were conducted at feeders with a fairly rich supply of storable food, while the former, reporting short carrying distances, describes encounters with natural food distributions. This difference in how far food is carried before storage may be due to how much storable food is available, how much has already been stored in the vicinity, or it may be a consequence of the presence of other birds at rich food sources (Sherry et al. 1982). Birds storing food are often pursued, usually by other parids or nuthatches which attempt to take the food or pilfer the cache after the food-storing individual has left (Löhrl 1950, Richards 1958, Sherry et al. 1982).

Even after food has been successfully stored, the level of cache pilfering may be quite high. A rate of loss of 20% or more per day was found for Marsh Tit caches (Sherry et al. 1982). Some of this food was taken by...
other birds, but the greatest source of loss was overnight pilfering by rodents.

Most available information indicates that food is recovered a few days after storing it, but these results do not rule out the possibility of long-term storage. In a study in which Marsh Tit cache sites were located by giving the birds sunflower seeds labelled with a low dose of radioactive technetium (Tc 99 m), it was found that stored seeds were taken within a few days after storing (Cowie et al. 1981). (Evidence that these seeds were recovered by the bird that stored them is described below.) Löhrl (1950) also reports that Marsh Tits collect their caches after several days. Stevens and Krebs (1986) equipped Marsh Tits with small magnets on their leg bands and placed detectors at cache sites to register visits by the birds. They confirmed that the bird that stores food returns to collect it, and that the interval between storage and recovery is rarely more than one or two days. Moreover, recovery attempts at the longest intervals were uniformly unsuccessful, because the caches had been pilfered in the meantime by other birds or rodents.

These results may not be the whole story, however. In captivity, Marsh Tits and Black-capped Chickadees (P. atricapillus) often retrieve food from one cache only to store it again elsewhere. This has also been reported in the wild (Haftorn 1954). It is therefore possible that food is taken from initial storage sites quite promptly but transferred to other long-term cache sites. Ludescher (1980) likewise suggests that there may be two modes of food caching in parids: long-term for winter food reserves and short-term to take advantage of encounters with rich food sources. There is presently no direct evidence that parids ever recover stored food after periods longer than a few days, largely because of the difficulty researchers have in tracking stored food for long periods. But there are indications of much longer term storage. Higuchi (1977) reports that 5% of the nestling diet of Varied Tits in May is made up of nuts of Castanopsis cuspidata which the adults store from August to February. Gibb (1960) reports Coal Tits (P. ater) eating caterpillars and pine seeds in winter, several months after these foods would be expected to be available. Haftorn (1956b) discovered Galeopsis seeds in the stomachs of Willow Tits in mid-winter, even though snow cover had prevented access to Galeopsis plants since the previous autumn. It is thus likely, though not conclusive, that in each case scarce foods were being taken from caches established several months earlier.

**HOW IS STORED FOOD RECOVERED?**

There are potentially many means by which caches of food could be relocated and exploited. Caches could be encountered at random during normal foraging like any other encounter with prey. By putting caches in
the kind of places where it normally forages, a chickadee or tit might eventually re-encounter most of its stored food. The major difficulty with this method is that other animals foraging in the same places would have an equal likelihood of finding the caches. A refinement on this method would be to store food only in particular locations, determined by some kind of "rule." The bird would have to search exhaustively at all sites satisfying the rule, but this would nonetheless confer an advantage over competitors searching for caches. The rule might differ among individuals, or it could vary within individuals from one bout of caching to the next. Alternatively, birds could mark caches in a distinctive way and search for these marks. If the marks were detectable from a distance, the bird could orient to them and quickly approach the cache. Finally, birds could remember the spatial locations of caches and return to them directly. Löhrl (1950) was the first to suggest seriously that chickadees and tits remember where they have cached food. In fact, he distinguished two kinds of memory that might be involved in relocating cache sites, the ability to recall spatial locations from memory (freie Erinnerung) and the ability to recognize a particular spatial location when it is encountered (gebundene Erinnerung). Much of the recent research on food storing by parids has examined these various means of cache recovery.

FIELD STUDIES

At cache sites found by searching for labelled seeds, as described above, Cowie et al. (1981) set up a simple field experiment. We placed two control seeds near the cache, at distances of 10 cm and 100 cm respectively, in sites that were as nearly identical as possible to the cache site chosen by the bird. Inspections of these trios of hidden seeds at intervals of three hours allowed us to monitor their disappearance. The logic of the experiment was that if Marsh Tits re-encountered their caches at random, then seeds in all three sites should disappear at the same rate. Any other animal taking seeds would also be expected to take cached and control seeds with equal frequency. We found that seeds stored by the birds were removed after a mean of 7.7 daylight hours, while the 10 cm and 100 cm control seeds remained in place for 13.5 and 20.4 daylight hours, respectively. On 93 out of 121 occasions, the cached seed was taken while the control seed 10 cm away was not. We interpret this result as showing that Marsh Tits do not re-encounter their caches at random, but that instead they return quite precisely to the place where food was stored.

These results, however, do not show unequivocally that memory is the means by which Marsh Tits return accurately to their cache sites. A number of laboratory studies of Marsh Tits and Black-capped Chickadees have addressed the question (Sherry et al. 1981; Sherry 1982; Shettleworth
and Krebs 1982, 1986; Sherry 1984a, 1984b; Sherry and Vaccarino, 1989; Baker et al. 1988). The basic design of these studies has been to compare the birds’ observed accuracy in retrieving stored food to the accuracy expected by chance encounter or other methods of cache recovery.

**LABORATORY STUDIES**

Both Marsh Tits and Black-capped Chickadees adjust well to captivity. In the laboratory, it is much easier to control the conditions under which the birds search for the caches they have made. In most of these experiments the birds cache seeds in suitable sites that are provided, such as beds of moss or small holes in tree branches, and after a delay of several hours to several days, search for their caches. Usually the stored food is removed in the interval by the experimenter, so that the bird cannot find the cache simply by seeing or smelling the food itself. To determine how likely the bird would be to search a particular place had it not stored food there, a variety of control procedures are used. One method is to allow the bird to search the empty aviary for a period of time immediately before each episode of food storing. This control period provides an estimate of any bias or preference to search particular places whether food has been stored there or not. Comparison of actual cache recovery behavior to behavior during the control period can be used as a measure of whether the birds remember the locations of their caches (Sherry et al. 1981; Sherry 1982, 1984a). Another method is to compare, during cache recovery, the probability of a bird’s visiting a site given that food has been stored there, to the probability of a bird’s visiting that site given no food storage (Shettleworth and Krebs 1982, 1986). The arrangement of moss beds or trees in the aviary can be changed between one caching trial and the next in an attempt to present the birds with a novel arrangement of sites in which to cache.

Both Marsh Tits and Black-Capped Chickadees perform well under these conditions and return to their cache sites much more accurately than would be expected from control data. They also return to caches at a much higher rate than expected by chance, which can be calculated from the total number of searches and the proportion of sites in which food had previously been stored. Birds can relocate their cache sites accurately when there is no stored seed that they might see or smell (Sherry et al. 1981; Sherry 1982, 1984a). Indeed they are not very adept at finding seeds stored by other birds or seeds moved to different locations by the experimenter (Shettleworth and Krebs 1982, Baker et al. 1988). Neither Marsh Tits nor Black-capped Chickadees have been observed to cover caches or to mark cache sites in any way.

The birds do not need to choose cache sites according to a rule in order
to perform well during cache recovery. First, sites do not vary much under laboratory conditions, whether they are beds of moss or holes in tree branches. Second, when the experimental arrangement of cache sites is slightly different for each bout of caching, the use of particular sites conforms to a Poisson random distribution, indicating that re-use of particular sites occurs on a chance basis rather than a rule-governed basis. Under a different experimental procedure, cache site preferences do develop (Shettleworth and Krebs 1982). However, the birds are more likely to search a site after food has been stored in it than when food has not been stored there, whatever the level of preference for that particular site.

It might be supposed that the birds would use the order in which seeds were stored as a mnemonic device to assist in returning to cache sites, but correlations between storage sequence and recovery sequence are sometimes positive, sometimes negative, and usually non-significant (Sherry 1984a, b). Birds are more likely to visit more recently made caches if an interval of a few hours intervenes between one bout of storage and the next, but this is probably an effect of decay or interference in memory, rather than reliance on the sequence of caching as an aid to recall (Shettleworth and Krebs 1982).

Convincing evidence that memory is the major means of cache recovery comes from experiments in which the birds are allowed to retrieve successfully some stored seeds. If memory is used to relocate cache sites, then it makes little functional sense for the bird to remember all cache sites it has recently established, because some of these will be empty as a result of the bird’s own retrieval behavior. Both Marsh Tits and Black-capped Chickadees handle this problem with little difficulty (Sherry 1982, 1984a). Birds were allowed to store about twelve seeds, and on the following day retrieve half of what they had stored. On the day after that, they were allowed to search for caches again, all remaining seed having been removed in the meantime by the experimenter. The birds returned to caches they had not previously harvested and did not search at caches they had. Neither the chance encounter nor the rule hypothesis can account for this result. Instead, sites which no longer contain food are distinguished in memory from sites where food remains, even though both kinds of sites were originally established during the same bout of caching. The same result occurs if birds simply discover that food has been removed from a cache (Sherry 1984a). That is, they do not have to retrieve the food themselves to be able to avoid subsequent visits to empty cache sites.

MEMORY AND THE HIPPOCAMPUS

A recent development in the study of memory in food-storing parids has been to look directly at structures in the brain with memory functions.
In mammals, the hippocampus plays an important role in memory. There are two dominant theories of the involvement of the hippocampus in memory, the cognitive mapping hypothesis (O'Keefe and Nadel 1978) and the working memory hypothesis (Olton et al. 1979). The cognitive mapping idea holds that the hippocampus processes spatial information and is essential to knowledge of places and relations among places. The evidence for this comes from the firing pattern of single cells in the hippocampus, some of which have receptive fields that are places. That is, a cell is active when the animal is in a particular place, for example a corner of its enclosure, and inactive when the animal leaves that place (O'Keefe and Dostrovsky 1971, Best and Ranck 1982). Surgical or neurochemical damage to the hippocampus can be shown to disrupt spatial orientation (Morris et al. 1982).

The working memory idea holds that memory can be dichotomized into two functions: reference memory, which retains information necessary to all performances of a particular task, and working memory, which only retains information about the current performance of the task (Honig 1978). For example, the rules of chess might be retained in reference memory, but how the board position of the present game developed is retained in working memory. The theory of Olton and his colleagues is that the hippocampus plays a role in working memory, regardless of whether the contents of memory are spatial. The evidence in support of this idea comes from studies of the behavior of rats on various tasks in which it can be shown that damage to the hippocampus disrupts memory for ongoing performance but not memory for the nature of the task (Walker and Olton 1984).

Because of the importance of the hippocampus in memory, we examined the effects of hippocampal aspiration on cache recovery by Black-capped Chickadees (Sherry and Vaccarino, 1989). The approach seemed promising because a study by Krushinskaya (1966) had shown that food-storing Eurasian Nutcrackers (Nucifraga columbiana) were unable to relocate their caches after lesions of the hyperstriatum, the part of the brain where the hippocampus is found in birds. Chickadees were allowed to cache and recover seeds once a day for five days. The hippocampus was aspirated bilaterally under anaesthetic, and the birds were allowed to recover from surgery. Three days later caching and recovery trials began again and continued for five days. We found that birds with hippocampal damage performed very poorly at cache recovery, compared to unoperated control birds and birds with aspirations of a comparable size in the hyperstriatum accessorium. They continued to cache seeds and search for them as intensely as other birds, but their cache recovery attempts were no more accurate than chance.
To determine whether this effect was due to disruption of cognitive mapping or working memory, or indeed whether it was due to a memory deficit at all, we conducted a further experiment. Chickadees were trained to locate seeds hidden by the experimenter in the same array of tree branches used for caching. In the Place task six seeds were hidden among the seventy-two holes available, but always in the same places. To perform successfully the bird had to remember which six places contained food. In the Cue task six seeds were hidden, but always in different places. Which six places held seeds was indicated by cues placed near each hole. The six holes with seeds had a small white card beside them, while all the other holes had small black cards. For half of the birds the colors of the cards indicating holes with seeds and empty holes were reversed.

Chickadees with hippocampal damage performed normally on the Cue task but were impaired on the Place task. Unoperated controls and birds with aspirations placed in the hyperstriatum accessorium performed both tasks normally. This is the result that the cognitive mapping account of hippocampal function would predict. To determine whether there was any detectable effect of hippocampal damage on working memory, we tallied all revisits to holes previously inspected. These revisits were regarded as working memory errors because the bird had already determined within that trial that the site had a seed in it (which it took) or was empty to begin with. Birds with hippocampal damage made far more revisits than control birds, a result predicted by the working memory account of hippocampal function.

These experiments showed that the avian hippocampus functions very much like the mammalian hippocampus with respect to memory. Experiments with homing pigeons have also shown that the avian hippocampus serves important memory functions, such as recognition of the home loft (Bingman et al. 1985). Although cognitive mapping and working memory are often presented as alternative accounts of hippocampal function, the results with chickadees, like other recent results with mammals (Jarrard et al. 1984), suggest that the hippocampus serves both functions. It is possible that the hippocampus has multiple memory functions (Sherry and Schacter 1987) or that cognitive mapping and working memory are two manifestations of the same underlying process. Because neurophysiological disruption of memory impaired cache recovery, the results also confirm that memory for cache sites is an essential component of cache recovery.

COMPARATIVE STUDIES OF THE HIPPOCAMPUS

Not all parids store food, and most avian families do not include food-storing species. Anthony Vaccarino and I compared the hippocampus of
storing and non-storing species, with interesting results. Prompted by studies of variation in the volume of song control nuclei of birds (Nottebohm et al. 1981), we compared the volume of the hippocampus in Black-capped Chickadees, Marsh Tits, Great Tits, and Blue Tits (the latter three kindly provided by John Krebs at the Edward Grey Institute, Oxford). Black-capped Chickadees and Marsh Tits store food, Great Tits do not, and the food-storing status of Blue Tits is uncertain. (There are several anecdotal reports of food storing by Blue Tits, but more extensive observations have failed to detect storing in this species; see Table 1.) We found that the hippocampus makes up about 5% of the telencephalon in the food-storing species, about 3% in the Great Tit, and is of intermediate size in the Blue Tit. Promising as this result is, without data on hippocampal size in more non-storing parids it is difficult to interpret. Hippocampal size in storing and non-storing families of birds is a better comparison, because it makes available a larger set of data to work with and permits a more rigorous treatment of allometric and phylogenetic effects (Harvey and Mace 1982). Comparisons of the size of the hippocampus among 13 families and subfamilies of North American passerines (Sherry et al. 1988) and nine families of European passerines (Krebs et al., in press) show that the three food-storing families, Paridae, Sittidae, and Corvidae, all have a larger hippocampus than expected for their body weight or for the size of their telencephalon. It is likely that reliance on stored food in these families has led to selection favoring memory capacities equal to the task of recovering stored food, and the effects of this selection can be seen in the size of the hippocampus, a structure intimately involved in memory for cache sites.

**WHY DO PARIDS STORE FOOD AND OTHER QUESTIONS**

Many questions remain unanswered about food storing in chickadees and tits. One of the clearest and perhaps the easiest to answer is, which species show this behavior and which do not? Food storing is not difficult to detect for an observer attuned to its possible occurrence, and the methods of Haftorn (1954), Moreno et al. (1981), and Cowie et al. (1981) can provide a great deal of descriptive detail about the behavior.

A more difficult problem, but the central one from an evolutionary point of view, is why do some parids store food while others do not? The one known non-storer *P. major* is larger than other European tits, which not only has energetic consequences, but also results in its being dominant to other tits at rich food sources such as artificial feeders. Large body size and dominance may remove some of the selective pressures that maintain food storing in other tits. The center of the Great Tit's distribution is farther south than those of other European tits (Perrins 1979), and this
may account for its being less adapted to seasonal fluctuations in food availability. The Great Tit’s range also extends farther north, however (Haftorn 1957), so exposure to seasonal fluctuations in food availability cannot be the whole answer.

In addition to variation within the Paridae, there is also variation among families of birds in the occurrence of food storing. Diet, body size, and seasonality of the food supply may all be important determinants of whether or not food storing occurs. Memory equal to the task of recovering scattered caches seems an evolutionary prerequisite for food storing, although an evolutionary scenario in which rudimentary food storing occurred first, followed by adaptive change in memory seems equally likely. Richards (1958) has raised the interesting possibility that some methods of feeding may lend themselves to leaving pieces of food behind to be collected later. Nuthatches, for example, wedge food into bark crevices to assist in handling it. The feeding methods of certain groups may provide the raw material for the evolution of more complex storing behavior.

A question alluded to earlier is: “how long after food stores are created are they harvested?” The interval appears to be only a few days for Marsh Tits, but there are indications of more long-term use of food stores in other species. This may vary between species, or it may be determined by local ecological conditions.

It is clear why storing food for long periods could increase fitness. There may be no food available in winter except that which was cached the previous autumn, and a supply of stored food could permit earlier breeding or feeding of the young than would be possible without such a reserve. It is less obvious what the fitness gains are from storing food for a period of a few days. Nonetheless, a number of benefits from short-term storing can be proposed. By storing food, small birds like chickadees and tits may be able to obtain a larger proportion of a rich food source than they would if they simply ate until other animals displaced them or depleted the source. Alternatively, there may be fluctuations in food availability on the scale of a few days, or even within days, that would be mitigated by a reserve of stored food. The effects of short-term fluctuations in energy requirements could also be reduced if stored food were available. Lack (1954) proposed that stored food allows rapid feeding in the morning following the overnight fast, though in fact the reverse appears to be true. Marsh Tits and some other food-storing birds do most of their cache recovery at the end of the day (Collopy 1977, Powlesland 1980, Rijnsdorp et al. 1981, Stevens and Krebs 1986). Caches are probably used as a reliable source of food to be eaten just before beginning the overnight fast. McNamara and Houston (1986) analyzed how food eaten at various times during the day contributes to overnight survival of small birds in
winter, and they found that food eaten just before nightfall can make a much larger contribution to survival than the same food item eaten earlier in the day. Short-term food storing may effectively raise the value of food items by deferring their consumption until the time when they make the greatest contribution to fitness.

In scatter hoarding species, the spacing among neighboring caches has a major effect on the loss of stored food to other animals. This density dependence occurs because animals finding one cache by chance search the surrounding area for more (Stapanian and Smith 1978, 1984; Clarkson et al. 1986). If neighboring caches are placed outside this zone of area-restricted search, then an animal finding one cache by chance cannot systematically pilfer others. Spacing caches is a way of safeguarding them (Vander Wall and Smith, 1987). Marsh Tits maintain a spacing among their caches that minimizes the loss of stored food to other animals (Sherry et al. 1982), but how they space their caches as they do is not well understood. Similarly, how far food is carried from the point where it was first encountered appears to be influenced by a variety of little-understood factors (Clarkson et al. 1986).

A bird makes a decision each time a food item is stored. This "decision" need have no element of reason or foresight (despite Pernau's intuitions quoted at the beginning of the article), no more so than reason or foresight are used, for example, by migratory birds to control their annual movements. But decisions about whether to eat a food item or store it, whether to place it a meter away or a hundred meters away, whether to hide it on the ground or high in a tree, whether to retrieve it promptly or to leave it in place, are going on continually. Behavioural ecologists have enjoyed some success in modelling such economic decisions (Stephens and Krebs 1986). A great deal more information is necessary before the consequences of various food-storing decisions can be analyzed, but a start has been made and this may prove to be a fruitful line of inquiry.

Finally, the food-storing habit may have far-reaching social consequences (Roberts 1979). Reliance on stored food has major effects on social organization in Acorn Woodpeckers (Melanerpes formicivorus) (Stacey and Bock 1978), and Ekman (1979 and this symposium) has suggested that dispersal patterns, site tenacity, and other features of Parid social organization may be adaptations to food storing.

Despite much recent progress, many questions about the ecology, behavior, and evolution of food storing remain unanswered. The Paridae are a group well-suited for examination of these problems, and as the members of this family of birds become better known, some answers may be forthcoming.
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LITERATURE CITED


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THE ORGANIZATION OF MAJOR VOCALIZATIONS IN THE PARIDAE

Jack P. Hailman

Abstract.—Vocal organization in Parus species is similar within subgenera, but differs among them. The Crested Tit, *P. cristatus*, has a weakly differentiated repertoire based on a unit-pattern consisting of a string of high-frequency (HF), tonal notes followed by a string of low-frequency (LF), noisy notes. The American titmice (*P. wollweberi, inornatus*, and *bicolor*) are similar, but have well differentiated songs and chick-a-dee-like calls. The Blue Tit, *P. caeruleus*, and probably one close relative, have differentiated song, alarm calls, and conflict calls, each based on vocal patterns similar to the one of the Crested Tit. The Coal Tit, *P. ater*, and its Eurasian relatives have well differentiated song-repertoires, have all but lost the LF-notes from their repertoires including alarm calls, and use calls consisting of a high diversity of single notes. The Great Tit, *P. major*, and its Asian relatives have similar song-repertoires, but use diversified LF-notes for alarm "churring," and combine other notes freely to make unit-calls. American chickadees and their European counterparts have secondarily simplified song, plus well-developed combinatorial chick-a-dee calls and semicombinatorial, complex gargles. Other subgenera are too little studied for characterization, but the first spectrographic evidence is provided for a number of species. Communicative functions served by "monolithic song" in migratory, north-temperate oscines appear to be divided among two or more major complex vocalizations in almost all species of the non-migratory, permanently mated Paridae. Parid "song," chick-a-dee calls, and gargles have functional equivalents among many parid species, but these are not necessarily phonological homologies. Parids have evolved information-laden vocal diversity both through phonological diversification and through combinatorial principles paralleling those of human language. These two kinds of diversity can be found in "song," chick-a-dee calls, and gargles (and their functional equivalents) in various species, making parid vocalization one of the most interesting and theoretically important communication systems known in the animal kingdom.

The last century of ornithology has witnessed an explosion in knowledge about vocalizations, so periodic summaries are useful for consolidating an ever-growing literature and directing attention to unsolved problems. The Paridae (taken here as coextensive with the genus *Parus*, although recent evidence suggests that genera such as *Sylviparus* should be included), is a particularly interesting family as most of its well-known members have not just one major vocalization ("monolithic" song) but two or more types of complex utterances. This is a preliminary survey aimed at understanding the organization of vocal communication and its evolution in the approximately 45 species of chickadees, tits, and titmice.

1 This paper is dedicated to the memory of my colleague and friend, Klaus Immelmann (1935–1987).
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The present paper is in many ways a descendent of Thielcke's (1968) pioneering review, although my emphases and goals are somewhat different from his primarily taxonomically oriented survey. More recently, Latimer (1977) provided a comparison of a number of parid vocalizations, with emphasis on phonological details and hypotheses concerning sound production. The principal motivation for the present ongoing survey is to trace the evolution of "chick-a-dee" calls and related combinatorial vocalizations. Due largely to their combinatorial properties, these calls of the Black-capped Chickadee (P. atricapillus) may constitute the most language-like system of animal communication thus far discovered (Hailman et al. 1985, 1987; Hailman and Ficken 1986). In addition the survey helps to elucidate how signal-system repertoires are organized, and how informational capacities of such systems were enlarged by evolution.

By "major" parid vocalizations I refer to sounds other than short, special-purpose calls (such as aerial-predator alarms, copulatory-solicitation calls and the like). Most of the major vocalizations are units composed of two or more different note-types put together in either a fixed sequence or a variable order governed by statistical "rules." For example, in the Black-capped Chickadee the major vocalizations are the whistled "fee-bee" (usually referred to as "song"), the semi-combinatorial "gargle" complex, and the manifestly combinatorial "chick-a-dee" call-complex. These three "major" vocalizations are among about a dozen vocal types used by this species (Ficken, Ficken and Witkin 1978).

METHODS

Recording instruments.—My field tapes were made with a Stellavox Sp7 reel-to-reel recorder or a Marantz PMD 430 Professional cassette recorder, with some tapes in mono but most in stereo with one channel being used for running commentary. All vocalizations were recorded with Sennheiser condenser, highly directional ("shotgun") microphones. Reel-to-reel recordings were made on Scotch 208 "mastering" tape, and cassette recordings used Maxell UR90 normal-bias tape. Once the frequency ranges of a species' vocalizations were determined spectrographically to be above low-frequency noise, subsequent recordings were sometimes made using the low-frequency roll-off filter of the Sennheiser ME88 microphone.

Recordings made by persons who have provided me with tapes were made with a wide range of recorders, microphones, and types of tape. In most cases I have copied their original tapes directly into the Marantz PMD 430, and probably in the majority of instances the original tapes were played back from the same recorder or recorder-type on which they were recorded. I have also surveyed recordings from the files of the Cornell Laboratory of Ornithology (hereafter "CLO") purchased by my coworker Millicent S. Ficken.

Recording sites and contexts.—My recordings of North American species were made at many sites, in eastern U.S. at all times of year, but in the west primarily in late summer. Timing is important because: (a) recordings may often include vocalizations of birds only 1–3 months old, and these vocalizations may not be typical of adult birds; and (b) vocalizations associated with advertising and territoriality may be rare in late summer. Species were flocking by late summer, which was ideal for my principal aim of recording chick-a-
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deep calls in those species that have them, but other major vocal types are undoubtedly under-represented in my own recordings, made beginning in 1983.

My recordings of European tits are from the period January to June 1987. During March–April 1987 I made field recordings on the continent near Groningen (Netherlands), Antwerp (Belgium), and Radolfzell and Tübingen (Germany). Most of my recordings were made in Norway, in Væretrøa (Ranheim) east of Trondheim, and at Målsjøen (Klæbu), south of Trondheim, but some recordings were made at other sites. At the two sites named I recorded from winter flocks, during mobbing experiments with stuffed owls (Pygmy Owl [Glaucidium passerinum] and Tawny Owl [Strix aluco]), and from birds at nest boxes (natural cavity in the case of the Crested Tit [P. cristatus]). Recordings from other persons were made at various times and sites, spanning a large period and a large geographic area. In some cases recordings were made of captive birds.

Spectrographing.—All spectral analysis was done with a Uniscan (Unigon Corp.) or Uniscan II (Multigon Corp.), the former used in Trondheim, the latter in Wisconsin. All of the figures herein were made with the latter instrument and printed out on an Epson FX80 printer. For illustration purposes the hard-copies were scanned by ThunderScanning (Thunderware, Inc.) to create digitized images in an Apple Macintosh-plus computer, where they were then labeled and printed on an Apple LaserWriter II.

RESULTS

Vocal organizations were found to group approximately according to Thielecke’s (1968:162–163) listing of subgenera, by which I present the data (using a different sequence of subgenera). There is a persistent structural theme in the phonology of complex vocalizations of Parus species: a series of higher-frequency (HF) notes followed by a series of lower-frequency (LF) notes. The acoustical frequencies differ among species, kinds of vocalizations within a species, probably individuals of the same species giving the same vocalization, and perhaps even repetitions of the “same” vocalization by the same individual. Nevertheless, vocalizations often follow this [HF]-[LF] plan, where the brackets indicate that there may be a number of HF- or LF-notes in a row. (For simplicity, such brackets are omitted from the remainder of the text except where necessary for clarity of a discussion.)

Furthermore, note-types tend to have certain consistent phonological characteristics. The HF-notes confine sound energy mainly in one frequency band, often with frequency modulation (FM). The FM pattern is commonly a chevron on a spectrographic display; when either the ascending or descending arm is emphasized (or the peak of the chevron is missing) I refer to the notes as “slurred.” By contrast LF-notes tend to have a wide frequency spectrum. When they are of fairly short duration, they tend to have a number of parallel frequency-bands (“banded” structure) consisting of “stacked” chevrons. Longer-duration LF-notes tend toward frequency-invariance, so that the frequency-bands look like pure-tone harmonics (which they are not: see Nowicki and Capranica 1986a, b; Nowicki 1987).
There may also be note-types intermediate between the HF- and LF-notes: the “IF-notes.” These intermediates may have intermediate characteristics, or they may be essentially compound notes, beginning as HF and ending as LF, depending upon the species. The IF-notes almost always occur between the other two types, so the typical parid pattern is [HF]-[IF]-[LF]. Finally, within these note-categories there may be several differentiated types, and in some cases graded series.

**Lophophanes and Baeolophus: American Titmice and Relatives**

Thielcke (1968:163) listed the Bridled Titmouse (*P. wollweberi*) in *Lophophanes* with the Crested Tit (*P. cristatus*) and Grey-crested Tit (*P. dichrous*) while placing the other North American crested forms in *Baeolophus*. I consider them together, and begin with this group because the Crested Tit appears to have the least differentiated vocal organization in the family. I found no information on the Grey-crested Tit’s vocalizations; all other species are covered here, with the form *atricristatus* treated with *bicolor*.

Crested Tit (*P. cristatus*).—The handbook of Bergmann and Helb (1982:333) characterizes the vocal repertoire of this European species as markedly sparse and weakly differentiated. “Singing” repeats a characteristic “unit-pattern” (Thielcke 1968:151, fig. 2f; Latimer 1977:421; Bergmann and Helb 1982:333, figs. a and b), consisting of a series of HF-notes followed by a series of LF-notes. I found in Norway that these two series could be alternated, with either beginning and either ending. Furthermore, the male of a pair I studied sometimes gave a repeated phrase of purely HF-notes (Fig. 1A, left part), which resembles “song” of many other parids. Sometimes these HF-notes were no different than those of the unit-pattern, at other times slightly more diverse, as figured.

Vocalizations used in winter flocks, disturbance at the nest-site and in response to a stuffed owl are similar to “singing” except that the LF-notes predominate (Thielcke 1968:154; Bergmann and Helb 1982:333, figs. c and d). Fig. 1A (right part) shows one unit of such a repeated vocalization given in response to nest-disturbance; both members of the pair I studied uttered this vocalization.

Latimer (1977:426) shows four repeated notes that look much like the last two notes shown in Fig. 1A (left). He lists these under “alarm and aggression calls.” These notes, beginning with a brief transient and continuing with a rising slur, might represent a slight phonological differentiation of special notes used in close aggressive contexts, as reported for other tits. Such a call, although rare, is known to occur in the Crested Tit (Perrins 1979, Dhondt pers. comm., Haftorn pers. comm.).

Bridled Titmouse (*Parus wollweberi*).—Gaddis (1983) reported that this
Fig. 1. Sound spectrograms of a sample of vocalizations from primarily European and North American parids other than chickadees and their close relatives (Fig. 2). Sounds were recorded by the author except as noted in the text; for categorization of sounds, see text.
species of Mexico and southwestern United States had three song-types of repeated single notes, which were given by all four of his marked males. One type is an upward slur and the other two are chevrons, one occurring as repeated couplets and the other as repeated notes (op. cit., p. 18). Figure 1B (left) shows an extract from the repeated-couplet type of song from CLO tapes. Gaddis found the three song-types tended to be used in different contexts: the slurred type in spontaneous advertising, the couplet-type in distant exchange (counter-singing by males), and the chevron-type in close exchanges and when approaching the nest.

The other published spectrogram of this species’ voice resembles the unit-pattern of the foregoing species (Robbins et al. 1966:216, repeated in the revised edition, 1983:230). Figure 1B (right) shows a typical call, with an opening slurred HF-notes, four chevron-shaped HF-notes and a string of LF-notes. Me recordings appear to show an intermediate between the chevrons and LF-notes. This call-type sounds very much like “chick-a-dee” calls of the Poecile (below), but I cannot say yet whether it has combinatorial properties.

Plain Titmouse (P. inornatus). — Dixon’s (1949) early behavioral study of this western United States species concluded that the Plain Titmouse had “two basic types” of songs that were used somewhat differently, plus “highly variable call notes.” Later, Dixon’s (1969) spectrographic study showed that songs consist of strongly slurried HF-notes of one type repeated or short, alternating phrases. Fig. 1C (left) from CLO tapes shows a repeated three-note phrase. Dixon identified no fewer than 17 “song themes” from a study of 12 males, and “the three males whose vocabularies appeared most thoroughly documented, uttered 11, 10, and 9 motifs, respectively” (pp. 96–97). He felt that there was some separation of usage, particularly between agonistic interaction and counter-singing. Gaddis (1983:19) showed similar song spectrograms, and found repertoires of individual males ranging from 5 to 11 of the 12 types he recorded from five individuals. His data indicate a statistical association between song-types and three contexts of use: advertising, exchanging (counter-singing) and approaching nest. Johnson (1987) found that of 14 song-types, five were statistically associated with one or two contexts while others were used interchangeably.

The only non-song spectrograms are four by Dixon (1969:97), only two of which are cited in the text. Three of the four appear to be like chick-a-dee calls, although only the call in his fig. 3C is so designated explicitly: one HF-note followed by four banded LF-notes. He mentions (p. 95) that both sexes give this call. His fig. 3B consists of two HF-notes, a pair of LF-notes, another HF-note, and then two more LF-notes. Finally, his fig. 3D consists of a series of HF-notes, which Dixon terms a “trill.” These
notes appear to be shorter than the HF-notes of the other calls, and the first note of this series is higher-pitched. My Fig. 1C (middle) shows the beginning of a call in which the banded LF-notes continued for about three times the duration of the string shown. There is a striking aural similarity of this kind of call with that of the Crested Tit (Fig. 1B, right). A recording from CLO tapes (Fig. 1C, right) shows longer LF-notes, which may also be of higher frequency. It is not possible to say if such variation represents different types of LF-notes, or is attributable to individual differences, geographic differences or other factors; nor is it clear whether these chick-a-dee-like calls are combinatorial.

Dixon's (1969:97, fig 3A) other non-song vocalization is "a characteristic utterance" consisting "of several similar, high-pitched notes, followed by two closely spaced, emphatic sounds" (p. 94). The figure-legend terms this "the 'call derivative' song of the Plain Titmouse." It seems possible that this vocalization represents the functional homolog of the Black-capped Chickadee's gargle (discussed below). This might be the same vocalization that Johnson (1987:27–28, figs. 2 and 4) termed song #14 "associated with attack on rival males."

Tufted Titmouse (*P. bicolor*).—The commonly phoneticized "peter" vocalization of this eastern North American species is so frequently uttered that other vocalizations are difficult to record (spectrograms in Robbins et al. 1966:216, 1983:230; Latimer 1977:421; Gaddis 1983:20; Schroeder and Wiley 1983a, b). These "songs" almost always consist of a repeated slurred note or an alternation of two fairly tonal and simple HF-notes. Fig. 1D (left) shows four slurred notes from a longer bout of song. The marked males of Gaddis (1983:19) had repertoires of 7, 12, 14 and 15 song-types; Schroeder and Wiley (1983a, b) report repertoires of 8–12 "song themes." Lemon (1968: plate I) shows spectrograms from the black-crested race of the Tufted Titmouse (*P. bicolor atricristatus*) in Texas, formerly considered a separate species. These songs are similar to those of the nominate race, and Lemon's birds had repertoires of 7–12 different types. Insofar as I can determine there are no published spectrograms of any vocalization besides song for the Tufted Titmouse. Fig. 1D (right) shows an example of its infrequently used chick-a-dee-like calls. At least three note-types make up these calls: a few HF-notes followed by one IF-note and ending with several LF-notes in the longest calls. I cannot say yet if these calls have combinatorial properties.

*Cyanistes*: Blue and Azure Tits

There are only two species in this subgenus. The Blue Tit (*P. caeruleus*) has a clearly differentiated repertoire, but major vocalizations are built on basic HF-(IF)-LF patterns like the single pattern of the Crested Tit
(above). The similar Azure Tit (P. cyanus) of Asia ranges westward to eastern Europe; Bergmann and Helb (1982:336) show spectrograms of song (fig. a) and calls (fig. b), indicating that the second might be a type of song.

Blue Tit (P. caeruleus).—I believe that this common European (and North African) species is especially important to the understanding of vocal evolution in the Paridae. Compared with the Crested Tit (above), the Blue Tit shows a markedly clearer differentiation of vocalizations into three major types, a pattern that characterizes even more strongly the remainder of the family.

In a novel analytical approach, Bijnens and Dhondt (1984) began by classifying “syllables” (what I term notes: continuous traces on the spectrogram, which may have disjunct frequency components, but are not continuous in time with other such traces). They identified two major types (“A” and “B” syllables), which correspond roughly with my HF- and LF-notes, and within each main type further identified subtypes. Finally, they characterized complex vocalizations according to the composition of note-types, thereby identifying eight alarm and antipredator calls with a broad-spectrum (LF) element (table 1 on p. 250), about 16 distinct combinations in which A- and B-notes (HF- and LF-notes) both occur (table 2 on p. 251), and at least 10 “song-types” (table 3, p. 251) made primarily of A–(HF-)notes.

Vocalizations of the Blue Tit that have been called “song” vary widely (Thielcke 1968:150; Latimer 1977:418; Becker et al. 1980; Becker 1982:228; Miller 1982:262–263; Bergmann and Helb 1982:337; Bijnens and Dhondt 1984). These songs are typically composed of two or three different note-types, commonly in the sequence of several HF-notes followed by several IF-notes, or less commonly LF-notes (but in some cases alternating between two types). The HF-notes are typically chevron-shaped or tonal, and the IF- and LF-notes range from those of broad-frequency, noisy or banded structure on the one hand, to short, nearly tonal notes on the other. Intermediate types range from downsllurs to short-duration, stacked chevrons. Within this vast diversity one can find at least one note-type resembling almost any kind of note given by any parid species. Fig. 1E (left) shows a typical song-like vocalization. It is clear that a given individual sings several types of these complex vocalizations (Becker et al. 1980; Bijnens and Dhondt 1984), and that marked geographic variation in song-structure occurs (Thielcke 1969b, Becker et al. 1980). Both sexes sing (Bijnens and Dhondt 1984), and some song-types tend to be used in different contexts, whereas others appear to be interchangeable.

In the contexts of predator-mobbing or disturbance at the nest, similar but more structured vocalizations are given (Thielcke 1968:154; Latimer
1977:423; Bergmann and Helb 1982:337, figs. d and e; Klump and Curio 1983:80, "scolding"; Bijnens and Dhondt 1984:248–249). All these calls are similar to "songs" in being composed of series of HF-, IF- and LF-notes, but with considerable variability and commonly emphasizing LF-notes. Fig. 1E (right) shows an alarm-type vocalization.

An interesting result from Bijnens and Dhondt (1984) is the isolation of a "conflict call" (fig. 13, p. 256), which they recorded "when tits had physical contact, or when one tit was approached by another one to within 0.5 m during foraging" (p. 257). This conflict call consists of five different note-types, with further variation evident within types. The B4-syllable appears trill-like. The curious notes shown in spectrograms 4 and 5 by Latimer (1977:425) under the title "alarm and aggression calls" resemble somewhat the B4 and B7 notes used in the conflict call of Bijnens and Dhondt (1984).

**Periparus:** Coal Tit and its Relatives

This subgenus now contains four species, the Rufous-vented Tit (*P. rufonuchalis*) having been separated from the Rufous-bellied Tit (*P. rubidiventris*) subsequent to Thielcke's (1968) listing. The better known vocalizations of the Coal Tit (*P. ater*) are presented first and the other three summarized in a second account.

**Coal Tit (P. ater).—** This Eurasian species (which ranges southward to the north coast of Africa and eastward to Siberia and Japan) has greatly elaborated the HF-notes and virtually eliminated the LF-notes from its vocalizations. Its vocal organization is like no other western European or North American species.

The Coal Tit has a well-differentiated song consisting most typically of an alternation of two or three types of slurred HF-notes (Thielcke 1968: 150, 151; 1969a: 1973; see also Gompertz 1968:78, figs. 3a and d; Jellis 1977:121, 122, 170; Bergmann and Helb 1982:334; and Martens 1975: 413—all based mainly on recordings by Thielcke and Martens—and Goller 1987). Figure 1F (left) shows two three-note phrases from a bout of singing in which the phrase was repeated over and over. Males may have a repertoire of at least six song-types but the existence of local dialects is problematical, as a given song-type may show up in a distant population. Haftorn (pers. comm.) has recently found in Norway that an individual male sings up to 14 distinct song-types, and there is further variation manifest in frequency-shifts (cf. Black-capped Chickadee account, below) and other small phonological changes in note-types. Goller (1987) found similar results in the Tyrolian Alps, where individual males had repertoires of 12–16 song-types and the acoustic frequency of notes varied through the season. Goller also found evidence for differences in the
contextual use of different song-types. The song of the Asian form, *P. ater aemodius* (Jellis 1977:170, figs. 65b and c; Martens 1975:412, 413) is quite similar to that of the nominate race in Europe (*P. a. ater*).

A remarkable characteristc of the Coal Tit is the constant production of extremely varied single HF-notes during social contexts in which most *Parus* use chick-a-dee calls or some other combination of notes (Bergmann and Helb 1982:334, figs. c–d and g–h). Fig. 1F (middle) shows these notes from my Norway tapes on which about two dozen more-or-less distinct note-types occur. The intervals between notes are variable, but do not group into short and long classes that would suggest intra- and inter-call intervals.

Equally remarkable is the near lack of LF-notes in scolding or mobbing contexts, where virtually all other parids commonly employ them. Instead, The Coal Tit utters primarily two types of loud HF-notes: one an inverted chevron on spectrographic display and the other a higher note with a long arm that descends in frequency (Thielcke 1968:153; Löhrl and Thielcke 1973:250; Jellis 1977:171; Bergmann and Helb 1982:334, fig. f). The latter note has two parallel energy bands beginning about 7 and 5.5 kHz. Löhrl and Thielcke (1973) report the use of rare LF-notes once in a “very excited” European Coal Tit. The second note in Fig. 1F (right) appears to be one of these rare LF-notes, which I recorded during an agonistic encounter. Interestingly, the North African subspecies (*P. ater atlas*) does use typical parid LF-notes in scolding (fig. c in Löhrl and Thielcke 1973:114). When birds from the nominate European race (*P. a. ater*) were caged with three individuals brought from Morocco and presented with a stuffed Tawny Owl, the European birds began using the LF-notes like the African subspecies (Löhrl and Thielcke 1973:114, fig. d; recounted in Jellis 1977:171, fig. 67d).

One further call requires mention. Bergmann and Helb (1982:334, fig. e) show a note termed “psich,” which resembles the two-banded note used in scolding but is lower-pitched and noisier. A somewhat similar note (first note in Fig. 1F, right), which I termed the “sharp note” in my field commentaries, often occurs during close agonistic encounters.

*Related species.*—The Black-crested Tit (*P. melanolophus*), restricted to the mountains ringing the north part of the Indian subcontinent, is exceedingly similar to an Asian race of the Coal Tit (Martens 1975), and its songs (Thielecke 1968:151; Martens 1975:415; Jellis 1977:170, fig. 65d) are virtually identical. The HF-alarm notes of *melanolophus* (Thielecke 1968:153 and 154; Löhrl and Thielcke 1973:250, fig. b; Jellis 1977:171, fig. 67b) are also highly similar to those of *ater*, having two or more parallel energy-bands and completely lacking LF-notes. Löhrl and Thielcke (1973) also caged Black-crested Tits with the African race of the Coal Tit,
which possesses LF-notes, and found that (like European Coal Tits) the Asian species at first responded to a stuffed owl in the usual species’ way but then began making the LF-notes. Based on hybridization evidence (Diesselhorst and Martens 1972) *melanolophus* should be considered conspecific with *ater*.

The Rufous-bellied Tit (*P. rubidiventris*) was once considered to range from western China westward to Pakistan, but the field research of Martens (1975) indicates that the western form should be considered a distinct species, *rufonuchalis* (below). The songs and calls shown in Thielcke (1968:151) under the name “rubidiventris” belongs to *rufonuchalis* (fide Martens, in litt.). Martens (1975:384, 389) shows songs of *rubidiventris* as now recognized; these songs are quite similar to those of the two preceding species. The alarm calls (Thielcke 1968:153, 154) have the parallel-banded HF-note structure like that of the two preceding species, with no indication of an LF-type of note. However, these calls may belong to *rufonuchalis*. Martens (1975:391) shows a trilled element from the subspecies *P. rubidiventris beavani*, which he considered a possible homolog with trilled song in *rufonuchalis* (see below). This might represent a third major type of vocalization, but at present may be considered a note-variant of song.

The Simla Black Tit (*P. rufonuchalis*), is a Karakoram-West Himalayan equivalent of the foregoing species. Its “trilled song” (Thielcke 1968:151, fig. 21; Martens 1975:382) contains an obviously trilled element of varying phonology, usually at or near the end of the vocalization. The “whistled song” (Thielcke 1968:151, fig. 2m; Martens 1975:383) is variable and shows similarities with song in the three foregoing species. As with *rubidiventris* immediately above, it is not clear if the “trilled” songs should be considered as fundamentally different from the “whistled” songs as a separate major vocalization type. If the alarm calls labeled “rubidiventris” in Thielcke (1968:153, 154) belong to *rufonuchalis* as I suspect, then this species resembles the Coal Tit and Black-crested Tit in having parallel-banded HF-notes and no indication of LF-notes.

**Parus**: Great Tit and its Relatives

Thielcke (1968) lists five species in the nominate subgenus, but the form *bokharensis* may be a race of the Great Tit (*P. major*) and is not treated here. The Yellow-cheeked Tit (*P. spilonotus*) does not appear in Thielcke’s list as it was formerly confounded with the similar Black-crested Tit (*P. xanthogenys*). The well-studied Great Tit is considered first, then related species are summarized in a second account.

Great Tit (*P. major*).—This is one of the largest, most widespread, and best known parids in the world, ranging from European and North Africa eastward across Asia and southeastward throughout the Middle East to
the Indian subcontinent. Its song has been studied more extensively than that of any tit, and its complex vocal repertoire was described verbally by Hinde (1952), and then became one of the first to be compiled for any bird after the sound-spectrograph became available (Gompertz 1961). It may therefore seem ironic that I remain uncertain about vocal organization in this species—but for a simple reason: it mimics other species, including other tits.

The repertoire was studied in detail by Gompertz (1961) early in the spectrographic era, and most of her illustrations are of song (see also spectrograms of Gompertz 1968; Thielcke 1968:150, 1969a:149, 151; Krebs 1976; Jellis 1977:55, 145, 167, 203; Hunter and Krebs 1979; Sasvári 1980:393, Bergmann and Helb 1982:335; McGregor et al. 1983; Baker et al. 1986; Klump et al. 1986:386). Song commonly consists of an alternation of two HF-note-types (Fig. 1G, left), or an alternation of couplets of those types. Males usually have a repertoire of 2–7 song-types and there is much geographic variation. Many of the above-cited papers are devoted to analysis and experimentation on Great Tit song (see also Lehtonen 1954; Sasvári 1971a, b; Krebs 1977a, 1977b; Krebs et al. 1978; Bergman 1980; McGregor et al. 1981; McGregor and Krebs 1982a b, 1984; Falls et al. 1982; Lambrechts and Dhondt 1988). Martens (in litt.) has pointed out that the grey forms of middle Asia, India, and the Himalaya (P. major cinereus-group) sing quite differently from the well-studied European subspecies.

Great Tits also employ LF-notes, called “churring” by Gompertz (1961), especially in alarm contexts (Löhr 1963:547; Thielcke 1968:154, Jellis 1977:81; Sasvári 1980:394; Bergmann and Helb 1982:335, fig. c; Klump and Shalter 1984:194, fig. 2b; Klump et al. 1986:386, two middle figures). With the possible exception of Bergmann and Helb (1982)—where one cannot tell if fig. c is a unitary call or three kinds of notes assembled for illustration—only Jellis (1977:81) shows HF-notes combined with the LF-churrs. I found in Norway that one or several HF-notes commonly preceded a train of LF-notes (Fig. 1G, right), thus conforming to the typical parid pattern. Literature suggests several kinds of LF-notes. Gompertz’s (1961) original descriptions were unsupported with spectrographic documentation, but she listed six types of churring and Jellis (1977:81), using recordings made by Gompertz, illustrated several kinds of churrs in small spectrograms. Associated contexts include territorial skirmishes, scolding, excited foraging, seeking contact with the mate, and “situation tricky but not dangerous.” Klump et al. (1986:386) distinguish “scolding” and “mobbing” calls given to a cat, and these are both quite noisy calls; neither type is identical with the calls I recorded (Fig. 1G, right). In summary, LF-notes vary greatly and a complete classification is not yet possible. A
great variety of other calls is described by Gompertz (1961), with a few spectrograms (see also Jellis 1977, Bergmann and Helb 1982:335). Many of these calls and notes, unlike notes of the Coal Tit (above), are commonly used in various combinations, and some undoubtedly are allied to combinations used in churring. Although not organized like chick-a-dee calls (below), the Great Tit's many LF-churrs and associated HF-notes clearly present at least a semi-combinatorial system of fascinating complexity.

Gompertz (1961:387–388) also describes a “muttered threat” call. This is a three-note phrase “which begins and ends on the same pitch, with the middle note lower.” This call is used in close-distance agonistic interactions. The “war-whoops” shown by Jellis (1977:80) might be this muttered threat, and she points out that each male is likely to have variants of this aggressive call. There thus appears to be a third major vocalization in the Great Tit's repertoire that is functionally, if not phonologically, similar to the gargles of species discussed later.

**Related species.**—The Black-lored Tit (*P. xanthogenys*) of Asia sings at least a three-note, repeated phrase similar to songs of the Great Tit (Fig. 1H, left, taken from CLO tapes). Thielcke recorded responses of captive birds to a stuffed owl and showed a spectrogram (Thielcke 1968:154) of three note-types in a sequence that shows permutation (1-2-1-3). In 1987 we copied his complete tapes of the experiment, and selected the recordings of one individual for extensive quantitative analysis (Hailman and Thielcke MS). Notes, as in the preceding Great Tit, show considerable variety, but there are four modal types, two of which are shown in Fig. 1H (right). Notes are combined in various sequences, which show permutation of order as well as combination of type, and Markov-chain analysis shows that statistical rules govern this combinatorial system.

The Green-backed Tit (*P. monticolus*) of the Himalayas and China signs an alternation of two whistled notes, one tonal and the other steady in pitch then slurred down to a new pitch (Thielcke 1968:151). It is within the variation of the Great Tit songs. Fig. 11, from CLO tapes and those provided by Jelle Scharringga, shows two phrases from each of three different songs. In all three cases the phrase is repeated over and over, but in the first two (left and middle) the phrase consists of only one note, whereas in the other case (right) it is a four-note phrase with two note-types. This is the sort of interesting song variety shown by the Great Tit. The alarm call (Löhrl 1963:547 and Thielcke 1968:154) is a repeated IF-note, tending toward banded LF-type but quite noisy. Is is similar to one of the several kinds of churring of the Great Tit.

The White-winged Tit (*P. nuchalis*) of the Indian subcontinent has a vocalization with notes similar to types used by the Great Tit and other species (CLO tapes). However, it is unclear whether this represents song
or a combinatorial system of call-notes. The Yellow-cheeked Tit (P. spi-
lonotus), of the Himalayas and Indian subcontinent through southwestern
China and southeast Asia, was recorded in the field by Jelle Scharringa,
who kindly provided tapes. Fig. 1J shows two extracts from songs, both
composed of repeated three-note phrases (one phrase shown at left and
two phrases shown at right). It is not certain that these two songs were
from the same individual, but these and other song-types on the tape
suggest the possession of repertoires.

Poecile: American Chickadees and their Old World Relatives

This is the largest subgenus, containing a dozen species as listed by
Thielcke (1968), all of which are considered here except Pere David’s Tit
(P. davidi). The well-studied Black-capped Chickadee (P. atricapillus) is
considered first, followed by species with similar vocal organizations,
finally by species with repertoire patterns that are obviously different or
incompletely described.

Black-capped Chickadee (P. atricapillus).—This widespread North
American species is the archetype of its major group, which includes all
New World forms known as chickadees and certain Old World tits. Per-
haps the first (prespectrograph) vocal repertoire of any bird was of this
species (Odum 1942); the modern spectrographic study by Ficken, Ficken
and Witkin (1978) still stands as one of the most complete repertoires for
any bird. All three of its major vocalizations—fee-bee, chick-a-dee calls
and gargles—have been subjected to extensive analyses.

Whistled “song” or “fee-bee” (known as “phoebe” in earlier literature)
has obvious homologs in closely related species to follow. That both sexes
give this vocalization was noted by Dwight (1897) in a two-sentence paper,
the second sentence of which was “I am not aware that record has ever
been made of this fact, which I determined some time ago by the judicious
use of firearms.” Many spectrograms have been published (Thönen 1962:
117; Robbins et al. 1966:214, repeated in 1983:228; Dixon and Stefanski
fig. 62f; Ficken, Ficken and Witkin 1978:36; Ficken 1981a:385; Ratcliffe
and Weisman 1986:362). The typical fee-bee consists of two tonal notes
of about 350 msec, separated by about 130 msec silence, the second note
about 0.5 kHz lower (Ficken, Ficken and Witkin 1978:35, table 1); the
“faint fee-bee,” which is given by both sexes, is treated as a distinct
vocalization. The fee-bee sensu stricto is apparently given only by males
(contra Dwight 1897); it is basically invariant, so there are no repertoires
or local dialects (but see below). This simple vocalization has been termed
the species' "song" because it is heard in spring from the male on territory—certainly not because of phonological complexity. The fee-bee has been the subject of much comment and a number of specific investigations (e.g., Dwight 1897; Lumley 1934; Desfayes 1964; Dixon and Stefanski 1965, 1970; Ward and Ward 1974; Ficken, Ficken and Witkin 1978; Ficken 1981a; Ratcliffe and Weisman 1985, 1986, 1988).

In an overlooked report, Bagg (1958) noted that birds on the island of Martha's Vineyard (Massachusetts) sing both notes on the same pitch. Leonard Peyton provided tapes from Alaska: Fig. 2A (left) shows one of several songs in which the two notes are obviously at the same frequency; there is also a tendency for each note to be followed by a very brief pulse at the same frequency.

Like the fee-bee, the chick-a-dee call was well known to field workers before the advent of tape recorders and has been subjected to several kinds of analytical studies. Published spectrograms are many (Thielcke 1968:154; Witkin 1977:490; Latimer 1977:426; Ficken, Ficken and Witkin 1978a:36; Dixon and Martin 1979:422, fig. 1c; Mammen and Nowicki 1981:180; Nowicki 1983:317, 1987:53; Hailman et al. 1985:194, 1987:67–71; Nowicki and Caprinica 1986a:1298; 1986b:3597, 3599, 3606). The four note-types composing calls are two HF-notes (labeled "A" and "B"), an IF-note ("C"), and a banded LF-note ("D"). Calls are highly combinatorial, with note-types virtually always occurring in the sequence A-B-C-D, from which any note-type may be missing entirely, given once or repeated a variable number of times. Calls have been studied specifically with respect to sound-radiation patterns (Witkin 1977), flock- and individual-specific structure (Mammen and Nowicki 1981; Nowicki 1983), sequential or syntactic structure (Ficken, Hailman and Ficken 1978; Hailman et al. 1985, 1987; Hailman and Ficken 1986), and mechanisms of phonation (Nowicki and Capranica 1986a b; Nowicki 1987).

The third major vocalization is the exceedingly complex gargle, first spectrographed by Dixon and Stefanski (1970:54), who termed it the "fighting call," and by Dixon et al. (1970:324), who termed it a "supplanting call" (see also Ficken, Ficken and Witkin 1978:36; Ficken 1981a:385; Ficken and Weise 1984:352–253; Ficken et al. 1985:147, 149). Gargles are jumbles of highly slurred, extremely brief notes decreasing in average frequency through the call, commonly ending with a low-pitched trill or banded note of longer duration than the introductory notes. Fig. 2A (right) shows a lengthy gargle, with a trilled note in the middle instead of near the end. The gargle may be given by females but is much commoner in males, and is clearly associated with agonistic encounters. There are 2–13 notes in a call, drawn from a local dialectical "pool" of 16–23 different note-types that are shared almost entirely by all local individuals.
Fig. 2. Sound spectrograms of a sample of vocalizations from North American chickadees and their close Eurasian relatives.
Dialects vary microgeographically, with marked differences in local “pools” of note-types found within 5.7 km. Specific analytical studies of gargles are by Ficken and Weise (1984) and Ficken et al. (1985, 1987).

Carolina Chickadee (*P. carolinensis*).—The vocal repertoire of this species of southeastern United States is similar to that of the parapatric Black-capped Chickadee, the two hybridizing in certain areas of contact but not in others. The major study of the Carolina Chickadee’s vocalizations is Smith (1972).

The tonal “whistled song” was long ago recognized to have about four notes in contrast with the Black-capped Chickadee’s two-noted fee-bee (Thönen 1962:117; Robbins et al. 1966:214, 1983:228, Ward 1966:141, 143, 146; Smith 1972:67–70; Ward and Ward 1974:351; Jellis 1977:164, fig. 62g; Latimer 1977:421). In addition abnormal songs from southern Pennsylvania are shown by Ward and Ward (1974:347), who state that these may be the result of hybridization or variants used to defend interspecific territories in an area of overlap. Although the song is typically a doubling of the Black-capped Chickadee’s fee-bee, with a drop in pitch for the second couplet, Ward (1966:134, table 2) showed that songs may range from one to 12 notes. Like the fee-bee, these songs are commonly sung on territory by males in spring.

Chick-a-dee calls have been published only as hand-traced spectrograms on a 0–8 kHz scale (Smith 1972:76–78), although emphasized components of some notes commonly lie above 8 kHz. Smith recognized three note-types: an HF-note (termed “High Tee”), an IF-note (“Chick”), and an LF-note (“Dee”). Her fig. 2.15C (p. 76) shows an HF-IF intermediate, and fig. 2.26C (p. 77) shows two longer-duration HF-notes labeled “High See.” The text (p. 49) states that these two note-types “intergrade completely.” Therefore, in a direct comparison with the Black-capped Chickadee, High See = A, High Tee = B, Chick = C, and Dee = D, except that the first two intergrade in the Carolina Chickadee but do so only rarely in the other species (Hailman et al. 1985). Figure 2B (left) shows a chick-a-dee call, where it can be seen that the first HF-note peaks at about 9 kHz and the three introductory notes appear to present a graded series.

Smith (1972:62–67) showed many spectrograms of obvious gargle homologs to which she gave a variety of names: T-slink, Click-rasp, Tee-rasp, Rasp-slink, and Slink-rasp-slink. The calls are composed of typically slurred notes that tend to decrease in frequency and end with some sort of trill. The note-types shown in 19 spectrographed gargles are more diverse than the verbal labels imply, and the gargoyle system of the Carolina Chickadee appears virtually identical with that of the Black-capped Chickadee. Figure 2B (right) shows a gargoyle following a chick-a-dee call; the apparent pause within the vocalization is due to rapid transients that do
not show on the spectrogram. This species sometimes runs together chick-
a-dee calls and gargles thus, or may have intermediate vocalizations. The
next species below sometimes inserts gargles into song, further demon-
strating some interesting vocal complexity in this subgenus.

Willow Tit (P. montanus).—Formerly classified as conspecific with the
Black-capped Chickadee, this widespread species is common in Europe
and ranges east across Asia. The vocal repertoire is very similar to those
of the Black-capped and Carolina chickadees. There are two major geo-
graphic variants of a simple song. One is a repeated, whistled downslur
ending in a pure tone (Thönén 1962:117; Thielcke 1968:151, 1969b:323,
figs. 6a and b; Ludescher 1973:13, figs. 4g–m; Jellis 1977:164, figs. 62b
and c; Latimer 1977:418 bottom; Romanowski 1978:248, 1979:60; Berg-
mann and Helb 1982:339, fig. a). The other is a succession of tonal notes,
much like the whistled fee-bee of the Black-capped Chickadee, but re-
maining on virtually the same pitch throughout (Thönén 1962:117;
Thielcke 1969b:323, figs. 6c and d; Jellis 1977:164, figs. 62d and e; Ro-
manowski 1979:56, 61; Bergmann and Helb 1982:339, fig. b). Thönén
(1962) found in Switzerland that the slurred song is characteristic of the
plains and the tonal song of the Alps. However, I have recordings from
Norway of nearly tonal notes (with a slight initial downslur). The literature
suggests that a male sings only one basic song, with minor variations, and
there are no local dialects, but as Haftorn (in litt.) points out, whether the
variants are minor variations or major song-types is a matter of definition.
Romanowski (1979) found by playback experiments that the downslurred
part of the first song-type was relatively unimportant in eliciting responses,
the important part being the pure-tone frequency at the end (which is
common to both songs).

The chick-a-dee calls are similar to those of the Black-capped Chickadee
(Thielcke 1968:154; Ludescher 1973:12, figs. 3m–o; Jellis 1977:171, fig.
68b; Latimer 1977:426; Romanowski 1978:249, figs. 14a and b; Berg-
mann and Helb 1982:339, fig. d). At least two note-types are revealed in
these spectrograms: an HF-chevron (the “zi” of Bergmann and Helb) and
an LF-note virtually identical with the D-note of the Black-capped Chick-
adee except for longer duration (about 400 msec). The LF-note in fig. 14b
of Romanowski (1978:249) is somewhat transitional from an HF-note.
My Fig. 2C (left) shows three HF-notes followed by the first two of three
LF-notes in a typical call. Ludescher (1973:12, fig. 3n) shows three short
notes before an LF-note, these consisting of stacked chevrons and prob-
ably representing a third type of (IF) note.

The gargle-equivalent of the Willow Tit has at least two interesting
properties (Ludescher 1973:12, figs. 3p–5; Romanowski 1978:249, figs.
14c and d; Bergmann and Helb 1982:339, fig. c). In the last reference, a
trill begins the call, and after a slurred note, a higher-pitched trill ensues, followed by a regular repetition of an HF-note that is so rapid as almost to be trilled as well. Ludescher’s fig. 3q and Romanowski’s fig. 14d also show imbedded trills. The Willow Tit’s gargles thus depart slightly from the generality of a jumble of diverse FM-notes of descending frequency followed by a terminal or subterminal trill. Fig. 2C (right) shows the trill near the end, after five introductory notes, but followed by a string of five notes of one type. The other unusual characteristic is that the Willow Tit commonly inserts gargles within its song (pers. obs.); indeed, Bergmann and Helb (1982) treat this vocalization as “song.”

Mountain Chickadee (P. gambeli).—The vocal organization of this western North American species is similar to that of the Black-capped Chickadee. The only published spectrogram of its whistled “song” appears to be in Gaddis (1985:32, fig. 2, lower right): three tonal notes at about 4.4 kHz. My tapes show that the number of notes in a song varies within one individual, thus suggesting some sort of song-repertoire. Figure 2D (left) shows one note from a vocalization of three identical notes, which are typically “broken” in spectrographic displays, suggesting amplitude modulation.

Chick-a-dee calls appear to have at least four different note types (Robbins et al. 1966:214, 1983:228; Thielcke 1968:154; and Gaddis 1985:32, left side of fig. 2). The two most evident types are a chevron-shaped HF-note (Thielcke 1968: Gaddis 1985:32, figs. 2A–F, H–J) and a banded-to-noisy LF-note (Robbins et al. 1966; Thielcke 1968; Gaddis 1985, fig. 2H and I). There is in addition a shorter-duration IF-note that often appears as a down-slur (Robbins et al. 1966, Thielcke 1968) or a noisy chevron (Gaddis 1985:32, figs. 2G and J). A type of note very common in this species is an “attached” HF/LF-note in which the last chevron of a series is continuous in time with the first LF-note. This HF/LF-note is shown in Gaddis (1985, fig. 2I and J, and in a lesser form in 2H). These three note-types (not counting the attached HF/LF) seem to occur always in the order HF-IF-LF. If there are no IF-notes in a call, there is almost always an attached HF/LF-note between the HF-series and the LF-series. Fig. 2D (right) shows a call with three introductory HF-notes, and “attached” IF-note, and two LF-notes. The first LF-note is banded and the second one noisy; in extreme cases, the banded variant becomes a single tone at about 3.7 kHz, thus reminding one of the song-notes (Fig. 2D, left) in this species.

A third category of major vocalization is somewhat problematical. Dixon (1972) first described the “attack call,” then Dixon et al. (1970:324, fig. 2A) showed the evidently identical “aggressive call” consisting of slurred notes that decrease in average frequency. Their fig. 2D of a “sup-
planting call” ends in partially trilled components, much like the Black-capped Chickadee’s gagle. Whether the calls shown by Gaddis (1985:32, figs. 2L–N, also fig. 5 on p. 39) belong to this same complex is difficult to decide. He divides them into three subtypes and attempts to correlate them with different behavioral contexts (p. 38, table 4) but the sample sizes do not allow firm conclusions. Gaddis identifies (p. 38) one component note-type with “close aggressive contact.”

White-browed Tit (P. superciliosus).—There are no published spectrograms for this species of western China, but I found one type of vocalization in the CLO tapes (Fig. 2E). The first note also occurs as a long repeated series, and I preliminarily interpret these vocalizations as song. The whistled notes at about 3 kHz are very similar to songs of the foregoing species in this subgenus, although the vertical “clicks” may be unique.

Marsh Tit (P. palustris).—The song of the Marsh Tit, a common European species that also occurs disjunctly in eastern Asia, is clearly elaborate with respect to foregoing chickadees and the Willow Tit (Thönen 1962:117; Thielcke 1968:151; Ludescher 1973:13, figs. 4a–f; Jellis 1977:164, fig. 62a; Latimer 1977:418, spectrogram 4 of this species; Becker 1978a, 1978b, 1982:224, Romanowski 1978, 1979:50; Bergmann and Helb 1982:338; Rost 1987). Perhaps the most typical song consists of repeating a downs pitching note somewhat like the plains’ form of the Willow Tit’s song. Many songs, however, are alternations between a downs pitching note and a tonal whistle, or in some cases even more complexly arranged with two slurs, or trills, or trills and slurs (see esp. Ludescher 1973, Romanowski 1978, Becker 1978b, Rost 1987). The trilled elements in song are unusual for a parid, and suggest affinities with gargles; recall that the Willow Tit inserts gargles within its singing bouts. Marsh Tit males have repertoires of up to 19 different learned songs. Although females sing less than males, the size of their repertoires and tonal quality of their songs are comparable. There are local dialects, and some indication that different songs tend to be used in territorial defense and courtship. Romanowski (1979) found by playback experiments that the most critical variables in song-recognition were the frequency modulation and the intervals between successive notes.

The Marsh Tit also gives typical chick-a-dee calls (Thielcke 1968:154; Ludescher 1973:12, figs. 3a–k; Jellis 1977:171, fig. 68a; Latimer 1977:425; Romanowski 1978:241, figs. 6c and 7a; and Bergmann and Helb 1982:338, fig. d). At least three, probably four, note-types can be separated. There is a broad HF-chevron and probably a separate HF-type with small-amplitude, rapidly-modulated FM-excursions superimposed on the shallow downslope following the chevron’s peak (the “pistjä” note in Bergmann and Helb). An IF-note is a simple, emphatic downs slur. The LF-note is
of short duration (50–100 msec), called “dā” by Bergmann and Helb, and its frequency banding consists of stacked chevrons. Fig. 2F (left) shows a chick-a-dee call, with introductory chevron followed by a downslur then two further small notes before the string of six LF-notes; another downslurred note concludes the call, showing permutation of note-types in this species. The close relationship between the chick-a-dee call and song in the Marsh Tit is illustrated by fig. 7 in Romanowski (1978:241), showing rare intermediate vocalizations as the bird switches between song and call.

The third major vocalization is included as “territorial song” by Latimer (1977) and as a call by Bergmann and Helb (1982); it appears to be the Marsh Tit’s functional equivalent of the gargo, and Ludescher (1973:12) says it is always associated with fighting (see Ludescher 1973:12, fig. 31; Latimer 1977, spectrograms 1–3 of this species; Romanowski 1978:241, figs. 6a, b and d; Bergmann and Helb 1982, fig. c). Ludescher phoneticizes it “si-illuoi,” Latimer “pitchew,” and Bergmann and Helb “pistjū.” Typical calls consist of a jumble of highly slurred notes that tend to decrease in average frequency. Terminal notes sometimes show rapid frequency modulations superimposed over a downslur (see esp. spectrograms 2 and 3 of Latimer), which are roughly the equivalent of terminal trills in gargles of other species. Fig. 2F (right) shows a typical example of the gargo, but with no indication of the trilling.

Sombre Tit (P. lugubris). — This Eurasian species ranges westward through Turkey to Greece. The phonology of notes in song is unlike that of any other tit voice I have seen (Latimer 1977:421; Bergmann and Helb 1982:340, figs. a and b): densely trilled HF-notes. Fig. 2G (left) from a tape provided by M. Duijim shows a double-chevron making a phrase that is repeated. The song seems always composed of such two- or three-note phrases repeated up to at least five times.

Alarm-type calls involve about four note-types (Thielcke 1968:154; Latimer 1977:426; Bergmann and Helb 1982:340, figs. c and d), including two HF-notes (“zi” and “tsi” of Bergmann and Helb, those in Thielcke being “tsi” and those in Latimer possibly being “zi”). Both are rapid trill-bursts. The simple, slightly noisy chevrons that Bergmann and Helb term “trerr” (fig. d) are those in Latimer’s call, and seem to be a low-pitched IF-note. The LF-note is called “trrr” by Bergmann and Helb, and is the long string illustrated in Thielcke. Figure 2G (right) shows such a string taken from tapes provided by Thielcke. As the number of notes of a given type and the note-type composition of calls clearly varies combinatorially, there seems little question that this is chick-a-dee system.

Mexican Chickadee (P. sclateri). — The spectrograms in Dixon and Martin (1979:422) document at least two major vocal types in this Mexican
species, which ranges northward barely into southern Arizona. A forthcoming study by M. S. Ficken (unpubl. data) on the entire species’ vocal repertoire will document separate song, chick-a-dee calls and gargles.

Dixon and Martin (1979:423, fig. 2) presented a variety of vocalizations “used in territorial defense” and attempted to show differential use (table I, p. 422), although samples are too small for drawing firm conclusions. They identified the “peeta-peeta” vocalization (fig. 2b) as song, noting that it was uttered at dawn and “functions both in attracting a rival to a boundary and in reiterating boundaries from a distance” (p. 422). Their fig. 2b, however, appears to be of two individuals calling simultaneously. Fig. 2d, which they term the “speetit-speetit” call, shows phrases of similar phonology. Ficken (unpubl. data) found autumnal songs to be relatively simple structures of one type of HF-note followed by several repetitions of a lower note. This song is similar to the vocalizations shown by Dixon and Martin. In spring, however, Ficken found that song was more elaborate, and had combinatorial properties. Her birds used three phrases: a chevron-couplet of higher then lower notes (S), a densely trilled tone (T), and a short, rapid phrase of a chevron with slurred notes (U). Songs consisted primarily of repeated S-phrases or alternating T/U combinations, with one song being SSSTUT. Insofar as I can determine, this combinatorial construction of song has been reported for no other species in the Paridae.

Chick-a-dee calls are composed of four note-types (Dixon and Martin 1979:422, fig. 1): two types of HF-notes, one IF-note and an LF-note. One HF-note is a rapid FM, low-amplitude trill with a steady carrier frequency of about 7 kHz, and the other is a chevron-shaped note. The IF-note is a downward slur, and the LF-note is typically banded. Ficken’s (MS) characterization of chick-a-dee calls is similar. A trilled HF-note I found on chick-a-dee calls of CLO tapes is reminiscent of more densely trilled HF-notes of the Sombre Tit.

There are also typical gargle vocalizations consisting of a jumble of different note-types, typically descending in average frequency and commonly ending in a trill-like utterance (Dixon and Martin 1979:422, figs. 2a and c: the “swehbegeet swehbegeet cheeyay” and “swehbegeet chee-yay”). In addition, the “sitchowee” (fig. 2e) seems to be a gargle with only a short concluding trill. Ficken’s (unpubl. data) spectrograms are similar.

Siberian Tit (*P. cinctus*). — Unless the Black-capped Chickadee and Willow Tit are considered conspecific, the Siberian Tit is the only *Parus* common to the Old and New Worlds, due to its quasi-circumpolar distribution that extends from Norway east to Alaska and western Canada. Its vocal repertoire was sketched by Haftorn (1973), revealing three major
vocal types, perhaps organized somewhat differently from all foregoing species.

The first major vocalization is what Haftorn (1973:94, fig. 1f) shows as the “p’tri poi”—an unusual vocalization that begins with a faint HF-note, followed by one or two broad-frequency notes of very short duration, and ending with a rising, tonal glissando. His spectrograph shows a tonal note at about 4 kHz overlying the first part of the call. A variant is phoneticized in the text (p. 95) as “p’tri-pyy.” Haftorn refers to this vocalization guardedly as “song” with analytical notes worth reading. Fig. 2H (left) shows this vocalization, taken from one of Haftorn’s recordings; two faint HF-notes begin this particular example. The “territorial song” pictured by Latimer (1977:421) does not show the faint introductory note, and the final note of his song falls rather than rising in frequency. The repeated “tschi” shown by Bergmann and Helb (1982:341, fig. a) is similar. Haftorn (p. 96) notes that this is usually a male vocalization but the “female can sing on rare occasion.” Bergmann and Helb (1982:341) also include as song combinations containing the LF “dschee” notes, which clearly belong to the chick-a-dee complex (below). Finally, Holm (1982), without citing Haftorn (1973), argued that the term “song” should be applied to the last of the three major vocalizations (discussed near the end of this account).

Combinatorial chick-a-dee calls involve several note-types (Haftorn 1973:94, Bergmann and Helb 1982:341). Calls tend to conclude with an LF-type of note termed “tae” by Haftorn and “dschee” by Bergmann and Helb. These are typical LF-notes whose structure ranges from banded to noisy (compare spectrograms in fig. 1a, b and c of Haftorn, loc. cit.). The middle note in Fig. 2H (right) is one of this LF-type. Notes associated with (and usually preceding) the LF-notes appear to be unusually diverse. The commonest, and one often given in isolation uncombined with other note-types, is a variable HF-note consisting of an emphasized chevron peaking at variable frequencies, with possible parallel components at higher and lower frequencies. This note-type is termed “piv” by Haftorn (1973:94, fig. 1e). Haftorn (fig. 1d) shows a noisier variant called “pév” and refers in the text to a yet hoarser variant (“pêv” not spectrographed); the last two notes in Fig. 2H (right) are of the “pév” type. A second kind of introductory note is termed “tsi” but not figured in Haftorn (1973). I believe this to be the shorter-duration, chevron-shaped HF-notes “zi, dü” and “ti” shown by Bergmann and Helb (1982:341, fig. d). The note “pst” preceding LF-notes in Haftorn (fig. 1b) appears to be identifiable with the “zi” of Bergmann and Helb. A third kind of chick-a-dee note is the “ti” of Haftorn (1973:94, fig. 1a), which is a noisy chevron of the IF-type
somewhat similar to the Black-capped Chickadee’s C-note. This “ti” is probably the “zit” of Bergmann and Helb (1982:341, fig. c). Haftorn (p. 96) refers to a double “titi” form of this note. The first two notes in Fig. 2H (right) may be this repeated “titi.” In addition to the four or more foregoing chick-a-dee notes, Haftorn detected combinations with other kinds of notes. He thus refers (p. 98) to a “sisitisææ” call combining the “hawk alarm” sisi with the tææ notes of the chick-a-dee call. Another variant mentioned is “pist pist tææ tææ tææ,” where the “pist” may be a variant of the pst-note mentioned above.

The third major vocalization is the “ttrrryy” trill shown in Haftorn (1973:94, fig. 1g), which he notes (p. 97) is a “warning or aggression call.” This call was given in response to playbacks near the nest site, and consists of a simple 300-msec trill centered at 3–3.5 kHz. There is no indication of this vocalization being used combinatorially, but it appears similar to trills concluding gargles of the Black-capped Chickadee; however, it may also be allied phonologically with the trills used in other vocalizations by the Sombre Tit and Mexican Chickadee. Holm (1982) argued that the trill (which he phoneticized “yrr”) is the true “song” of the Siberian Tit, as he could hear it over relatively long distances in spring. What I have listed at the outset as “song” (and Holm phoneticizes “titsiloi”), he says is used in direct aggressive interactions. Clearly, further study of this species is warranted.

**Boreal Chickadee (P. hudsonicus).—** McLaren (1976) remains the sole modern study devoted to vocalizations of this basically Canadian species. It has been recorded recently and extensively by M. S. Ficken (pers. comm.). Early field workers reported that the Boreal Chickadee lacked simple whistled songs of more familiar chickadees, and used more-or-less in its place a varied “warbling song” (e.g., Allen 1910). McLaren (1976:455, fig. 2A) stated that this was the vocalization she spectrographed and termed the “musical call.” The call or song consists of a repeated sequence of about four highly slurred HF-notes that descend in frequency through the phrase. It thus has phonological affinities with the gurgle of the Black-capped Chickadee and similar species. The musical call is given only by males in territorial situations.

A chick-a-dee call of HF-LF notes was first published as a tiny spectrogram in Robbins et al. (1966:214, 1983:228); see also Thielcke (1968:154) and Latimer (1977:426). McLaren (1976:452, figs. 1A and B) provided two other spectrograms ending in LF-notes, but pointed out that two further note-types are commonly incorporated into chick-a-dee calls. The introductory HF-notes appear as chevrons of decreasing peak frequency, the last emphasizing the descending arm so as to appear almost as a downward slur (esp. her fig. 1B) or being virtually continuous with the first LF-note (esp. fig. 1A). The LF-notes have a broad frequency range
and are distinctly banded. A longer-duration HF-note, which McLaren calls the "seep" (fig. 4C, p. 459), may be incorporated into chick-a-dee calls or given as common, separate notes. Also, the "chit" (fig. 4E, p. 459) may be a component of chick-a-dee calls; it is a short-duration IF-note with noticeable banding in the lower frequencies and upward frequency modulation. McLaren mentioned several ways in which chick-a-dee calls vary. Fig. 2I (left) shows a typical chick-a-dee call, provided by Leonard Peyton from Alaska. The near attachment of the last HF-note to the first LF-note is typical for this species, and reminiscent of the Mountain Chickadee's calls.

Similar in usage to the musical call, but distinct phonologically, is the "trilled call" (McLaren 1976:455, figs. 2C and D). This trilled call consists of a jumble of highly slurred notes ending in a trill of distinct notes. The jumble is highly variable, and this call seems equivalent with the gargle of the Black-capped Chickadee. Furthermore, I think it likely that what McLaren termed the "rapid musical call" (fig. 2B) is in fact a gargle lacking the terminal trill, as it is a jumble of notes unlike the repeated phrases of the musical call. Fig. 2J (right), taken from CLO tapes, shows a trilled call that is nearly identical with McLaren's fig. 2C (p.455). In fact, it is not certain that the musical and trilled calls represent separate vocal systems; if they are all allied to gargles of typical chickadee species, then the Boreal Chickadee could be said to lack separate song.

Chestnut-backed Chickadee (P. rufescens).—I cannot find spectrograms from this species of the Pacific coastal region of Canada and northwestern United States. Bowles (1909:56) likened the "very pleasing and quite lengthened song" to that of the Chipping Sparrow (Spizella passerina). Bent (1946:390), quoting a description by Dawson, added a repeated double-noted song "ch lulip, chulip," etc. Figure 2J (left) shows a five-noted phrase from repeated song on CLO tapes.

Early workers also realized that the Chestnut-backed Chickadee possessed a chick-a-dee-like call (Bent 1946:389). Figure 2J (middle) shows a short chick-a-dee call from my tapes that suggests at least three note-types are used. Figure 2J (right) shows part of an apparent gargle taken from CLO tapes, consisting of a typical jumble of notes decreasing in average frequency. However, this type of call is so similar to the apparent song of this species that they may simply be variants of one vocalization type.

Melaniparus: African Tits

All the Parus of Africa south of the Sahara, about a dozen species, are in this subgenus. For no species could I find a published spectrographic study. No distinction is made below between afrer and the South African African endemic cinerasens, as the two were not distinguished at the time
recordings available to me were made. The survey lacks several African forms: griseiventris (a South African endemic), leucomalas, leuconotus, the niger-carpi complex, and rufiventris. The species treated are presented in alphabetic order of their Latin names, and spectrograms are from CLO tapes except where noted.

Tapes of the African Grey Tit (P. afer) made by H.-W. Helb were supplied by G. Thielcke. Fig. 3A (left) shows a repeated note, which apparently represents song. Figure 3A (right) shows the last part of a chick-a-dee-like call; it was preceded by two HF-notes similar to the first shown. There are thus at least an HF- and LF-note, with some tendency toward intermediates between the two strings.

The White-bellied Tit (P. albibventris) of east Africa possesses a chick-a-dee-like vocalization (Fig. 3B). All but the first slurred note show signs of frequency-banding, and there seems to be a variety of LF-type notes. The fourth note from the left (complexly banded and at higher frequencies) appears to belong to another bird (probably another species) calling at the same time. Fig. 3C shows two chick-a-dee-like calls taken from CLO tapes of the Striped-breasted Tit (P. fasciiventer). The calls suggest a combinatorial system with at least two types of HF-notes and an LF-type. Figure 3D shows a chick-a-dee-like call from the Red-throated Tit (P. fringillinus) with at least one HF- and one LF-note and a possible intermediate type.

The Dusky Tit (P. funereus) is the only species besides the African Grey Tit for which I have evidence of possible song (Fig. 3E, left). Whether or not this four-note phrase actually is used like song remains to be determined; similar phrases repeat on the tape in the manner of a perched male singing. The Dusky Tit also has a chick-a-dee-like call (Fig. 3E, right). Here the double couplet of unstructured introductory notes is shown with the first two of a long string of virtually identical LF-notes, which show typical frequency-banding.

Paradaliparus: Three Far-eastern Endemics

Little is known of the voice of the Palawan Tit (P. amabilis), a Philippine endemic from the island of Palawan. Tapes provided by Jelle Scharringa contain at least two types of song-phrases (Fig. 3F). One consists of two notes repeated over and over (left) whereas the other is a repeated note (right); these songs were adjacent on the tape so probably came from the same individual, suggesting the possession of song-repertoires.

The Elegant Tit (P. elegans) of the Philippines was also recorded in the field by Scharringa. Fig. 3G (left) shows an extract from one of several song-types, consisting of a two- or three-note phrase repeated over and over. Fig. 3G (right) shows a call composed of two LF-notes that strongly
Fig. 3. Sound spectrograms of a sample of vocalizations from parid species that do not occur in North America or Europe.
resemble the terminal notes of typical chick-a-dee calls in other species. There is no evidence, however, of this type of note being combined with HF-notes.

The Yellow-bellied Tit (*P. venustulus*) is a species of China which Hans Löhrl had in captivity at Vogelwarte Radolfzell. Through the aid of Gerhard Thielcke and Roland Rost I recorded in a room where many adults and juveniles were caged together. The birds gave spontaneous notes not assembled into calls (Fig. 3H, left), and hence reminiscent of the Coal Tit (cf. Fig. 1F, middle). Thielcke and I copied his tapes of these birds. Figure 3H (middle) shows a commonly occurring series of HF-notes; another form simply repeats the same note in very long strings. These might represent forms of song. That the species also has banded LF-notes is shown by Fig. 3H (right). However, I could not find in any of the tapes indications of combinatorial or semi-combinatorial call structures resembling chick-a-dee calls or gargles.

*Machlolophus* and *Sittiparus*: Two Monotypic Subgenera

Scharringa provided the tapes of the Yellow Tit (*P. holsti*), a Formosan species which clearly has some kind of song-repertoire, as continuous recordings reveal switches in song-types. Tapes show at least two kinds of phrases, one of three HF-notes and another of four. It is typical that the last two notes of a phrase are of the same type. A given phrase is repeated over and over again without pause. The Yellow Tit also possesses combinatorial calls. Fig. 3I (left) shows five note-types in a seven-note call, of which the first three notes are HF-types, the next repeated doublet is more like an IF-type, and the final doublet is one kind of LF-note. There seems to be another LF-like note, shown in Fig. 3I (right), which occurs in long strings (only the first five notes of the call are shown). In a preliminary search I was unable to find this second kind of LF-note combined with any other notes. This situation is reminiscent of the Great Tit, where several kinds of churring occur, not all of which are known to be combined with HF- or IF-notes.

The Varied Tit (*P. varius*) of Japan and Formosa has vocalizations that remind me of no other tit. Fig. 3J (left) shows a repeated two-note phrase that may be song; the doublet of a chevron-like note followed by a W-shaped note occurs commonly in isolation on the CLO recordings. The three-note phrase shown in Fig. 3J (right) is also repeated, and may thus also be song.

**DISCUSSION**

Perhaps the most striking characteristic of vocal organization in the Paridae is that no tit is known to have just one major complicated vo-
calization as songbirds are "supposed" to have. All well-studied parids have at least two distinct, complicated vocalizations or vocal complexes.

What is song?—There are many discussions in the parid literature concerning how "song" is used (Dixon and Stefanski 1965, 1970), which vocalizations should be considered "song" (Haftorn 1973:95–96, Holm 1982), whether "song" is being evolutionarily reduced (Ficken, Ficken and Witkin 1978, Ficken 1981a), and whether certain species even have "song" (McLaren 1976). A phonological approach views oscine song as the longest and most complicated vocalization in the species' repertoire. Such a view is patently inapplicable to tits; e.g., the Black-capped Chickadee's fee-bee "song" fits neither stipulation: it lasts less than 1 sec, compared with some chick-a-dee calls that have durations of 4–5 sec (longer in bouts of mobbing: K. Apel pers. comm.), and chick-a-dee calls are much more complicated (and even they are simple compared with gargles). There exists no single vocalization that is both the longest and most complicated in the repertoire. If one takes a more functional view that "song" is an exclusively male-uttered, long-distance advertising vocalization used simultaneously to repel neighboring territorial males and attract unmated females, the definition again utterly fails with parids. In most parids that have been studied carefully both sexes are known at least occasionally to give all the species' major vocalizations. Furthermore, in some species (especially cinctus, hudsonicus and rufescens), no vocalization seems to carry far enough for long-distance advertising.

The problem with a monolithic view of "song" is that it stems largely from sexually dimorphic, north-temperate, migratory passerines—in which males tend to arrive on the nesting grounds and set up territories before females arrive. Virtually all the world's tits, by contrast, are sexually monomorphic, non-migratory and permanently paired. When the winter flocks break up into pairs, the pairs nest in the same general area. The birds usually already know their neighbors individually so have less need for typical long-distance territorial advertising to newly arriving, unfamiliar males from distant wintering grounds. And males have less need to attract unfamiliar females to their territories.

Haftorn (1973:95–96), following Thielcke (1970), articulated the problem of parid "song" clearly by listing some known functions of song: (1) territorial defense, (2) mate-attraction, (3) strengthening of the pair bond, (4) stimulation of conspecifics in colonial nesters, and (5) synchronization of reproductive development in the mate. The list could be augmented, but its point is clear enough: the usefulness of a signal needs to be judged by the behavioral needs of the species. The present survey shows that almost all parid species possess two or more major vocalizations, suggesting that parid life history is such as to promote evolution of several
major signals in place of monolithic song in many other oscines. I envision a contextual or functional hyperspace into which the communicative domains of major vocalizations map differently in different parids, but all within the domain of monolithic vocalization of most oscine birds. That is, if we could identify the variables defining contexts in which vocalizations were given, these variables would probably be more than three in number, so define a hyperspace. Monolithic song of most passerines would plot over a large portion of this hyperspace; in tits, that portion would be broken into three or more parts for the major vocalizations, but in each species the partitioning of the hyperspace would be somewhat different.

Communicative functions of the major vocalizations.—Based on obviously fragmentary evidence I will speculate about the communicative functions of the three classes of major parid vocalizations: (1) What has been termed "song" is given more commonly by males than females and more commonly on spring territory than at other times of year or elsewhere. Such song is elaborated differently in different species: some have only a single kind (e.g., the Black-capped Chickadee's fee-bee), others have several song-types that tend to be used in different contexts (e.g., Blue Tit), and still others have repertoires that are apparently not contextually differentiated (e.g., Great Tit). At heart, what unites "songs" is their species-specificity: closely related sympatric species can be separated readily by song. Whatever else they do in a given species, songs may insure that mistakes in mate-choice are rarely made. My colleague Charles T. Snowdon (pers. comm.) trapped reputed Carolina Chickadees near Philadelphia at the study site of Smith (1972), and his caged birds formed pairs. When spring came one male unexpectedly began singing the fee-bee song of the Black-capped Chickadee and his mate suddenly and permanently deserted him. (2) The chick-a-dee call-complex sensu stricto occurs only in certain species but roughly equivalent vocalizations of various degrees of "alarm" exist in most parids. These are the vocalizations given in mobbing of predators by almost all tits, but clearly used in a variety of other contexts depending upon the species. This is the functionally most complicated major vocalization in many tits, and may be related primarily to movements of the birds in space. (3) Gargles have been studied intensively only in the Black-capped Chickadee, but many other species possess an equivalent vocalization and still others a probable equivalent (e.g., "conflict call" of Blue Tit, "muttered threat" of Great Tit, "call derivative" of Plain Titmouse). These usually complex calls are uttered in very-short-distance communication: commonly accompanying physical combat or in propinquitous agonistic encounters, but also reported in some species as given by mates at the time of copulation.
What is vocal homology?—Various kinds of vocal "equivalencies" do not covary in tits. For example, "song" may be roughly equivalent functionally but is phonologically so diverse that no individual note-homologies can be drawn among any but closely related species. Another kind of equivalency is the basic HF-(IF)-LF plan, which underlies nearly all parid vocalizations: "song" of the Blue Tit, churring of the Great Tit, all chick-a-dee calls and gargles of species that have them, as well as functional equivalents in other forms (e.g., "conflict" call of the Blue Tit). The very fact that the same organizational plan underlies all major vocal types shows that there is no contextual homology. Furthermore, phonological similarity in specific notes occurs among different major types of vocalizations; e.g., diverse notes in Blue Tit songs may be likened to notes found in chick-a-dee calls of other species. Ficken (unpubl. data) found that one "simple" call of the Black-capped Chickadee's repertoire is missing from that of the Mexican Chickadee, yet in the latter species another call's domain of contextual use is expanded to cover the context of the "missing" vocalization. Indeed, some calls are phonologically different in the two species while having the same use-pattern, whereas other calls that are phonologically very similar have different uses in the two species. In sum, to draw a parallel (Hailman 1976): a bird's wing and a bat's wing are not homologous structures as wings but they are homologous as vertebrate forelimbs. When one asserts that two vocalizations appear to be "homologous" it is necessary to make clear in what way they are homologous.

Types of vocal diversification.—Vocalizations are virtually always communicative; communication is the transfer of information; information is variety; therefore, vocalizations must vary in some way in order to communicate information. The differentiation of two or more kinds of major vocalizations in parids is itself a form of information-laden variety, but within kinds can be seen two principles of vocal diversification.

First is variety of phonological structure. This is the common pattern in song of oscines, where repertoires are almost always strictly non-combinatorial. Each song-type may be composed of two or more kinds of note-types, but usually those note-types are unique to that song-type and not used in some different pattern of another song-type. Note-diversity is also evident in the large repertoire of isolated call-notes of the Coal Tit.

The other principle is analogous with human language: a relatively few acoustical elements are used combinatorially to produce a far larger diversity of unit-utterances. Thus in the Black-capped Chickadee's chick-a-dee call-system four distinct note-types are used in combination to produce hundreds of different call-types. In fact, mathematical analysis
shows that there is no limit to the number of different chick-a-dee calls—the repertoire is "open" or theoretically "infinite" (Hailman et al. 1985). Note-types virtually always occur in a fixed sequence within the call, but in the Black-lobed Tit's mobbing calls note-sequences are not so constrained: permutation can also diversify vocal systems beyond the variety created by combination alone. The principle of combination-permutation can also occur in parid song, as evidenced by the Mexican Chickadee—highly unusual for an oscine.

These two principles of vocal diversification can also operate together as in gargles of the Black-capped Chickadee. Here there exists a local "pool" of phonologically distinct note-types. A given gargo utterance draws notes from this pool and strings them together according to a pattern of decreasing average frequency, commonly ending with one of the trill-types from the "pool." This vocal procedure produces a huge variety of gargles, with nearly every utterance sharing at least one note-type with most other such utterances.

It is possible that acoustical variety represents information at a different level: instead of each variant representing a different message, it is the ensemble's diversity per se that is informative. For example, several hypotheses have been proposed to account for diversity of song in tits (see, for example, the following references on the Great Tit: Baker et al. 1986: Krebs 1976, 1977a, 1977b; Krebs et al. 1978; Lambrechts and Dhondt 1988; McGregor and Krebs 1982a; and others cited in the species-account above). These hypotheses include: (1) avoiding habituation in the receiver by frequent switching of song-types; (2) deceiving neighboring males into believing that many different males are present; (3) stimulating females, which reputedly prefer males with large repertoires, perhaps because these correlate somehow with good genes for passing to the offspring; and (4) avoiding motor-exhaustion of the muscles of the syrinx, necessitating switching to a new vocalization in order to keep singing. Whether or not other parid vocalizations similarly show variety "for the sake of variety" is unknown but it seems possible. For example, gargles of the Black-capped Chickadee show immense variety based on combinatorial principles and it seems unlikely (to me) that every combination could "mean" something different.

Vocal evolution in the Paridae. —Finally, I attempt a tentative overview of the evolution of vocal organization in the Paridae, restricted to the six subgenera in which vocalizations have been studied extensively. (1) The Crested Tit must be something like the ancestral parid, with a weakly differentiated vocal repertoire consisting of the basic HF-LF unit-pattern shown in Fig. 1A (above). Advertising seems to consist of repeating this unit; alarm-calling consists of giving fewer introductory HF-notes and
extending the train of LF-notes. Shorter calls consist of weakly modified "extracts": several HF-notes, or several LF-notes or a few of each in the sequence HF-LF. The transition between the two note-types often produces phonologically distinct notes, and these proto-IF-notes may sometimes be used in short calls. However, Martens (in litt.) points out that the vocalizations of *cristatus* might be secondarily simplified, as its poorly studied relative *P. dichrous* apparently has rich song.

From this poorly differentiated vocal organization, evolution appears to have taken at least two initial routes. (2) The American titmice possess more clearly differentiated vocalizations of songs and complex calls. The songs, emphasizing repeated HF-notes, form large repertoires in some species, and song-types tend to be used differentially in different contexts. The calls seem to be intermediate between the unit-pattern of the Crested Tit and the chick-a-dee calls of chickadees and their close relatives. (3) The Blue Tit has differentiated and more-or-less stabilized several versions of the unit-pattern. A number of these versions are used as "song," where LF-notes tend to be dropped and HF- and IF-notes differentiated. As in the titmice, these versions are not song-repertoires in the usual sense of equivalent vocabularies, but rather tend to be used in different behavioral contexts. Other variants concentrate on the LF-end of the continuum, yielding "alarm" vocalizations that are not as chick-a-dee-like as those of the titmice. Still a third vocal type may be differentiated into the "conflict" call used for social interactions at close quarters. The result of these evolutionary changes is differentiation of the forerunners of three major types of vocalizations that characterize many of the remaining parids.

The remaining three paths lead to more complex vocal organization. (4) In the Coal Tit and its relatives the presumed ancestral diversity of contextually different songs is solidified into a repertoire of more-or-less equivalent song-types. Probably quite independent is the near loss of LF-notes from mobbing and alarm vocalizations, with the elaboration of isolated HF-notes in this context and in general social interactions covered contextually by chick-a-dee calls in other species. (5) The Great Tit and its relatives represent a similar route of development, having solidified a song-repertoire parallel with that of the Coal Tit. Alarm and mobbing, however, have gone exactly in the opposite direction, emphasizing the "churring" LF-notes with apparent reduction of the HF-introductions. And unlike the isolated-note calls of the Coal Tit, the Great Tit has evolved fewer note-types but uses them together to make calls of various combinations. Finally, (6) typical chickadees and their European counterparts are characterized by usually simple song, well-differentiated chick-a-dee calls, and well-developed gargles. Typically there is only one song-
type—thus rendering the distinction between differential usage and repertoire-equivalents a moot question. The Marsh Tit's more repertoire-like organization suggests primitiveness within the subgenus. These species are also characterized by the evolution of a manifestly combinatorial chick-a-dee call-system employing four (or more) stable note-types. Finally, the chickadees have well-developed gargles based on structural rules for selecting a diversity of note-types from a shared “pool” which shows microgeographic dialectical variation.

Figure 4, a tentative model of parid vocal evolution, takes a novel approach by creating a matrix of song-organization vertically and call-organization horizontally, with gargoyle-like vocalizations omitted due to the uncertain comparative evidence available. Species are placed together in the most appropriate cell(s); in some cases there is sufficient diversity within a group that not all species fall unambiguously into one cell, even though placed there together; in the case of chickadees and related species the song-diversity is sufficiently great that I have scattered the species into subgroupings in the rightmost column of the figure to suggest this diversity.
All groupings are shown by the vertical arrows as independently evolved from a common ancestor, with the horizontal juxtaposition of arrows suggesting affinities of groups (thus the caeruleus-cyanus group may be close to the major-monticolous-xanthogenys group, and cristatus may be close to the North American titmice). When an arrow passes through a cell, this suggests that an intermediate ancestor may have possessed the cell's vocal organization (e.g., the immediate ancestor of the ater group may have had contextual songs, and its ancestor may in turn have had a “unit-vocalization” of the cristatus type). Fig. 4 is a crooked wheel, but as it is the only wheel in town it may be sufficient to get us to the next way-station of understanding parid vocal evolution.

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I want to express special thanks to Stephen Nowicki, M. Duijm, Leonard Peyton, and Jelle Scharringa, who all provided tapes of various species. Yngve Espmark was my supportive host for a productive semester in Europe, supported by the Fulbright program and the University of Trondheim. American field work was supported in part by grants from the Wisconsin Alumni Research Foundation administered by the Graduate School of the University of Wisconsin-Madison, and further support came from the Department of Zoology. Among those who helped importantly in numerous ways (especially field work) are Thomas Bicak, Tor Bollingmo, Eberhard Curio, André A. Dhondt, Robert W. Ficken, Karl A. Hailman, P. Eric Hailman, Olav Hogstad, Donald Jenni, Jaap Kruijt, Randi Reinertsen, Roland Rost, Klaus Schmidt-Koenig, Nathan Shambaugh, and the late Klaus Immelmann, in whose memory this paper is dedicated. Among undergraduate assistants who have logged and spectrographed tapes I single out Randall Detmers, Timothy Fenske and Ilse Olson as especially helpful and competent; my graduate student P. Janine Clemmons also provided key help late in the game.

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SHORT COMMUNICATIONS

Black-capped Chickadee summer floaters.—Summer floaters are sexually mature birds which, although physiologically capable of breeding, are prevented from doing so by some factor such as the territorial behavior of others. Floaters are sometimes referred to as surplus birds or population reserve (Brown 1969).

At one time, it was considered sufficient proof of the existence of floaters if removed birds were replaced during the breeding season, even if the replacements were all unbanded (e.g., Hensley and Cope 1951, Stewart and Aldrich 1951). However, replacement birds can come from a variety of sources. Krebs (1971), who removed 13 breeding pairs of Great Tits (Parus major) and got rapid replacement of both sexes, found that his replacements were not true floaters but were instead birds that had occupied inferior territories nearby. More recently Dhondt and Schillemans (1983) have shown that some populations of Great Tits can have highly complex social systems permitting a number of classes of sexually mature, breeding individuals to live within areas defended by others; most of these classes are not floaters at all. Even in recent removal experiments, reports of unbanded replacements that are almost certainly floaters are common (e.g., Gauthier and Smith 1987, Pedersen 1988). However, only when replacement birds are individually marked and their previous behavior known (Smith 1978, Saether and Fonstad 1981, Beletsky and Orians 1987), can one be sure that they are, in fact, true floaters.

In most cases, very little has been reported of the past history of floaters. Clearly, this is most easily studied in resident species where individuals can be marked early in their lives and followed year-round. The Black-capped Chickadee (Parus atricapillus), being resident over most of its range, is thus an excellent subject for this sort of study. I report here on the summer floaters in my Massachusetts study area over a period of nine summers (1980–1988).

Study area and methods.—The study area, approximately 35 ha composed of about one third mixed woods, one third old field, and one third residential area, located adjacent to Mount Holyoke College in western Massachusetts, has been described in some detail elsewhere (Smith 1984). The winter population has varied from 37 to 72 chickadees with an average of 55; the breeding population has varied from 12 to 16 pairs with an average of 13.4 breeding pairs. I have color banded the chickadees in this area each year since the fall of 1979. Throughout each fall, winter, and spring, observations were made at least once weekly; through June and July, data were collected approximately every two weeks. Because I am also studying long-term survivorship, I have made no removal experiments during the breeding season.

Results.—Table 1 shows the numbers and identity of the summer floaters found within the study area from 1980 through 1988. This includes seven males and four females, a total of 11 floaters in nine summers.

No unbanded summer floaters were seen in the study area in any year. Hence all summer floaters, at least in this period and location, came from the birds that were present locally the previous winter.

Neither sex had floaters every year: male floaters were found in five of the nine summers and female floaters in only three of the nine. Male floaters were fairly easy to find and to follow. Indeed, three males actually sang in certain areas, typically the least used corners of breeding territories, and especially once incubation had begun. The other four males were not heard singing during the summer. Nevertheless, even these males were easily found after sufficient time. By contrast, female floaters were very much harder to locate and
TABLE 1
OBSERVED SUMMER FLOATERS

<table>
<thead>
<tr>
<th>Year</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1981</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1982</td>
<td>—</td>
<td>AG RK</td>
</tr>
<tr>
<td>1983</td>
<td>AY RO</td>
<td>—</td>
</tr>
<tr>
<td>1984</td>
<td>AY RO</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>AR BG</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>AK RO</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>AY RR</td>
<td>—</td>
</tr>
<tr>
<td>1985</td>
<td>AY RG</td>
<td>AR BO*</td>
</tr>
<tr>
<td>1986</td>
<td>AO KK*</td>
<td>AO OO (f.s.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AO BB*</td>
</tr>
<tr>
<td>1987</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1988</td>
<td>AK OY (f.s.)</td>
<td>—</td>
</tr>
<tr>
<td>Totals</td>
<td>7 (2)*</td>
<td>4 (0)</td>
</tr>
</tbody>
</table>

* Indicates a summer floater that replaced a breeder during the summer. (f.s.) indicates a former flock switcher.

b Number of repeats are in parentheses.

Extremely difficult to follow, as they were almost entirely silent for much of the breeding season. I am thus fairly certain of having an accurate census of males, but I feel the female data may represent just minimal numbers. Nevertheless, in two years, 1981 and 1984, a female breeder disappeared before the end of egg laying but was not replaced; similarly in 1987, a male territory owner vanished, and the widowed female remained unpaired all summer. This strongly suggests that no floaters of that sex were available in those areas during those summers.

All but two of the 11 birds were floaters for just one summer (their first). The two exceptions, both males, were repeats, spending both their first and second summers as floaters before, as three-year-olds, finally obtaining a territory and breeding. One of these bred for two years before his death; the other is still alive, having bred in the study area for the last three years.

Three of the floaters (two females and one male) succeeded in becoming members of territorial pairs following the summer deaths of breeding birds. Both successful females replaced birds that died before their eggs had hatched. Each started a new nest less than a week after replacement, one approximately 80 m and the other over 100 m from the old nests. In 1986, a breeding male disappeared less than a week after his young had fledged and was replaced by the floater AO KK (Table 1). On at least 12 occasions after this replacement, I saw AO KK bring food to the offspring of his new mate, i.e., young presumably fathered by another bird. The newly formed pair did not breed together until the following year.

One of the most unexpected findings of this study concerns the source of the summer floaters. In the nonbreeding season, my study population contains what is probably an unusually high proportion of flock switchers or winter floaters (Smith 1984, 1987); these may be similar to those found in various European parids (Ekman 1979). I expected that
any summer floaters found in my study population would likely be drawn from those switchers that had survived the previous winter, especially as more than 30 such birds were alive over a total of 9 springs. In fact, however, only two of the 11 summer floaters (one male and one female) were former flock switchers; the other nine had all been regular members of particular winter flocks, too low-ranked to obtain breeding territories in the spring (Tables 1 and 2).

Only one floater, a male, died during the summer. The others all survived and joined the winter flocks more highly ranked than in the previous winter (Table 2). All eventually joined the breeding population. Interestingly, the eventual rank achieved varied markedly with sex (Table 2). Thus all four female floaters rapidly became the top-ranked females in their flocks. By contrast, only one of the five males for which I have data became the dominant male in his flock. Indeed, three others, including the two males who were floaters for two consecutive years, were in later winters subordinate to younger birds, something rarely seen in parids (Dhondt and Hublé 1968, Glase 1973, Smith 1976).

Home ranges of summer floaters were anywhere from three to five breeding territories. These were always contiguous; I found no evidence of disjunct home ranges such as I found in certain Rufous-collared Sparrow (Zonotrichia capensis) floaters (Smith 1978). Within these ranges, ten of the 11 birds appeared always to avoid any contact with the resident pairs. The exception was a young male former switcher that spent much of his time following one particular breeding pair; he regularly pursued this pair until they would drive him away. Similar following behavior has been reported for a Black-capped Chickadee summer floater by Ficken et al. (1981).

**Discussion.**—Dhondt and Schillemans (1983) found a highly complex social system in some Great Tits, where a given area might be used regularly by several breeding adults (i.e., not floaters) other than the pair that “owned” the territory. No evidence of any such system

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**Table 2**

<table>
<thead>
<tr>
<th>Individual</th>
<th>Rank of initial pair</th>
<th>Next rank</th>
<th>Highest achieved (if different)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Female floaters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AG RK</td>
<td>5 (5)*</td>
<td>1 (4)</td>
<td></td>
</tr>
<tr>
<td>AR BO</td>
<td>2 (2)</td>
<td>1 (2)</td>
<td></td>
</tr>
<tr>
<td>AO OO</td>
<td>f.s.</td>
<td>2 (5)</td>
<td>1 (5)</td>
</tr>
<tr>
<td>AO BB</td>
<td>4 (4)</td>
<td>1 (5)</td>
<td></td>
</tr>
<tr>
<td>B. Male floaters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AY RO</td>
<td>4 (6)</td>
<td>3 (6)</td>
<td>2 (3)</td>
</tr>
<tr>
<td>AR BG</td>
<td>5 (6)</td>
<td>3 (4)</td>
<td>1 (3)</td>
</tr>
<tr>
<td>AK RO</td>
<td>3 (4)</td>
<td>2 (5)</td>
<td></td>
</tr>
<tr>
<td>AY RR</td>
<td>5 (6)</td>
<td>Died over the summer</td>
<td></td>
</tr>
<tr>
<td>AY RG</td>
<td>6 (6)</td>
<td>2 (2)</td>
<td>2 (3)</td>
</tr>
<tr>
<td>AO KK</td>
<td>3 (4)</td>
<td>2 (6)</td>
<td></td>
</tr>
<tr>
<td>AK OY</td>
<td>f.s.</td>
<td>No data</td>
<td></td>
</tr>
</tbody>
</table>
seems to have been found in any Black-capped Chickadee population. Nor is there any account of helpers in this species, although a report exists of possible helpers in the congeneric Tufted Titmouse (Parus bicolor) (Brackbill 1970). Therefore, in the breeding season, any chickadees other than the resident pair but living regularly in an area are apparently always floaters.

Several reports of such birds have been published. In general, they have found, like the present study, that summer floaters typically occur in low numbers, are not necessarily found every summer, and are birds that had been present locally during the previous winter. Thus Odum (1942) found unmated, nonterritorial chickadees in both summers of his study as did Smith (1967). In the latter study I found two females, banded in the area the previous fall that ranged over several breeding territories, that for the most part avoided contact with territory owners. Weise and Meyer (1979) reported six yearling chickadees, nonterritorial during their first breeding season, that all later obtained breeding territories within their previous (last summer’s) home range. Finally, Ficken et al. (1981) describe a banded female summer floater that had been a regular member of a local winter flock prior to that breeding season.

In the current study, the number of summer floaters has varied markedly from year to year, and in several years there were apparently none of one or both sexes. Odum (1942) also found strong changes in floater numbers from year to year. It is interesting that the year when I had the most male floaters there were evidently no local female floaters at all—apparently factors affecting the presence and abundance of floaters may vary with sex. I could find no obvious correlation between floater numbers and any fluctuations in local breeding population. How various social, weather-related, or other ecological factors affect floater abundance in this species remains an interesting area for future research.

Three of my 11 floaters were able to replace territory owners that had disappeared during the breeding season. The two female replacements are relatively unremarkable, each occurring sufficiently early to permit their starting new nests right away. The male replacement is more interesting, since it occurred while there were still dependent offspring fathered (presumably) by another bird. The replacing male fed these offspring, yet he did not get to breed with his new mate until the following year. Similar care of another’s offspring has been found in this species by Odum (1941) and Howitz (1986), although in each of those cases the replacing male was not a summer floater but a neighboring male that had lost his mate. In Odum’s case, the new pair finished raising the first bird’s brood, and they then raised another of their own that same year. By contrast, Howitz’s case, like mine, had the replacing male not breeding with his new mate until the following summer. As Howitz points out, such replacement, even without breeding right away, is still potentially advantageous for the male, since older females are more efficient breeders, and chickadee pair-bonds, once formed, are typically maintained for life.

Given the two repeats, I have observed a total of 13 summers of floating by 11 birds, with only three replacing others over the summer. However, a number of other advantages are potentially available to birds that become summer floaters. One often mentioned possibility involves seeking extra-pair copulations (EPCs) with members of breeding pairs within a floater’s home range. While often suggested for male floaters, this seems unlikely in chickadees. Female Black-capped Chickadees apparently take an active role in selecting partners for EPCs, and they typically choose males that ranked above their own mate the previous winter (Smith unpubl. data). Floater males, being either from the lowest-ranked pairs in the winter flocks or even more lowly flock switchers, will always have ranked below a breeding female’s mate. Therefore a male summer floater’s chances of being accepted for an EPC by a resident female are extremely slim. Nevertheless, it is not inconceivable that
female floaters might engage in EPCs with resident males, especially in light of the rapidly growing body of evidence of within-species social parasitism and multiple maternity (Gowaty and Karlin 1984, Wrege and Emlen 1987, Kendra et al. 1988).

Besides the short-term benefits of possible EPCs as a floater, at least two longer-term benefits may be gained: achieving higher rank in subsequent winter flocks and eventually obtaining a local breeding territory. At first glance, the data seem to suggest a sex difference in eventual winter rank achieved, since all four females rapidly became the top-ranked female in their flocks, while only one of the males did so. Yet there seems no obvious reason why female floaters should be more successful in this respect than their male counterparts. Possibly this apparent difference is only an artifact due to my very small sample size—especially since both the female floaters that were replacements over the summer paired with alpha males.

A consequence of achieving higher winter rank is having an increased chance of obtaining a breeding territory the following spring (Smith 1984). Every bird that survived its first summer as a floater did eventually breed in the study area, although two males did not manage this until their third summer.

Nine of the 11 summer floaters had been low-ranked regulars during the previous winter, with only two having been flock switchers or winter floaters. Yet in all but one year, more of both low-ranked regulars and flock switchers were alive at the end of March, although they left without gaining a territory or becoming a summer floater (Smith, in press). The very fact that so few switchers manage to stay on as summer floaters, whereas so many more low-ranked regulars do, may suggest some competition for the chance to stay on in the spring. Since low-ranked regulars always rank above switchers of their own sex, such regulars could conceivably drive away switchers that might otherwise have stayed on as summer floaters.

This casts an interesting new light on the position of low-ranked regulars in winter flocks. Such birds have more ways of achieving breeding status (Smith, in press) than I had initially thought (Smith 1984). Becoming a summer floater is yet another route whereby chickadees with low winter rank can eventually obtain a local breeding territory.

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LITERATURE CITED


**Boreal Chickadees eat ash high in calcium.**—Birds sometimes eat materials that are not normal food items, compensating for a nutrient deficiency (Kare 1965). In the present instance, Boreal Chickadees (Parus hudsonicus) were observed spending long periods of time eating ash. Observations were made at Newman Sound Campground in Terra Nova National Park, Newfoundland (80 km S. of Gander), from 11 to 16 October 1988. Boreal Chickadees, abundant in the area, foraged in small flocks, often low in black spruce (Picea mariana) and balsam fir (Abies balsamea). Numerous small patches of ash occurred in the campground,
presumably from burned charcoal briquettes. Chickadees ate the ash at only one very small site (about 0.3 m by 0.3 m and several cm deep). This ash was different from nearby ash where chickadees did not feed as it had a consistency appearing as if liquid had been poured on it.

The chickadees spent up to about 1 h at a time, mainly in the morning and late afternoon, feeding solely in the small patch of ash during the six days of observation. They probed their bills into the substance, and tongue movements could be seen. During one 40 min observation period, 64 visits were made, indicating the high intensity of use. The average number of pecks per visit was about 10 per bird (range 4 to 32). As the birds were unbanded, it was impossible to determine if several flocks were feeding there, but at any one time at least five different individuals were present.

When feeding in the ash, the birds showed greatly reduced fear and allowed approach to within about 15 cm. This incredible tameness is indicative of the strong motivation to feed on the ash, as otherwise they had a flight distance of about 2 to 5 m. Usually only one fed at a time, others often waiting nearby. When a chickadee approached a feeding individual, aggression, particularly Gargles (Ficken et al. 1978) and supplanting were common. When the same birds fed away from the ash site, aggression was very rare.

The only other species seen near the ash was a pair of Gray Jays (Perisoreus canadensis) which pecked the ash once or twice on the first day of observation and were never observed there again. Possibly they were attracted to the site by observing the chickadees.

Small samples of ash were removed from the site where the chickadees were pecking and from an adjacent patch of ash where they never fed. Levels of P, K, and Mg were very similar in the two samples, but there was 2580 ppm Ca in the ash where the chickadees fed vs 600 ppm from the nearby ash. The sample was not analyzed for elements other than those noted, so possibly some other minerals may also have had higher levels in the area where the chickadees fed.

Some birds in far northern areas seem to require supplementary calcium during the breeding season, and many reports document consumption of specific items that are rich in calcium (and possibly some other minerals). For example, the insect food given nestling Lapland Longspurs (Calcarius lapponicus) near Barrow, Alaska, was low in calcium, and the birds ate bones and egg shell fragments (Seastedt and MacLean 1971). Parrot Crossbills (Loxia pytyopsittacus) and Common Redpolls (Carduelis flammea) ate decaying wood in subarctic Finland in summer, and nutrient analyses indicated that the ash was primarily a source of calcium (Pulliainen et al. 1978). A Red Crossbill (L. curvirostra) ate mortar from a wall, presumably for its calcium content (Susic 1981). Pulliainen et al. (1978) suggested that such nutrient needs are prevalent in granivorous birds, as well as in reindeer (Rangifer tarandus) in the subarctic. My observations indicate that calcium may be sought during the nonbreeding season, although the other observations indicate that during the breeding season calcium needs for egg laying may be particularly high.

Soils in the Newfoundland study site are mineral deficient (Damman 1964), particularly in calcium (Brinkmann pers. comm.), and chickadees were probably eating the ash because of its high calcium content. Evidently the liquid used to extinguish the charcoal fire in the one small area was high in calcium (and possibly other minerals), because nearby ash was not consumed.

One of the advantages of sociality may be that if one individual finds a scarce but important resource, other group members can benefit in locating the resource. For example, Great Tits (P. major) in a laboratory experiment found clumped food faster through social foraging (Krebs et al. 1972). An interesting question is whether scarcity of certain minerals such as calcium affects the distribution and/or fitness of subarctic birds. McNaughton (1988) sug-
gested that the spatial distribution of African ungulates is influenced by the mineral content of vegetation.

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A case of polyandry in the Black-capped Chickadee.—Black-capped Chickadees (Parus atricapillus) have been studied extensively in the breeding season (e.g., Odum 1941, Smith 1967, Ficken et al. 1981) and all studies have reported the species to be monogamous, forming permanent pairbonds in winter. Here, we document the first reported case of polyandry in the Black-capped Chickadee.

We studied chickadees on a 500-ha area at the Meanook Biological Research Station of the University of Alberta, near Edmonton, Alberta, Canada, from March 1985 to September 1987. The area was a mosaic of poplar (Populus tremuloides and P. balsamifera) woodland interspersed with fields (20% of the area). One hundred fifty pairs were studied and the majority of nests were located; most individuals were captured with mist nets and nest box traps and were color banded.

In late winter 1987, male A was apparently paired with a banded female (they were frequently seen foraging together), and his neighbor, male B, was paired with an unbanded female. We saw the banded female on 7 April, but she was not seen thereafter. On 30 April and 2 May, male B was chased by male A off the latter’s territory. Six days later, the unbanded female (presumably the mate of male B) was in male A’s territory, and he was
engaged in courtship-feeding with her, indicating that they were paired. On that occasion, male B was foraging a few meters away. The "trio" was observed for 55 min. The two males were observed foraging together on 10 May; male A then visited the nest of the unbanded female located within his territory. On 16 May (a.m.) during incubation, male A fed the unbanded female at the nest. Fifteen min later, both males came near the nest with food, each giving "faint feebee" calls (Ficken et al. 1978). The males remained on their perches for a few minutes. They then dropped their food to the ground and left together. At 1200, the same day, male B fed the same female. On 21 May, male A was observed bringing food to the nest. On 29 May, the unbanded female and male B were feeding the nestlings. Four days later, after a severe windstorm, the nest tree was broken and the nest destroyed. The female was killed, and six dead nestlings, approximately 8–10 days old, were found in the cavity. Male A was singing nearby; male B was not seen after 29 May.

Thus, although we did not observe actual copulations, the behavior of the males suggested that they had both bred with the female. Because of the extensive natal dispersal in Black-capped Chickadees (Weise and Meyer 1979), the two males were probably not siblings. It is unlikely that either male was "cooperating" as a helper in the sociobiological sense (Emlen 1984). Polygyny has occasionally been reported in the genus Parus (Great Tit P. major; Gooch 1935; Saitou 1979; Blue Tit P. caeruleus: Dhondt et al. 1983). Polygyny is a common reproductive tactic in African Black Tits (P. niger) in which breeding units can include one to three helper males (Tarboton 1981). However, we found no case of polyandry in the literature on Parus, even though unpaired males have been reported occasionally on territories of Black-capped Chickadees (Ficken et al. 1981), suggesting a male-biased sex-ratio in the breeding season. Over the 30 months of our study, we have observed 14 non-breeders: nine yearling males, three adult males, one male of unknown age, and one female. However, none of these non-breeders was seen approaching active nests.

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CORRECTION

Recently (Scott, Wilson Bull. 100:323–324, 1988), I erred in omitting a record of a female House Sparrow (Passer domesticus) feeding two juvenile Brown-headed Cowbirds (Molothrus ater). This record (Dexter, Bird-banding 25: 112, 1954) was kindly brought to my attention by the observer. It is missing from the important papers on cowbird hosts written by Herbert Friedmann (e.g. Friedmann et al., Smithsonian Contr. Zool., 235: 1–75, 1977.—David M. Scott, Dept. Zoology, Univ. Western Ontario, London, Ontario, N6A 5B7, Canada.)
ORNITHOLOGICAL LITERATURE

A FIELD GUIDE TO HAWKS OF NORTH AMERICA, by William S. Clark and Brian K. Wheeler. Houghton Mifflin, Boston, Massachusetts. 1987:xii + 198 pp., 26 plates (24 in color), 42 pp. of black-and-white photographs. $13.95 (paper). HAWKS IN FLIGHT. By Pete Dunne, David Sibley, and Clay Sutton. Houghton Mifflin, Boston, Massachusetts. 1988:xviii + 254 pp., 92 black-and-white drawings, 78 pp. of black-and-white photographs. $17.95 (cloth). — Both of these books are very useful but irritatingly flawed works. My review will concentrate on the flaws. I wish that we had one excellent guide instead of two imperfect ones. I find it incredible that the first two field guides to the identification of North American hawks appear within a few months of each other, both by the same publisher, both by authors with long associations with Cape May, both with introductions by Roger T. Peterson, and that the senior authors of both books collaborated in a critique (Clark and Dunne, Amer. Birds 33: 909, 1979) of my paper on the identification of accipiters (Mueller, Berger, and Allez, Amer. Birds 33: 236–240, 1979).

The two books differ considerably, with Clark and Wheeler (CW) emphasizing "... the latest in tried and proven field marks ..." and Dunne, Sibley, and Sutton (DSS) favoring more subtle and subjective aids to identification: a bird could be identified "... because it seemed to have this feature or tended to exhibit this particular behavior ...." I hope that users of DSS will read and remember this because the uncertainty of identification is not stressed sufficiently in the species accounts. CW do not believe in caution; they simply and boldly state that their book,"... should enable anyone, with a little practice, to accurately identify [sic] most flying and perched diurnal raptors when they are seen clearly."

Raptors rarely permit close and prolonged examination in the field, and the “field marks” are frequently variable and qualitative characteristics. The perception of these “field marks” is often largely in the eye of the beholder, and they may have limited basis in reality. Individuals vary in their perceptions, and, as DSS note in their discussion of the identification of accipiters, “even veteran observers do not always agree.” I am unfamiliar with more than a few of the “field marks” depicted by CW and DSS. I delayed the completion of this review until I could check out some in museums, and, more importantly, in the field. These efforts have further convinced me that both books should be used with care. Space prohibits the discussion of all of the field marks that I have studied; a few examples should suffice to show the problems involved in the use of field marks in the identification of diurnal raptors.

A “black” or dark patagium is indicated as diagnostic for the Red-tailed Hawk (Buteo jamaicensis). The extent, position, and apparent darkness of this mark is highly variable, and it is often not nearly as obvious in juveniles (“immatures”) as shown in Plate II of CW and certainly not as prominent as shown on p. 21 of DSS. Occasional “immature” Broad-winged Hawks (B. platypterus), and even a few Red-shouldered Hawks (B. lineatus), have diffuse patagial marks that appear to be more prominent to me than those of some young Red-tails. As another example of the problems involved, I will reopen my arguments with the senior authors on the identification of accipiters. CW simply states that Sharp-shinned Hawks (Accipiter striatus) have square tails and that Cooper’s Hawks (A. cooperii) have rounded tails. DSS allow that some sharp-shins have slightly rounded tails and that “1 in 8” Cooper’s has a tail that seems slightly square. I accept the fact that Cooper’s tails are more rounded than those of sharp-shins but continue to maintain that the dichotomy of round and square leads to misidentifications. CW present 5 photographs with a view of sharp-shin tails; two of these (8b and 9f) appear rounded to me, and the latter appears at least as rounded as any Cooper’s in a photograph in either guide. Similarly, the sharp-shin
in the photograph on p. 191 of DSS appears to have a tail as rounded as that of any Cooper’s in either book. CW indicates that Cooper’s have squarish heads. Cooper’s do have a pronounced tendency to raise the feathers of the nape when in the hand, or in enforced proximity to a human, but I have seen this behavior very rarely in the field, and then only when a Cooper’s was struggling with large prey or being attacked by another bird. In short, this characteristic is useless in the field, as is the apparent position of the eye in the head. Both species have relatively small heads when the nape feathers are not raised, and the eyes are placed in about the same place in the head in both species. Both guides indicate that, in the adult plumage, the dark cap of a Cooper’s contrasts more with the color of the back than that of a sharp-shin. DSS note that there is a less of a contrast in female Cooper’s than in males. In actuality, the same is true of sharp-shins, and a dark cap is more of a character denoting sex rather than species, although Cooper’s caps of each sex are darker than sharp-shin caps of the same sex. Further criticism of some of the characters used for identification in CW and DSS can be found in Mueller, Berger, and Allez (Amer. Birds 36:340-341; 1982), a rebuttal to Clark and Dunne (1979). To summarize: all characters useful for distinguishing between the two species are relative and not absolute. All characters aid in identification, but no simple combination of “field marks” provides for correct determination. The same holds true for most other species of raptors, particularly under the conditions under which they are usually observed.

CW has the advantage of color plates and accounts depicting all 39 species of Falconiformes that have been recorded in North America north of the Mexican border. The paintings and the verbal descriptions present considerably more detail about plumage characteristics than can be found in DSS. The distribution maps are useful, although they suffer from the generalizations necessary to construct such large scale maps and offer only a little more detail than the verbal account in the descriptions accompanying the plates or in the text. The book, 11.4 x 18.3 cm, easily fits in most pockets.

DSS depicts only 23 species; missing are accidentals and those species of limited distribution in the southwestern United States and Florida. The 14.5 x 22-cm size of this book fits in few pockets. The large print and ample margins result in less than 75% of the words on a page than does the smaller CW. The black-and-white drawings in DSS are superb, much better than the wooden paintings in CW. Sibley has succeeded in capturing the “jizz” of flying hawks far better than the artist of any other field guide to North American birds. In comparison, I rank Wheeler’s illustrations only slightly better than the worst (those of the National Geographic Society’s Guide 1983) in spite of the generally excellent attention to details of plumage coloration. The paintings simply do not have the appearance of live hawks. The verbal descriptions in DSS are also markedly superior to those of CW. Dunne has a gift for describing hawks in flight; Clark is often confusing, misleading, and sometimes incomprehensible. For example, consider the following descriptions of the Turkey Vulture (Cathartes aura): “Turkey Vultures often bow their wings in a ‘flex’ until the tips almost meet.” The illustration in Plate 1 shows the wings bowed downward in a continuous curve, an anatomical impossibility. Compare this with the description by DSS of presumably the same behavior: “Turkey Vultures also have the curious habit of drooping their wing tips and quickly straightening them in a sort of mock-flap. The arm remains rigid; the hands simply wilt and then snap back.” Although an aerodynamically unlikely description, this is an apt characterization of a flight behavior that I have seen performed by Turkey Vultures; CW’s description left me mystified. The behavior probably is a forceful downstroke of the primaries to gain air speed and lift and not a passive “wilt.” CW states that Turkey Vultures “. . . are reportedly able to locate carrion by smell . . . .” This ability is much more certain than many things that CW assert without qualification. CW further states: “Turkey Vultures eat smaller prey than Black Vultures (Coragyps atratus) . . . .” Carcasses are not “prey.”
Black Vultures are uncommon at small carcasses; where both species occur, Black Vultures outnumber Turkey Vultures at large carcasses or other concentrations of food.

Most of the photographs in DSS are good, and some are excellent. Many of the photographs in CW are poor, and some are wretched. In more than a few cases, the arrows point to “field marks” that cannot be seen in the photograph. The black-and-white photographs in CW were made from color slides. It is an exacting art to produce a good black-and-white print from an excellent color slide. The editors and publisher should be reprimanded for failing to invest in better processing of the photographs and for subjecting both the photographers and the users of this guide to an atrocity.

The illustrations of the five species of falcons in flight on p. 80 of DSS are mislabeled: C is a Prairie Falcon (Falco mexicanus), D is a Gyrfalcon (F. rusticolus), and E is a Peregrine Falcon (F. peregrinus). Broad-winged Hawks and Swainson’s Hawks (B. swainsoni) have only three emarginated primaries, not four as indicated on p. 14 of DSS.

Plate 20 of CW shows an “immature” Golden Eagle (Aquila chrysaetos) in dorsal view without a white patch at the base of the primaries and secondaries. A separate painting of a wing on the plate shows this patch and the text on the facing page indicates that the patch is “sometimes” present. I assume that CW is following the usual perversion of field guides in using the term “immature” for raptors in the juvenile plumage instead of “juvenal” or the less preferable “juvenile.” I have never seen a juvenile Golden Eagle that lacked the white at the base of the proximal primaries and adjacent secondaries on the dorsal surface, and I have been unable to find a reference in the literature that indicates the possibility of such a lack. The amount of white shown is variable, it is reduced with each molt, it may not be visible dorsally in the first basic (“subadult”) plumage, and it disappears entirely by the time the definitive basic (adult) plumage is attained (Glutz, Bauer, and Bezzel, Handbuch der Vogel Mitteleuropas, Vol. 4, 1971; The Birds of the Western Palearctic, Vol. II, 1979; Palmer, Handbook of North American Birds, 1988).

The best field guide to raptors is for Europe (Porter, Willis, Christensen, and Nielsen, Flight Identification of European Raptors, 3rd Ed., 1981). DSS resembles Porter et al. except for the larger print and the inclusion of much material irrelevant to identification. I wish that DSS had not tried to entertain the reader with, e.g., a page of text on how the introduction of firearms, Bibles, and domestic chickens by European colonists had an impact on the Cooper’s Hawk, and instead had imitated Porter et al. more closely. Porter et al. provides all of the information on a species, including illustrations, in 2–5 pages, a format that greatly facilitates comparing the descriptions of two similar species in the field. For example, Porter et al. provide more useful information for the three species of European accipiters in nine pages than DSS provide for the three North American species in 23 pages. The organization of CW also makes for difficult use in the field: there are two plates of accipiters, with very brief descriptions on the facing pages; eight pages of more detailed descriptions are separated by more than 50 pages from the plates. CW also contains considerable information of no use in identification, and some of this is in the species accounts, providing little more than additional pages to turn when one is trying to identify a bird. Generally, I found DSS easier to use than CW when I was trying to compare two species.

Both DSS and CW appear to be overexertions to produce sufficient pages to provide the appearance of a “book.” DSS does this by stretching species accounts with verbiage unrelated to problems of identification which some may find entertaining when reading the book at home, but all will find annoying when trying to identify a hawk in the field. The abundant and large photographs are an expander that at least is of arguable value. CW uses a number of devices to expand to book size: repeated illustrations (“generic” silhouettes, topography of a bird), almost 20 absolutely blank pages, the etymology of scientific and common names and a glossary that is misnamed “Topography of a hawk” and largely repeats what can be
found in the illustrations including, e.g., such entries as “Leg. See Fig. 5.” Fig. 5 indicates that the “leg” is the tarsus or, more properly, the tarsometatarsus—the foot of a chicken, in common usage. The “leg feathers” of Fig. 5 appear to be largely those originating on the portion of the leg of which the femur is the skeletal element—the thigh of the chicken in your supermarket. CW also lists 24 pages of “References” compared to the modest 2.2 page “Bibliography” of DSS. I hardly expect a field guide to be a reference work, but CW begs to be examined as such. I have written only one paper on hawk identification (Mueller et al. 1979); this is cited in the brief bibliography of DSS but not in the extensive references of CW. DSS (appropriately) do not cite any of my other papers; CW cite five where I am sole or senior author. CW amplify their book with a nine page “Index to references by species and topic,” permitting me to see why my five papers were selected for citation. Three are listed under “plumage.” Mueller, Berger, and Allez (Bird-Banding 47:310–318; 1976) do present 0.6 pages on how to determine the age of Goshawks (Accipiter gentilis) in the hand, but is essentially useless for aging birds in the field. The same is true of the half page of plumage description of the Cooper’s Hawk in Mueller, Berger and Allez (J. Field Ornithol. 52:112–126, 1981). The third paper (Mueller, Berger, and Allez, Wilson Bull. 93:491–499, 1981) contains absolutely no mention of plumage. All three papers deal with age and sex differences in measurements and not with description of plumages. My note on an isolated incident of a Rough-legged Hawk’s catching fish (Mueller, Mueller, and Mueller, Wilson Bull. 78:470, 1966) is one of five references on the behavior of this species; several of the other references are of similar, dubious importance. My note presenting an aerodynamical hypothesis for similarities in the wing dihedral and flight behavior of Turkey Vultures and Zone-tailed Hawks (B. albonotatus) might be an appropriate listing, but the text in CW only mentions the other hypothesis, that Zone-tailed Hawks are mimics of the Turkey Vulture (Mueller, Condor 74:221–222, 1972). I did not find the list of references in CW very useful in trying to find support for statements in the text of the book; the list appears to be a random sample of some of the literature.

Both of these books are significant contributions to the art of hawk identification (field identification approaches becoming a “science” only when one recognizes one’s limits as an “artist”). The color illustrations and verbal descriptions of the details of plumage characteristics in CW are useful hints (but only occasionally definitive field marks). The illustrations and verbal accounts in DSS are very useful in conveying the “jizz” of each species of raptor that permits a reasonable guess as to its identity when seen under the conditions that usually prevail in the field. If your finances or limits of transporting a library into the field limit you to one of the two books, DSS is the obvious choice. Neophytes will be attracted to CW because of its Peterson Guide imprimatur, its format, and its promises of relatively easy identification. DSS would serve them better in their efforts to become experts. Serious hawk watchers may wish to purchase Porter et al. (1981), as well as the two American guides, to help them identify the increasing number of exotics that escape from falconers. No guide will suffice to identify the hybrids produced by artificial insemination. For example, a hybrid Peregrine Falcon (Falco peregrinus) × Merlin (F. columbarius) exhibited by a falconer at the 1988 A.O.U. meeting had the general appearance of a giant male American Kestrel (F. sparverius).—Helmut C. Mueller.
groups then "linked" closely by taxonomists. In the intervening period, many studies of the biology of these birds have been published, taxonomists have isolated the auks from the other groups, and even a common ancestry of the loons and grebes has been debated. Although Palmer (Handbook of North American Birds, Vol. 1, Yale Univ. Press 1962) compiled the information on loons and grebes 25 years ago, Paul Johnsgard's book is the first attempt at a modern synthesis of these groups together. As the author points out in his preface (p. xi), this artificial "lumping" seems justified because "such coverage would emphasize the impact of convergent and parallel evolution better than would dealing with the patterns of adaptive radiation within a single phyletic group as has been the typical approach of my earlier books."

The book consists of six summary chapters (74 pp.), 31 species accounts (198 pp.), and four appendices (11 pp.). Johnsgard's coverage of the North American literature is reasonably comprehensive, up to about 1983, and several important European and Asian papers are included. However, publication proceeded at a time when several other syntheses of the auks were coming out, and although some of these were cited, they were not summarized because of his publication deadline. Thus, parts of the book are already out of date.

In the first chapter, Johnsgard addresses the controversy surrounding the evolutionary relationships among and within the loons, grebes, and auks by examining the fossil record and morphological variation, but he only alludes to current electrophoretic and DNA-DNA hybridization studies. Evidence that suggests that loons and grebes are monophyletic is compared with that which argues for convergence in their similarities. The author notes that, while some workers support a charadriiform origin of loons, others favor an origin from the penguins and tube-nosed swimmers. With no consensus, Johnsgard's gut reaction is a charadriiform ancestry, but he indicates this with a question mark in his "hypothetical evolutionary dendrogram" (Fig. 1 in the book). A charadriiform ancestry of the auks, specifically larid, is accepted despite the inability of recent workers to identify the closest charadriiform relatives of the group (see Strauch, Auk 102:520–539, 1985). The "dendrogram" is confused further. Interpreting the fossil record, the author concludes wrongly that *Nautilornis*, from the Eocene of Utah, is the earliest known aleid fossil. He overlooked Feduccia and McGrew (Contrib. Geol. 13:49–61, 1974) who showed that *Nautilornis* actually is referable to the genus *Pterygornis*, now known to be a charadriiform near the ancestry of the Anseriformes (Olson and Feduccia, Smithson. Contrib. Zool. 323:1–24, 1980). Finally, the author summarizes long-held ideas concerning the zoogeography and relationships within the alcids that now must be modified because of newly discovered fossils from the Atlantic (Olson, Avian Biol. 8:79–238, 1985).

The recurrent theme of Chapter 2 is relative size, shape, and flying/diving performance. The specializations that characterize these groups for locomotion on, under, and above water are compared in the context of the evolutionary development of underwater locomotion, wing-propelled in the auks and foot-propelled in the loons and grebes. Overlooked is Olson's (1985) evidence that suggests that loons also are specialized for wing-propelled underwater locomotion. The information in this chapter especially is discussed at a simplified level, and the author frequently refers rather subjectively to aspects of relative size. For example, he states (p. 20) that "... wing shape of grebes varies from moderately long to distinctly short and elliptical," and "... supported by a long and fairly weak ulna."

"Egocentric behavior" is defined (p. 26) in Chapter 3 as "those categories of individual survival and maintenance behaviors that are exclusive of ... aggressive, sexual, and parental behaviors." Thus comfort movements are described although only sunbathing behavior in grebes has been studied quantitatively. The suggestion that Western Grebes (*Aechmophorus occidentalis*) become flightless while nesting is intriguing. The indication (pp. 33, 34) that Ancient Murrelets (*Synthliboramphus antiquus*) feed their young at sea has not been reported.
previously, to my knowledge, and the author does not cite a source. Such behavior, however, has been observed in the closely related Craveri’s Murrelet (S. craveri) (DeWeese and Anderson, Trans. San Diego Soc. Nat. Hist. 18:155–168, 1976). Dive/pause ratios are examined for several species but the author questions their use for measuring diving stress directly. Implicitly, more research on this subject is needed, with complete sequences of dives to known depths and prey of known abundance and dispersion.

Much of the tabulated information on diets in Chapter 4 is of limited value because only the families of the prey groups, i.e., fish, crustaceans, etc. are listed and the species that have been preyed upon are not indicated. Prey of different sizes taken in different seasons and localities are lumped. Information compiled in Tables 14 and 18 apparently confirms for loons and grebes, despite sparse data, what is established for auks, namely, that the smaller species tend to feed on plankton and other invertebrates and the larger species on fish. The correlative evidence the author presents in Chapter 1 purporting to demonstrate the relationship between oceanic productivity levels and the distribution of major alcid colonies is too simplistic. The availability of appropriate nesting stations, patchiness of food resources in the sea, etc., surely must be considered.

Pair-forming and copulatory behaviors (Chapter 5) are best known among the grebes. In the case of the loons and most auks much uncertainty still exists about the mechanisms of pair bonding, although monogamy seems to prevail. The tendency for nest-site tenacity to promote long-term mate fidelity is an important observation that deserves more attention (see also Morse and Kress, Auk 101:158–160, 1984). Vocal communication, apparently especially important in the loons, is poorly documented. The elaborate displays of pairing and paired grebes are species specific, and their taxonomic utility is well known.

Life history and reproductive success data for loons and grebes are sparse, and European papers are used to round out Chapter 6. The more intensively studied auks receive the most attention. Loons and auks are long-lived, enjoy high annual adult survival, and lay clutches of 2 and 1–2 eggs, respectively, but the alcids exhibit highly variable nesting periods that continue to intrigue biologists. The shorter-lived grebes lay larger, more variable clutches, generally hatch their young asynchronously, and divide their broods and care for them for extended periods. Johnsgard’s interpretations in this chapter are couched in terms of the influence of food supply, especially during the breeding season. For example, he suggests (p. 74) that the 2-egg clutches most guillemots (Cepphus spp.) lay is a “gamble” that pays off occasionally when 2 young are reared. Ainley’s (Pacif. Seabird Grp. Bull. 13:16, 1986) long-term study of the Pigeon Guillemot (C. columba) seems to bear this out—2 young are reared in years when pelagic schooling fishes are available.

The bulk of the book consists of the species accounts which complement nicely, and provide the basis for, the earlier chapters on comparative biology. The Pacific Loon (Gavia pacifica) and Clark’s Grebe (A. clarkii), recognized recently by the 35th Supplement (1985) to the A.O.U. Check-list, are mentioned in footnotes (p. 4) but not treated separately. Surprisingly, the author neither summarizes the recent accounts of the Great Auk’s (Pinguinus impennis) biology nor addresses the current debate as to why this species became extinct.

Taxonomy ostensibly follows the 6th edition (1983) of the A.O.U. Check-list, but the spelling of many scientific and common names do not conform to it, and some generic names are misspelled (e.g., Pinguinus, pp. 8, 9; Ptychoramphus, pp. 6, 41; Cyclorrhynchus, p. 8). For each species, a list of vernacular names is followed by the ranges summarized and mapped for each North American subspecies. The Pacific Loon’s breeding range in British Columbia (Campbell et al., Can. Field-Nat. 99:337–343, 1985) is omitted, and it is mapped in northeastern Alberta instead of northwestern Saskatchewan. Western Grebes do not breed in southeastern Alaska (p. 141), and some of the largest colonies of the Crested
Auklet (Aethia cristatella), north of the Pribilof Islands, are mapped (p. 235) but not summarized. The range maps of the Atlantic (Fratercula arctica) and Horned (F. corniculata) puffins (pp. 253, 259) are inverted. Breeding and wintering adults, downy young, and, in some species, juveniles of each species are described; measurements of presumably adults (from live or dead birds?) and eggs are followed by body weights from the literature. Estimated egg weights are used in many accounts even when published data were available. Thorough sections follow on "Ecology and Habitats," "General Biology," "Social Behavior," "Reproductive Biology," "Evolutionary History and Relationships," and "Population Status and Conservation." Molts, migrations, and overwintering biology clearly require further study. As elsewhere, errors and misleading statements exist. Logging of coastal old-growth forest may be the major, not "lesser," threat (p. 198) to the Marbled Murrelet (Brachyramphus marmoratus). Incubation shifts of 72 hours are reported for the Ancient Murrelet, not Marbled Murrelet (p. 205).

The appendices are of limited value. The key (App. II) to the species is designed for identifying living or recently dead adults in alternate plumage. It worked for skins of loons and most grebes (keys to the Western and Clark's grebes are inverted), but problems arose with the alcids. The "total culmen length" (="exposed culmen" used elsewhere?) of the Marbled Murrelet is under, not "at least 25 mm," even in the Asiatic subspecies perix. "Underparts" of the Least Auklet (A. pusilla) are white in juvunal and basic plumages but not in the alternate plumage. The black-and-white sketches of a downy loon and some of the auks do not reveal the subtle differences in pattern that exist among the species and thus cannot be used to identify them. The "head profiles" show different plumages, but the outmoded terminology oversimplifies the complex plumage generations characteristic of these species. Estimates (individuals? pairs?) of the sizes of the "major" auk colonies in North America (App. III) do not list all of the species, and serious students will have to consult the catalogs listed on p. 274 for extended information on colony sizes, species composition, and census methods. The index lists only scientific and common names. Finally, the painting by John Felsing, Jr. on the dust jacket is attractive, but the direction of the action is wrong. Horned Puffins pursued by a Gyr Falcon (Falco rusticolus), in real life, would fly toward the ocean, with the falcon in pursuit, not land on or remain standing on a boulder.

I am not sure for whom this book was written. Many of the photographs, some by the author which include birds in captivity, lack the visual quality one associates with a collectable book. Although each species account has a section on "identification" in the field and in the hand, the book is too bulky for birdwatchers to use in the field. Much published information on these groups is summarized, apparently for the professional, but generally at a simplified level, and almost no new information is presented. Serious students of alcids have available other more exhaustive, up-to-date treatments of the topics covered. The 14 pages of references, nevertheless, will assist those initiating new research. The many errors and misleading statements in the text demand caution by readers who may use it as a reference book. University undergraduate, museum, and field station libraries should have this book, and ornithologists in general and students of loons and grebes in particular will find it useful, but students of alcids less so.—SPENCER G. SEALY.
catcher genus *Polioptila* is a small, well-defined group of species of similar appearance. In such a genus, species level problems are inevitable—but now there is one fewer. Reversing an incorrect lumping of years ago, this paper definitively separates two species of gnatcatchers with mainly black tails currently treated in most literature as a single species, and clarifies the English as well as the scientific nomenclature. *Polioptila melanura* Lawrence, 1857, the Black-tailed Gnatcatcher, occurs in the Sonoran and (disjunctly) Chihuahuan desert regions of the southwestern United States and northern Mexico. *Polioptila californica* Brewster, 1881, the California Gnatcatcher, is restricted to southwestern California and Baja California. A third “sibling” (but white-tailed) species, *P. nigriceps*, the Black-capped Gnatcatcher of northwestern Mexico, was included in the study for comparative purposes.

Atwood’s taxonomic decision is based primarily on behavioral and ecological evidence. The mainly allopatric species come into contact regularly in a small area in northeastern Baja California, where assortative mating occurs. In that area, *melanura* can be distinguished by its brighter (whiter) breast color. Much of the ecological (habitat) difference is related to geographical separation. There are minor differences in breeding biology, and there are differences in vocalizations.

The basic taxonomic work is accompanied by an extensive (nearly half the text) univariate and multivariate analysis of morphological character variation. Univariate analyses showed consistent patterns of intraspecific geographic variation in morphological characters. Sonoran and Chihuahuan desert populations of *melanura* differ markedly in some characters and are treated as subspecies, *melanura* in the Chihuahuan Desert, and *lucida* in the Sonoran. Both *nigriceps* and *californica* show north-south clinal variation in many characters; the latter consists of two subspecies, *californica* in the north and *margaritae* in the Cape Region of Baja California. Actual statements of morphological differences between the species, or between populations within the species, are scattered throughout this section and can be picked out only with careful reading.

Populations from islands in the Gulf of California were not included in the statistical analysis, primarily because of small sample size, although some mainland populations with equally small or smaller samples were included. Also, mean values from those populations tended to “obscure” (read “screw up”) patterns of variation based on mainland samples. This exclusion is unfortunate, because eventual recognition of subspecies is based on this analysis, and at least one such insular population (on Isla Tiburón) has been named as a subspecies (*curtata*) of *melanura*; there is no way to judge its validity in the context of other intraspecific variation, but Atwood recognizes it tentatively.

Although I accept the taxonomic conclusions of this study and admire the thoroughness of the statistical analysis, some aspects of this monograph bother me. Aside from mean values for a few characters, there are no data. For example, although Chihuahuan Desert samples of *melanura* are said to be longer winged, longer tailed, and heavier than Sonoran desert samples of that species, there are no tables that give ranges of measurements, standard deviations, etc., that would help the reader judge the degree of overlap or independently assess the geographic variation. Thus, accepting Atwood’s statements about the patterns of variation becomes an exercise in faith. Although light on data, the paper is very heavy on statistical treatment. This tells a lot about what one can do with data, but tells relatively little about the birds.

Patterns of variation in a few characters are mapped after a fashion. The entire range of means in a character—for all three species—was divided into fifths, and the symbol for an individual population indicate into which fifth it falls. I’m not sure I see the point of that; I would rather know how a population fits variation in its species, not the species complex. Patterns in other characters are tabulated in similar fashion, showing the number of populations in selected areas of each black-tailed species that fall into each fifth of the range of
variation for that species. I find it difficult to get much useful information from any of this. Is this ornithology or numerology?

Vocalization playback experiments were conducted on all three species and suggested that differences in vocalizations might serve as an isolating mechanism for the black-tailed species. There is no indication, however, whether these experiments were done in the area of contact or on allopatric populations. Because vocalizations were presented with visual models, morphological as well as vocal differences may have influenced the results.

The final di-, tri- or quadri-chotomous key "correctly identified 97 percent of the specimens that were examined with 90 percent accuracy." Aside from the ambiguity of that statement, the key leads to a mainland (not the insular) race of melanura but only to the species californica. With bad luck the key will leave you at 5C, "Not as above . . . unknown."

In summary, I am glad to have a definite statement that melanura and californica are specifically distinct. I wish I had been told that in a shorter paper. The rest of this monograph, including brief sections on species concepts and biogeography, leaves me with a funny unsatisfied feeling. Did the author not make a point, or did I miss it? Probably you should get it and read it, and judge for yourself. I suspect this will be a much cited paper, one that you should be familiar with.—RICHARD C. BANKS.

WATERFOWL: AN IDENTIFICATION GUIDE TO THE DUCKS, GEESE, AND SWANS OF THE WORLD. By Steve Madge and Hilary Burn. Houghton Mifflin Company, Boston, Massachusetts. 1988. 298 pp., including 47 color plates, 152 range maps, and 25 unnumbered black-and-white text figs., $35.00.—This book by two Britishers is a guide to the semiaquatic birds typically known as waterfowl in North America and wildfowl in Britain and other European countries. However, coverage includes the Family Anseranatidae (the Magpie Goose, Anseranas semipalmata, of Australia) but excludes the Family Anhimidae, the screamers (genus Chauna) of South America. Considering its worldwide coverage, it is compact (ca 16 × 24 cm), well designed and printed, and with a small but readable text printed with narrow margins to maximize space use on a heavy grade paper. It will be useful in the museum or at the zoo, but its hard cover will need protection in the field for the wet weather often associated with waterfowl.

The book is divided into two sections, a sparkling array of 47 color plates illustrating all species and selected subspecies, and a systematic section made up of species treatments. The plates by Hilary Burn include many plumages and sometimes color variants, and remind one of the coverage established by F. H. Kortright's "Ducks, Geese and Swans of North America" (Wildlife Management Institute, Washington, D.C., 1942) where identification in the hand or at close range was expected. Illustrations are bright, colorful, and distinctively rendered for identification while being quite detailed and artistic. Many of the outstanding bird artists of the world have found waterfowl their greatest challenge and their chief failure. Burn has done an exceptional job, and although each person who knows a certain species may find fault, they are overall the best collection of waterfowl paintings in a guide book.

The text by Steve Madge is separated from the paintings so that the range maps and commentary could be opposite the color plates. But this is where the arrangement is disconcerting, for many of the range maps are out of sequence with the paintings on the opposite page. This is a product of the fact that the species are numbered, and the range maps are given numerically, whereas the paintings are not in the same order. To assist the less experienced reader, the numbers should either have been deleted and the range maps arrayed to match the plates, or the species arranged on the plates in sequence—probably the more difficult challenge.

The species treatments in the text average nearly a page of small text and seem up-to-
date but general—as would be expected in a guide. They include field identification, description of the “bare parts,” measurements, geographic variation, habits, habitat, distribution, populations (status), and a few key references. References are listed in an abbreviated bibliography at the end of the text and include compendia and original citations. A glossary at the end seems short and not very helpful for those familiar with terms such as sympatric, holarctic, etc., but it will aid the bird-watching public in clarifying abbreviated descriptions and ranges.

The taxonomic arrangement and the sequence of species will be the most disruptive aspect of the book for many readers, since it follows a recent paper (Livezey, Auk 103:737–754, 1986) that makes major changes in species grouping in tribe and adds numerous subfamily taxonomic treatments. Several tribes are thereby deleted, and earlier generic names such as Olor, Nomonyx, and Mergellus are resurrected. This will not affect the usefulness of the book for identification, but many readers will be surprised to find new scientific names for familiar species as well as changes in tribes; e.g., many species previously in the Tribe Cairinini (perching ducks) are included with several aberrant forms like the Blue Duck (Hymenolaimus malacorhynchos), Pink-eared Duck (Malacorhynchos membranaceus), and Torrent Duck (Merganetta armata) in the Subfamily Tadornini. This subfamily should have been divided into two tribes, but a subheading is missing on page 163 so that all the shelducks and sheldgeese seem to be in the Tribe Sarkidiornini (Comb Duck [Sarkidiornis melanotus]) rather than the Tadornini. Other species of the former Cairinini tribe are placed among the dabbling ducks (Anatini). A systematic list would have been helpful; the Table of Contents could have served this role if modified.

Use of this classification system must have been a difficult choice for the author, who made a concerted effort to have data, references, and approaches up-to-date. Arrangements of species in the color plates suggest that the acceptance of this ordering was made after the plates were finished. Madge expressed the hope that this would be the system to be followed for many years, but, unfortunately, two recent papers demonstrate that this is not to be: Sibley et al. (Auk 105:409–423, 1988) and Madsen et al. (Auk 105:452–459, 1988).

Vernacular names tend to be those from “official” regional check-lists and guides, presumably to be useful to local bird watchers. Thus, Hardhead is used for the Australian (White-eyed) Pochard (Aythya australis) but Johnsgard’s (Ducks, Geese and Swans of the World, Nebraska, Lincoln, 1978) terminology is used for the Australasian Shoveler (Anas rhynchos). This could be confusing in viewing a large, labeled waterfowl collection.

Guides to groups of birds are less common than guides to birds of regions, but waterfowl have had a large following among both aviculturists and hunters. All worldwide guides seem to have had their origins in England. One of the oldest was by Frank Finn (Wildfowl of the World, Hutchinson, London, 1921), with most species listed but only a few illustrated with black-and-white photos. Peter Scott’s outstanding illustrations in the comparative “Key to the Wildfowl of the World” (Wildfowl 2, Plates 1–23, 1949) was reprinted in black-and-white, bound, and sold for use at the Wildfowl Trust at Slimbridge. It was soon followed by “A Coloured Key to the Wildfowl of the World” (Royle & Sons, London, 1957), which has been available from various publishers for many years. A more general descriptive work by O. J. Merne (Ducks, Geese and Swans, Hamlyn, London, 1974) lacked the detailed illustrations useful in species identification. It was superceded by a good photographic treatment (Soothill and Whitehead, Wildfowl of the World, Blandford, Poole, 1978).

Madge and Burn have assembled the most complete and compact guide to waterfowl of the world now available. I recommend the book for all who wish to identify and compare waterfowl, their ranges, and their general characteristics over several broad geographic areas. It will work well for specific areas such as North America or Europe, but other guides will do those areas in greater detail. World travelers with a special interest in waterfowl will find the book extremely useful.—Milton W. Weller.
Voices of the Wrens, Family Troglodytidae. By J. W. Hardy and Ben B. Coffey, Jr. ARA-2 (revised). ARA Records, P.O. Box 12347, Gainesville, Florida 32604-0347, 1988: Monaural cassette, normal bias tape (approx. 40 min/side). $10.00—J. W. Hardy continues to render a valuable service to the ornithological community with the production of recordings at the Bioacoustic Laboratory of the Florida State Museum. These productions, which today number eleven, are comprehensive surveys of the vocalizations of entire groups of birds. Hardy’s monographs provide amateur ornithologists with examples of vocal variation within and across groups and are of value to the professional who wishes to conduct an initial comparison of closely related forms for taxonomic and behavioral purposes. In addition, the recordings provide documentation of the vocalizations of many groups that exist in ecologically endangered regions. This is certainly true for the wrens in the recording under review here, as over 70% occur in the New World tropics.

The first collection of wren vocalizations appeared as an LP record in 1977 (“The Wrens,” reviewed by Stuart Keith, Wilson Bull. 90:148–150). That edition featured 43 of the then-recognized wren species. The revision has increased the number of species to 71, with all but three presently recognized species represented (omitted are: Niceforo’s Wren [Tryothorus nicefori], the Gray Wren [T. griseus], and the Tepui Wren [Troglodytes rufilus]). Thirty-eight new recordings appear on the cassette tape; 31 are of species not in the first edition, and seven replace recordings of species on the LP. The wren vocalizations included in this production were obtained by more than 20 recordists. A nucleus of 30 recordings was made by Ben Coffey (the next largest contribution by any one recordist consisted of five recordings). The quality of the recordings, with few exceptions, is good. This is rather remarkable considering the number of contributors and the difficulty of obtaining some recordings. After careful comparison, both by ear and by analysis with a digital spectrum analyzer (Kay DSP Sona-graph Model 5500, Kay Elemetrics Corp., Pine Brook, NJ), we concluded that the cassette production compares well with the original LP format.

However, there are some noticeable differences between the two editions. Narration on the cassette is restricted to voicing the common and scientific name of each species. This is in contrast to the LP where commentary was extensive, providing information about habitat and vocal behavior as well as species identity. For the revised edition, some of this information has been placed in a small, folding brochure accompanying the cassette. Here each species is listed with its distribution and data supporting the recording (location, date, and recordist). Most, if not all, of the recordings now reside in an archive, and it would have been appropriate to include the archive identity and archive number with the text accompanying each recording.

Omitted from the brochure, except for a few remarks following the species list, are some of the more valuable comments on the LP, especially those on habitat which were originally given for all species. More critical is the omission of information on the number of birds vocalizing in any cut. Duetting and group chorusing are especially common in tropical wrens. Without reference to the LP, we were not always certain when duetting occurred on the cassette, especially if the duet was antiphonal. Approximately 14 species were noted to be duetting on the LP, yet only one is so indicated in the text remarks accompanying the cassette. For the Rufous Wren (Cinnycerthia uniura), not represented on the LP, we were certain that duetting was involved only after consulting Dr. Hardy.

The text is further marred by organizational and production problems. Remarks relegated to a separate section in the brochure certainly would have been more valuable if incorporated in the species listing. Furthermore, the species list in the brochure lacks any indication of where side A ends and side B begins. Most annoying is the brochure’s nearly illegible print size.
Despite these shortcomings, we recommend this cassette to all with an interest in the vocal behavior of this most accomplished group of songsters. Dr. Hardy reports that a recordist has come forward with a sample of the previously unknown song of the Tepui Wren. We can only hope that the remaining two unrecorded wrens will soon be added and that a final, third edition of the "Voices of the Wrens" will appear.—SANDRA L. L. GAUNT AND ANDREW D. THOMPSON, JR.

BIRDS TO WATCH. The ICBP World Checklist of Threatened Birds. By N. J. Collar and P. Andrew (eds.). ICBP Technical Publication No. 8, Cambridge, U.K. 1988:xvi + 303 pp. £9.50 (For U.S. and Canada order from Smithsonian Institution Press, Washington, D.C.).—Over the last two decades the ICBP has published several lists of endangered and threatened bird species. The Red Data Book, in loose-leaf form, appeared from 1964–1971, with a second loose-leaf edition in 1978–1979. This last was later converted to a hard-back book. More recently, the Red Data Book has been expanded into a series of four volumes embracing different geographical regions. A volume on Africa (Collar and Stuart, 1985; see review, Wilson Bull., 99:736–737, 1987) has appeared and one on the Americas is in preparation. These compilations have been criticized on the grounds that the effort in preparing these detailed summaries precluded rapid transmission of information on a subject where changes are occurring rapidly. The present publication is an attempt to bring out the vital information quickly in less elaborate form. It is hoped to have updated versions at regular intervals.

After a brief introduction outlining both the purpose of the publication and the criteria used in establishing the list, the main portion of the text gives the World Checklist of Threatened Species, which lists 1029 species (over 11% of the world's avifauna). The 1978–79 edition of the Red Data Book had listed only about 290 species. Each species is discussed in a paragraph of 5–10 lines outlining the recently known status of the bird and some remarks about the threat facing it. The information is about as up to date as is possible, and there are numerous entries giving the 1988 status of species.

There are two useful appendices. The first lists the threatened birds by geopolitical unit, and the second lists 637 additional species which are "Near-threatened." A Bibliography in 25 pages of small type is included.

Indonesia with 126 species and Brazil with 121 species are the geopolitical units with the most threatened species. The United States and Canada have 15. The family Psittacidae with 71 species on the threatened list and 29 on the additional list is the taxon with the largest number of endangered species.

If there is an underlying theme that runs throughout the book it is the destruction of habitat, particularly forest. For species after species, this is listed as the main threat the species faces. In many cases of little known island species, it is reported that no forest remains on the island concerned. Many other species may face this threat in the future. A large number of species, particularly in the tropics, are either known from only a few specimens (often only one) or else have not been reported for many years.

The Psittacidae, and to a lesser extent some others, are chiefly threatened by the wild bird trade which flourishes despite the increasing amount of legislation against it. On the other hand, no species is currently threatened by overzealous collecting.

There are a few less dark (I hesitate to say bright) spots in this picture. The Mauritius Kestrel (Falco punctatus) and the Chatham Island Robin (Petroica traversi) have both responded to intensive management and have increased in numbers.

This is a valuable and informative publication.—GEORGE A. HALL.
ANNOTATED CHECKLIST OF THE BIRDS OF KENTUCKY. By Burt L. Monroe, Jr., Anne L. Stamm, and Brainard L. Palmer-Ball, Jr. The Kentucky Ornithological Society (9101 Spokane Way, Louisville, KY 40241). 1988:xi + 84 pp. $6.00.—With a broad longitudinal range and elevations ranging from the lowlands of the Mississippi Embayment in the west to the high country of the Cumberland Mountains in the east, Kentucky has been blessed with a rich avifauna. For many years Robert Mengel’s classic, “The Birds of Kentucky” (1965), has been the benchmark for the study of the state. Now the Kentucky Ornithological Society has brought out an updated list incorporating the numerous additions and changes of the last 25 years. Mengel had recognized 296 species for the state. The present list contains 340 species, eight of which are either extinct or extirpated in the state.

After an eight-page introduction which gives a map of the state and its avifaunal regions and defines the terms used, the main portion of the text is a standard set of species accounts. The annotations are very detailed and include references, mostly in “The Kentucky Warbler.” For those species which have an endangered or threatened status, both on the state and federal level, that status is given. A Hypothetical List of ten species is appended, and a novelty for this type of checklist is a list of ten “What will be next . . . ?” species, that can be expected to occur within the state in the near future.

Part 2 of the booklet consists of the usual set of bar graphs summarizing the seasonal occurrence and abundance. One feature not usually found on such graphs is the inclusion of dates for out-of-season records and those species of casual occurrence.

This compilation should be very useful not only for Kentucky birders but also for people in neighboring states.—GEORGE A. HALL.

BRIEFLY NOTED

AN EAGLE IN THE SKY. By Frances Hamerstrom. Nick Lyons Books, 31 West 21st St., New York, 10010, 1988:xxv + 142 pp. Black-and-white photos and sketches. $10.95 (paperback).—This reprint of a book originally published in 1970 recounts the author’s experiences with two captive golden Eagles (Aquila chrysaetos). In her usual delightful style, Dr. Hamerstrom recounts her attempts to breed one captive female and to rehabilitate and release a tick-infested eagle taken from a nest.—G.A.H.

INVERNADA DE AVES EN LA PENÍNSULA IBERICA. By José Luis Tellería (Ed). Sociedad Española de Ornitología, Monografía No. 1 (Facultad de Biología 28040) Madrid, 1988:208 pp. 2400 ptas (£12) paperback. (In Spanish and Portuguese with English summaries.)—This work presents 14 papers on the wintering of birds in the Iberian Peninsula originally given at a symposium held in December 1987. Included are discussions of both waterbirds and landbirds, with three papers on conservation problems.—G.A.H.


The following publications are available from the Publications Unit, U.S. Fish and Wildlife Service, Room 148 Matomic Building, Washington, D.C. 20240.

CHEMICAL CHARACTERISTICS OF PRAIRIE LAKES IN SOUTH-CENTRAL NORTH DAKOTA—THEIR POTENTIAL FOR INFLUENCING USE BY FISH AND WILDLIFE. By George A. Swanson,


ANNOUNCEMENTS

Hawk Mountain-Zeiss Raptor Research Award

The Hawk Mountain Sanctuary Association awarded its 1989 research grant to Suzanne M. Joy, a M.S. candidate at Colorado State University. Her project is entitled "Nest-site characteristics and foraging behavior of Sharp-skinned Hawks in mature aspen and conifer habitats."

The Hawk Mountain Sanctuary Association is now accepting applications for its thirteenth annual award to support student research on birds of prey. Support for this award is provided by Carl Zeiss Optical, Inc. Up to $2000 in funds are available and will be awarded to one or two recipients. To apply, a student applicant should submit a brief description of his or her research program (five pages maximum), a curriculum vitae, a budget summary including other funding anticipated, and two letters of recommendation to Dr. James C. Bednarz, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529, USA. The deadline for applications is 15 November 1989. The Association's board of directors will make a final decision in February 1990. Only undergraduate and graduate students in degree-granting institutions are eligible to apply. The awards will be granted on the basis of the project's potential to improve understanding of raptor biology and its ultimate relevance to the conservation of raptor populations. The funds are no longer restricted to studies in North America and applications from anywhere in the world will be considered.

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THE WILSON BULLETIN

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THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.
Taxa of the Rusty-faced Parrot (Hapalopsittaca amazonina) superspecies of the northern Andes of South America: (upper left) H. a. amazonina; (upper right) H. a. velezi ssp. nov.; (middle left) H. a. theresae; (lower left) H. pyrrhops; (lower right) H. fuertesi. From a mixed media painting by John P. O'Neill.
A NEW ALLOPATRIC TAXON IN THE
HAPALOPSITTACA AMAZONINA (PSITTACIDAE)
SUPERSPECIES FROM COLOMBIA

GARY R. GRAVES¹ AND DANIEL URIBE RESTREPO²

ABSTRACT.—Hapalopsittaca amazonina velezi, a new subspecies of Rusty-faced Parrot, is described from the Central Cordillera of the Colombian Andes. H. a. velezi apparently occurs sympatrically with H. fuertesi, which is raised to species level along with H. pyrrhops of southern Ecuador and northern Peru. Received 15 March 1988, accepted 15 July 1988.

In the autumn of 1911, Arthur A. Allen and Leo E. Miller collected birds and mammals for the American Museum of Natural History along the centuries-old Quindío trail. Among their many discoveries in the forests below the snow-capped volcanoes of Tolima and Santa Isabel was the Azure-winged Parrot (Hapalopsittaca fuertesi), the only member of the genus in the Central Cordillera of Colombia (Chapman 1912, 1917). Although H. fuertesi has not been collected since September 1911, recent sight records of Hapalopsittaca between Manizales and Salento (Fig. 1), below the Parque Nacional Los Nevados, have been attributed to H. fuertesi (see Ridgely 1980a). Unbeknownst to King (1981) and other ornithologists, four specimens of Hapalopsittaca collected in 1969 and 1976 near Manizales were deposited in the Museo de Historia Natural, University of Caldas. We were greatly surprised to find that these did not represent H. fuertesi, but instead, a new subspecies of H. amazonina (Rusty-faced Parrot).

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Hapalopsittaca amazonina velezi, new subspecies

HOLOTYPE.—Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá 29823; adult male (115 g) from Cuenca Hidrográfica de “Rio Blanco,” Municipio de Manizales, 2450 m, Departamento de Caldas, Colombia; collected 20 July 1976 by Javier Arango.

PARATYPES.—National Museum of Natural History (USNM), Smithsonian Institution 606024 and 606025; adult males from Hacienda La Morena (Bosque del Taira), Municipio de Manizales, 2400 m, Departamento de Caldas, Colombia; collected December 1969 by Jesús and Jairo Vélez E.

DIAGNOSIS.—Hapalopsittaca amazonina velezi is similar to H. a. theresae but may be distinguished from that taxon and H. a. amazonina, H. pyrrhops, and H. fuertesi, by having a golden olive hindneck and nape that contrasts sharply, instead of being concolorous, with the bright green mantle.

DESCRIPTION OF HOLOTYPE (rounded skin).—Forehead dark reddish brown becoming olivaceous on crown and olivaceous yellow (Analine Yellow; capitalized color names are from Ridgway 1912) on nape and hindneck. Hindneck contrasts sharply with mantle. Mantle, upper back, rump, upper tail coverts, scapulars, secondary coverts, posterior median wing covert, and tertials bright green, bases of feathers darker. Bend of wing, shoulder, lesser underwing coverts, and anterior median wing coverts Scarlet. Alula and primary coverts dark blue, brightest on outer webs and blackish near shaft. Carpal edge of wing mixed pale blue and pink. Primaries dull black with dark blue outer webs. Secondaries bright green with bluish tips and black or bluish black inner webs. From below, inner webs of primaries bright dark blue. Greater underwing coverts and inner webs of secondaries, from below, pale greenish blue. Dorsally, tail dull red at base with bright blue tips, and diffuse greenish band between red and blue portions of inner rectrices. From below, colors of rectrices paler. Lore and extremely narrow band of feathers above cere cream-colored. Cheek dark reddish brown, gradually becoming olivaceous rufous on lengthened feathers of auriculars. Basal portions (most concealed) of cheek feathers and upper chin brighter, varying in color from Flame Scarlet and Orange Chrome to Mars Orange. Chin, throat, upper breast, and breast olivaceous yellow (slightly darker than hindneck), which contrasts with bright pale green abdomen, lower belly, flanks, thighs, and undertail coverts. No contrasting mid-abdominal patch. Soft part colors in life: bill ivory, horn-colored at base; cere dark gray; iris greenish white; feet and tarsi gray; narrow periophthalmic ring dark gray.

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Fig. 1. Distribution of the Hapalopsittaca amazonina superspecies in the Andes of northwestern South America based on specimens examined and literature (Chapman 1917, 1926; Phelps and Phelps 1958; Ridgely 1980b; Ridgely and Gaulin 1980; Hilty and Brown 1986; S. Hilty, in litt.; Parker et al. 1985): triangles = H. a. theresae; solid circles = H. a. amazonina; squares = H. pyrrhops; question mark = unidentified Hapalopsittaca; H. a. velezi and H. fuertesi in inset. Symbols may represent two or more localities.

The continuous lines within the inset approximate the 11,000 ft (3354 m) contour interval. Hatched areas represent the snow-covered volcanic cones of (counter-clock wise from top) Nevada del Ruiz, Nev. de Sta. Isabel, Nev. del Quindío, and Nev. del Tolima, in the Central Cordillera of Colombian Andes. Specimens of H. a. velezi have been collected at: (1) Cuenca Hidrográfica de “Rio Blanco,” and (2) Cuenca Hidrográfica de Gallinazo. H. fuertesi was collected below Nev. de Sta. Isabel and at Laguneta in 1911. Unidentified Hapalopsittaca have been observed at (3) Santa Rosa de Cabal.
DESCRIPTION OF PARATYPES (taxidermy mounts).—Paratypes differ from the holotype only in minor details: the nape and hindneck of USNM 606024 and 606025 are brighter yellow. Bases of breast feathers are brighter yellow and the distribution of Mars Orange and Orange Chrome on the chin and malar region in USNM 606024 is slightly more extensive.

MEASUREMENTS (mm).—(Holotype; USNM 606024; USNM 606025): wing chord (152, 151, 147); tail (84, 86, 85); culmen from anterior margin of cere (17.6, 18.4, 17.7); greatest width of upper mandible (11.0, 10.9, 10.5).

DISTRIBUTION.—Known only from remnant cloud forest and Alnus acuminata reforestation plots (2250–2650 m elevation) above Manizales on the northwestern flank of Nevado del Ruiz, Departamento de Caldas, Colombia.

ETYMOLOGY.—We take sincere pleasure in naming this parrot for Jesús H. Vélez E., Director of the Museum, University of Caldas. He collected the paratypes, prepared the type series, and assisted the research of Uribe in the Río Blanco watershed thus making this description possible.

SPECIMENS EXAMINED.—Hapalopsittaca a. amazonina. COLOMBIA: Buenos Aires, Norte de Santander (USNM, 2 ♂♂); Alto del Pozo, Norte de Santander (USNM, 2 ♂♂); El Roble, Cundinamarca (AMNH. 1 unsexed); “Bogota” (USNM, 1 unsexed).

H. a. theresa. VENEZUELA: El Escorial, Mérida (USNM, 1 ♂; AMNH, 3 ♀♀); El Walle, Mérida (AMNH 1 ♂, 1 unsexed); Culata, Mérida (AMNH 1 ♂).

H. a. velezi. COLOMBIA: type locality (Museo de Historia Natural, Univ. Nacional de Colombia, holotype; Museo de Historia Natural, Univ. de Caldas, 1 ♂); Hacienda La Morena, Caldas (USNM, paratypes 2 ♂♂).

H. a. pyrrhops. ECUADOR: Jima, Azuay (AMNH 1 unsexed).

H. fuertesi. COLOMBIA: Laguneta, Quindío (AMNH, 4 ♂♂, 1 ♀, including holotype); Santa Isabel, Risaralda (AMNH, 1 ♀).

DISCUSSION

Ecology.—Data on the ecology and population status of H. a. velezi are scarce. Hapalopsittaca sp. have been reported intermittently in the remnant forests and plantations above Manizales since 1969. J. Vélez and Uribe observed five or six flocks each, between 1980 and 1985; the last sighting consisting of a flock of 25 birds observed by both individuals in a planted woodlot (Alnus acuminata) in the Gallinazo watershed.

The testes of the holotype were in non-breeding condition (drawings on label: 3.5 × 1.5 and 4.5 × 2.0 mm) and its stomach contents were reported to be “seeds and fruit.”

Systematic relationships.—Hapalopsittaca pyrrhops (Salvin 1876) (Red-faced Parrot) and H. fuertesi were considered to be species before Meyer de Schauensee (1966) merged them with H. amazonina, which consisted of H. a. amazonina and H. a. theresa (Hellmayr 1915, Peters 1961). Although Meyer de Schauensee presented no rationale for this revision, his taxonomy, which appears to be unjustified, was unchallenged by Forschaw (1973) and Morony et al. (1975). Taxa in this group are undoubtedly more closely related to one another than to H. melanotis or species of
Pionopsitta (Peters 1961). This fact and the allopatric distribution of the taxa were probably the reasons for Meyer de Schauensee’s merger.

H. fuertesi and H. pyrrhops are clearly divergent from one another and the amazonina group of subspecies, but share several plumage characters (e.g., blue feather margins on crown; traces of red on the abdomen; lack of extensive deposits of melanins on the forecrown, cheeks, and auriculares) not found in the amazonina group. These character states, however, cannot be considered synapomorphies because they occur in Hapalopsittaca melanotis and species in the closely related genera, Pionopsitta and Gyropopsitta. While we are unable to confirm the sister-group relationship of fuertesi and pyrrhops, the “rusty-faced” amazonina group of taxa appears to be monophyletic. We thus consider the H. amazonina superspecies to be composed of three allospecies: H. amazonina (H. a. amazonina, H. a. theresae, H. a. velezi); H. pyrrhops; and H. fuertesi.

The discovery of H. a. velezi on the western slope of the Quindío Andes suggests that H. amazonina and H. fuertesi are sympatric (Fig. 1). The distance between collecting localities for the two taxa is small (<25 km) relative to the dispersal capabilities of Hapalopsittaca (pers. obs.), and no geographic barriers occur in the intervening area. The chronology of collections, however, necessitates the consideration of other hypotheses. The failure of Allen and Miller to procure H. a. velezi in 1911, and its subsequent discovery in the same area some 50 years later may suggest that H. a. velezi is a recent immigrant that either replaced or displaced H. fuertesi. Because the avifauna of the Central Cordillera is still imperfectly known, we consider the chronological coincidence to be the result of sampling artifact (cf. Hilty and Brown 1983). For instance, Allen and Miller also failed to collect the parakeet, Bolborhynchus ferrugineifrons, at Santa Isabel where it is now locally common (Graves and Giraldo 1987). Miller’s field catalog (deposited in the American Museum of Natural History) indicated that all specimens of H. fuertesi were collected by their field assistant, Roso, and that neither Miller nor Allen observed the species. We note the possibility that H. a. velezi (observed 2250–2650 m) and H. fuertesi (collected at ca 3140 and 3810 m) replace each other elevationally. A. A. Allen observed (report dated 29 September 1911, deposited in the American Museum of Natural History) that forest was mostly cleared below 9300 ft (2835 m) on the trail to Santa Isabel. Whether the lower elevational limits of H. fuertesi below Santa Isabel were truncated by deforestation can only be surmised.

Recent sightings of Hapalopsittaca in the Quindío Andes were identified as H. fuertesi with the belief that it was the only member of the genus to occur there (Orejuela and Alberico, unpubl., in Ridgely 1980a; Hilty and
Brown 1986). Although populations of *H. fuertesi* may still survive, we know of no verified records in the past 75 years. Ridgely and Gaulin (1980:382) reported sight observations of *Hapalopsittaca* at Finca Merenberg, Department of Huila, with “considerable red on the face.” These and additional sightings of *Hapalopsittaca* sp. in the Parque Nacional Cueva de los Guacharos (Hilty and Brown 1986) may indicate that the range of *H. a. velezi* extends south along the eastern slope of the Central Cordillera to the head of the Magdalena Valley.

**Morphology.**—The dearth of sexed specimens with locality data precludes a detailed analysis of morphology. Of interest here is the observation that culmen measurements of *H. a. velezi* do not overlap those of the other taxa (Table 1). Whether this reflects some ecological difference among populations is unknown.

**RESUMEN**

Se describe una nueva subespecie de loros, *Hapalopsittaca amazonina velezi*, a partir de especímenes colectados en 1969 y 1976 de bosques nublados en la Cordillera Central de los Andes Colombianos. *H. a. velezi* se asemeja a *H. a. theresae* de los Andes Venezolanos, pero puede diferenciarse de este taxón y otras poblaciones de *Hapalopsittaca* del norte de los Andes (*H. amazonina, H. fuertesi, H. pyrrhops*) por poseer la nuca y cuello posterior oliva dorado contrastando fuertemente, en vez de ser concoloros, con el manto verde brillante.

Bandadas de hasta 25 individuos de *H. a. velezi* han sido observadas en los remanentes

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### Table 1

**Ranges and Means of Measurements (mm) of Taxa in the H. amazonina Superspecies**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Sex</th>
<th>N</th>
<th>Wing</th>
<th>Tail</th>
<th>Culmen</th>
<th>Width upper mandible</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. a. velezi</em></td>
<td>♂♂</td>
<td>3</td>
<td>147-152</td>
<td>84-86</td>
<td>17.6-18.4</td>
<td>10.5-11.0</td>
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<tr>
<td><em>H. amazonina</em></td>
<td>♂♂</td>
<td>4</td>
<td>147-151</td>
<td>82-84</td>
<td>17.0-17.5</td>
<td>10.6-11.4</td>
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<tr>
<td><em>H. theresae</em></td>
<td>♂♂</td>
<td>3</td>
<td>146-151</td>
<td>84-85</td>
<td>15.0-17.0</td>
<td>10.0-11.0</td>
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<tr>
<td><em>H. fuertesi</em></td>
<td>♂♂</td>
<td>4</td>
<td>150-155</td>
<td>87-98</td>
<td>14.9-17.3</td>
<td>10.5-11.9</td>
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<tr>
<td><em>H. pyrrhops</em></td>
<td>unsexed</td>
<td>1</td>
<td>140</td>
<td>77</td>
<td>16.0</td>
<td>10.7</td>
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de bosque natural y plantaciones con “Aliso” (*Alnus acuminata*) en las cuencas hidrográficas de Río Blanco y Gallinazo y en el Bosque del Taira, en las cercanías de Manizales, Departamento de Caldas.

La presencia de *H. a. velezi* a menos de 25 kms de las laderas del Nevado de Santa Isabel, sitio donde *H. fuertesi* fue colectada en 1911 por última vez, sugiere que los dos taxones son simpátricos. Los reportes visuales de *Hapalopsittaca* hechos recientemente en la región de Salento (Ridgely 1980 a, King 1981) pueden tratarse de *H. a. velezi* en vez de *H. fuertesi*, esta última quizás hoy extinta.


**ACKNOWLEDGMENTS**

We thank the curators and staff of the American Museum of Natural History (AMNH), Museo de Historia Natural, University of Caldas, and the National Museum of Natural History (USNM), Smithsonian Institution, for permission to examine specimens in their care, and Steve Hilty for providing detailed records of *Hapalopsittaca* in the northern Andes. We are especially grateful to Jesús Vélez for depositing the holotype in the Museo de Historia Natural, Universidad Nacional de Colombia, and for donating two specimens of the new subspecies to the Smithsonian Institution.

For assistance in Colombia, Graves thanks Gonzalo Arango, INDERENA, Pablo Medina and the Comité de Estudios Vulcanológicos, and Jesús Vélez. Uribe thanks the staff of the Central Committee for Scientific Research and College of Veterinary Medicine, University of Caldas, and the Fundacion Herencia Verde for assistance and support. Graves was supported by grants from the Smithsonian Research Opportunities Fund and from the Frank M. Chapman Memorial Fund of the American Museum of Natural History.

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Ridgway, R. 1912. Color standards and color nomenclature. Published by the author, Washington, D.C.

BIOLOGY OF THE AUSTRAL PYGMY-OWL

JAIME E. JIMÉNEZ and FABIAN M. JAKSIĆ

ABSTRACT.—Scattered information on the Austral Pygmy-Owl (*Glaucidium nanum*), published mostly in Argentine and Chilean journals and books of restricted circulation, is summarized and supplemented with field observations made by the authors. Information presented and discussed includes: taxonomy, morphometry, distribution, habitat, migration, abundance, conservation, reproduction, activity, vocalization, behavior, and diet. The first quantitative assessment of the Austral Pygmy-Owl’s food habits is presented, based on 780 prey items from a single central Chilean locality. Their food is made up of insects (50% by number), mammals (32%), and birds (14%). The biomass contribution, however, is strongly skewed toward small mammals and secondarily toward birds. Received 13 Jan. 1988, accepted 29 Jan. 1989.

The Austral Pygmy-Owl (*Glaucidium nanum*) is a little known owl of southern South America (Clark et al. 1978). During a field study on the raptors of a central Chilean locality, we found a small population of Austral Pygmy-Owls which were secretive but apparently not scarce. Because the literature on this species is widely scattered, mostly in little known and sometimes very old Chilean and Argentine books and journals, we decided to summarize it all in an account of what is known about the biology of this interesting species and to make this wealth of information available to interested ornithologists worldwide. We present a summary of our review of the literature, supplemented by our own observations. In addition, we report firsthand biological information that we have collected on Austral Pygmy-Owls in our study site, including an analysis of the first quantitative data on the food habits of the species.

METHODS

We made a literature search in the international literature, as well as in Argentine and Chilean books and journals, gathering information on the biology of Austral Pygmy-Owls. Our search was greatly facilitated through use of the Ornithological Gazetteers of Argentina and Chile (Paynter 1985, 1988). We also surveyed specimen holdings of the species at museums in Argentina, Chile, and the United States. We directed letters of inquiry to curators in the respective countries (Appendix I), asking for data reported in museum tags (catalog number, sex, locality, collector, date of collection, weight if reported, miscellaneous observations) and for direct measurement of tail length and wing chord.

We made field observations at our study site in Auco (31°31’S, 71°06’W) on the coastal ranges of north-central Chile between February (austral summer) 1987 and August (austral winter) 1988. The study site has a rugged physiognomy with mountains and ravines and almost no flat areas; it has a semi-desertic climate with usually scarce rainfall concentrated

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in winter months, and has a thorn-scrub vegetation with spiny shrubs, bromeliads, and cacti.

We searched for and found a number of bird plucking places under *Maytenus boaria* trees at the bottom of local ravines and under *Acacia caven* trees in slightly flatter areas. Under these same plucking places we found regurgitated pellets of *G. nanum*, which were transported to the laboratory. They were identified, measured, and analyzed with standard procedures (Marti 1987). Prey size of items taken by Austral Pygmy-Owls was estimated from our field data on weights of local vertebrates.

**RESULTS AND DISCUSSION**

*Taxonomy.* —Since its description by King (1827) until the early 1950s, the Austral Pygmy-Owl (*G. nanum*) was considered a species separate from the Ferruginous Pygmy-Owl (*G. brasillianum*) (e.g., Dabbene 1902, Wetmore 1926, Chapman 1929, Bullock 1929, Hellmayr 1932; Housse 1945; Barros 1950; Olrog 1948, 1950). Later authors considered it a subspecies of *G. brasillianum* (e.g., Olrog 1963, Johnson 1967, Markham 1971, Texera 1973, Clark et al. 1978) or no subspecies at all (Burton 1973). Recent South American authors, have again regarded *G. nanum* a legitimate species (e.g., Olrog 1979, 1984, 1985; Araya and Millie 1986; Olrog and Capllonch 1986; Narosky and Yzurieta 1987). However, following Short (1975), Vuilleumier (1985:292) stated that *G. nanum* is an allospecies together with the Andean Pygmy-Owl (*G. jardini*) (which inhabits forests in the high Andes) and *G. brasillianum* proper (which inhabits woodlands in Central and South America). To date, no definitive agreement has been reached with respect to the specific status of *G. nanum* and *G. brasillianum*.

Wetmore (1926) noted that *G. nanum* has a darker dorsum and heavier markings on the underparts than *G. brasillianum*. Chapman (1929) remarked that in addition to these characteristics, *G. nanum* had also heavier spotting on the breast sides and rufous tail barring. Hellmayr (1932) stated that *G. nanum* could be distinguished from *G. brasillianum* by having rufous-brown upperparts and often more than eight rufous tail bands instead of grayish-brown upperparts and generally six white tail bands, typical of the latter species. Meyer de Schauensee (1982) added that *G. nanum* is also separated from *G. brasillianum* in having numerous white spots on the wing coverts and by the comparatively narrow tail bands.

Finally, until now, these two species were supposed to be essentially allopatric in both Chile and Argentina (see distributional maps in Short 1975 and in Narosky and Yzurieta 1987). However, a recent collection of pygmy-owls from Chile, analyzed by Kiff and associates (Marín, Kiff, and Peña in litt.), produced some significant findings. First, four specimens from two localities (Rio Lluta and Quebrada Parca) in the Tarapacá Re-
region were clearly ascribable to *G. nanum*, thus representing a northward distributional extension of some 1200 km from Copiapó in the Atacama Region. It is interesting that Chapman (1929) had reported a pygmy-owl captured in Moquegua (southwestern Peru) and ascribed it to *G. nanum*, but this unusually disjunct specimen had not been considered to date in drawing distributional maps for the species. Second, four specimens from the same two localities in Tarapacá Region were clearly ascribable to *G. brasilianum*, which is no surprise in distributional range for the species. Third, six other specimens from those localities were intermediate between *G. nanum* and *G. brasilianum* in both coloration and markings. Fourth, a single specimen from Punitaqui in Coquimbo Region, well within the distributional range of *G. nanum*, had a coloration more typical of *G. brasilianum*. Marín et al. (In litt.) proposed the hypothesis that these *Glaucidium* owls are dichromatic, with the rufous-backed, rufous-tailed, highly barred birds (*nanum* morph) being more frequent toward southerly latitudes and with the *brasilianum* morph prevailing toward the north. According to Marín et al. (In litt.), *G. nanum* does not deserve even subspecific recognition. Our use of the specific epithet *nanum* throughout this paper is not a taxonomic statement. We discuss biological information on the southernmost *Glaucidium* populations in South America.

*Morphometry.*—*Glaucidium nanum* is among the smallest owls in southern South America. Measurements (from Hellmayr 1932) are: males, wing length 97.9 ± 5.9 mm (\(\bar{x} \pm SD, N = 19\)), and tail length 68.4 ± 4.3 mm (N = 19); females, wing length 106.9 ± 5.9 mm (N = 14), and tail length 74.3 ± 4.9 mm (N = 14). Goodall et al. (1957) apparently combined males and females and reported the following figures: wing length 103.6 ± 1.0 mm, tail length 69.3 ± 0.7 mm (N = 27), and total length 200–210 mm (range). Araya and Millie (1986) and Narosky and Yzurieta (1987) reported slightly smaller means for total length: 200 mm and 190 mm, respectively. The only weights reported in the literature are those of Humphrey et al. (1970) from Tierra del Fuego Island: 72.6 g (each of two males), 62.0 g (one female), and 83.3 g (another female).

We were provided with distributional and morphometric data of 195 specimens deposited in different museums and collections. The usable sample for morphometric analysis consisted of 164 specimens which were separated by sex and by distributional range. We recognized four distributional quarters for *G. nanum*, based on biogeographic, climatic, and vegetational features: a) Northern quarter: From latitude 17° to 27°; mainly warm desert areas, including oases and puna. b) Central quarter: From latitude 27° to 37°; mainly warm shrubland areas. c) Southern quarter: From latitude 37° to 43°; mainly temperate forest areas. d) Austral quarter: From latitude 43° to 56°; mainly cold *Nothofagus* forests interspersed with
Table 1

Morphometry of Austral Pygmy-Owls in Their Distributional Ranges in Chile and Argentina

<table>
<thead>
<tr>
<th>Range</th>
<th>Wing chord (mm)</th>
<th>Tail length (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>103.8 ± 3.8 (4)</td>
<td>79.4 ± 3.5 (4)</td>
<td>76.3 ± 6.0 (3)</td>
</tr>
<tr>
<td>Male</td>
<td>97.5 ± 0.0 (1)</td>
<td>75.5 ± 0.0 (1)</td>
<td>62.0 ± 0.0 (1)</td>
</tr>
<tr>
<td>Central:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>110.7 ± 4.5 (22)</td>
<td>81.2 ± 6.8 (19)</td>
<td>75.0 ± 0.0 (1)</td>
</tr>
<tr>
<td>Male</td>
<td>102.6 ± 3.9 (31)</td>
<td>77.4 ± 6.5 (25)</td>
<td>74.0 ± 0.0 (1)</td>
</tr>
<tr>
<td>Southern:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>102.9 ± 4.7 (52)</td>
<td>68.9 ± 5.9 (49)</td>
<td>95.5 ± 58.7 (2)</td>
</tr>
<tr>
<td>Male</td>
<td>96.3 ± 3.9 (31)</td>
<td>63.7 ± 4.8 (29)</td>
<td>66.5 ± 6.4 (3)</td>
</tr>
<tr>
<td>Austral:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>101.7 ± 4.8 (10)</td>
<td>68.6 ± 4.5 (10)</td>
<td>72.8 ± 3.2 (2)</td>
</tr>
<tr>
<td>Male</td>
<td>95.2 ± 2.5 (13)</td>
<td>61.9 ± 5.5 (13)</td>
<td>59.0 ± 3.6 (3)</td>
</tr>
</tbody>
</table>

* Mean ± one standard deviation, sample size in parentheses.

Steppe areas. All morphometric data were subjected to ANOVA procedures with Duncan’s Multiple Range Test as the a-posteriori algorithm to detect which data sets differed from others.

Together, the 88 females had longer wing chords and tails than did the 76 males ($P < 0.001$ in both cases); they also appeared to be heavier (Table 1), but the small sample size available (8 males and 8 females) did not result in a significant figure ($P > 0.11$). Given this sexual dimorphism, we analyzed females and males separately (Table 1). Females from the central distributional range had longer wing chords than females elsewhere; both northern and central females had longer tail lengths than those from southern and austral ranges; no significant differences were detected in body weights owing to the small sample sizes available. On the other hand, males from the central distributional range also had longer wing chords than males elsewhere; both northern and central males had longer tail lengths than those from southern and austral ranges; again, no significant differences were detected in body weight owing to the small sample sizes available. In sum, males parallel females in their morphometric trends but at significantly smaller sizes; central and northern individuals have longer wings and tails, and likely heavier weights, than southern and austral individuals.

One unsexed specimen captured alive by us near Santiago weighed 94.5 g and had 295.5 cm² total wing area. This renders a wing load of 0.320
g/cm²; or in standardized form (Jaksić and Carothers 1985), a linearized wing load of 0.265. This latter figure is the highest of all those reported by Jaksić and Carothers (1985) for other owls.

**Distribution.**—Until now, northernmost records were in Chile’s Atacama Region (Goodall et al. 1957), but Marin et al. (in litt.) have extended its distribution to Arica in Chile’s Tarapacá Region. In Argentina, northernmost records are from Córdoba province and from Neuquén and Rio Negro provinces southwards (Hellmayr 1932). Southernmost records are given as Cape Horn for both Chile and Argentina (Dabbene 1902), with numerous intermediate localities (e.g., Hellmayr 1932; Barros 1950; Olrog 1950, 1984; Goodall et al. 1957; Johnson 1967; Texera 1973; Meyer de Schauensee 1982; Hudson 1984; Narosky and Yzurieta 1987). Altitudinal records are from sea level to 1700 m (Barros 1950), 1800 m (Housse 1945), and 2000 m elevation (Goodall et al. 1957, Johnson 1967, Araya and Millie 1986) in Chile and up to 1500 m elevation in Argentina’s Patagonia (Vuilleumier 1985).

**Habitat.**—All authors (e.g., Clark et al. 1978, Meyer de Schauensee 1982, Araya and Millie 1986) concur that the Austral Pygmy-Owl inhabits forests and thickets, sometimes parklands, and that it is also found in city parks and gardens (Housse 1945, Goodall et al. 1957, Johnson 1967, Solar 1975). The forests inhabited may vary in character, however. In central Chile, the Austral Pygmy-Owl has been reported in evergreen shrublands (particularly in ravines, Barros 1950); in southern Chile, in rain forests; and in southernmost Chile, in *Nothofagus* forests (Humphrey et al. 1970, Markham 1971, Texera 1973, Venegas and Jory 1979, Vuilleumier pers. comm.). In Argentina, it is considered to inhabit *Nothofagus* forests (Narosky and Yzurieta 1987), and Patagonian scrub (Olrog and Capllonch 1986). Vuilleumier (1985), on the basis of a variety of sources reported the species to be found in mesophytic forests, montane forests, parklands, openings within forests, forest/steppe ecotones, and shrublands. Our own observations throughout Chile agree well with previous reports. In Aucó, Austral Pygmy-Owls are found in ravines with clumps of 5-m high *Maytenus boaria* trees, the tallest tree in our study site, and also in smaller *Schinus polygamus* trees in south-facing slopes, and in *Acacia caven* trees in north-facing slopes.

**Migration.**—Goodall et al. (1957) reported that *G. nanum* is a summer visitor in the northern ranges of its distribution in Chile (Atacama Region). Populations in Chile’s southernmost Magallanes Region are said to be permanent residents (Markham 1971, Venegas and Jory 1979). But just across the strait of Magellan, in Tierra del Fuego Island, Humphrey et al. (1970) considered the Austral Pigmy-Owl to be a “summer breeding visitor,” which “probably leaves the Island during the winter.” In agree-
ment, Vuilleumier (1985) considered it as a partial migrant, whose southern populations migrate northwards in late fall (see also Olrog 1963, 1979; Narosky and Yzurieta 1987). Olrog (1963) and Meyer de Schauensee (1982) reported that the final destinations of those winter migrants are in Buenos Aires, Santa Fe, Entre Ríos, and Tucumán provinces, all in Argentina. Hudson (1984) reported that overwintering Austral Pygmy-Owls migrate from Entre Ríos, Santa Fe, and Tucumán back to Neuquén, Rio Negro, and Tierra del Fuego, in southern Argentina.

Abundance.—Hellmayr (1932) reported that the Austral Pygmy-Owl is common throughout Chile. It is indeed considered the most abundant Strigidae in Chile, although it becomes rather scarce from Atacama south to Coquimbo during the winter, whereas toward the south of the country it is always an abundant nesting bird (Goodall et al. 1957, Johnson 1967). Barros (1950) added that the species is more abundant in southern than in central Chile. It is also common in southernmost Chile: in Magallanes and Tierra del Fuego (Markham 1971, Venegas and Jory 1979). Jaksic and Jiménez (1986) evaluated its abundance throughout Chile. They reported that its population status in northernmost Chile is unknown, that in central and southernmost Chile it is common (1 to 5 individuals can be seen or heard daily), and that in southern Chile it is frequent (one individual can be seen or heard weekly). Based on our observation in Aucó, Austral Pygmy-Owls seem to be abundant during summer, fall, and winter, as judged from vocalizations and sightings. Either they leave the area during spring to reproduce elsewhere, or they become very secretive. In Argentina, it has been reported as abundant from Neuquén and Rio Negro southwards (Johnson 1967) and even more common in forests of Tierra del Fuego (Olrog 1948, but see Vuilleumier 1985 to the contrary).

Conservation.—Jaksic and Jiménez (1986) considered G. nanum as a resident and breeding bird throughout Chile between latitudes 18°–55°. They also reported that the abundance status of populations of the Austral Pygmy-Owl is stationary in the entire country, except in central Chile, where it appears to be increasing despite being killed by country people because of its reputation as a bird of ill omen. Jaksic and Jiménez (1986) commented that “Glaucidium brasilianum [=nanum] seems to be relatively indifferent to (or tolerant of) human-induced habitat perturbations,” and suggested that “Gardening has apparently increased the prey (passerines, including House Sparrows) for the human-tolerant” owl.

Reproduction.—According to Barros (1950), males are fiercely territorial, pairing and mating by the end of July (austral mid-winter), nesting mainly between October and November (austral spring), and laying a single clutch. Goodall et al. (1957) and Johnson (1967) reported that
nesting begins earlier, in September. According to Housse (1945) the nest is re-utilized over several years. Barros (1950) and Housse (1945) disagreed as to the tolerance of Austral Pygmy-Owls to conspecific neighbors: while the former reported that they nest far apart, the latter reported that they may coexist peacefully in a single tree. Nests are placed inside hollowed tree trunks, sometimes in branch bifurcations, and also in road banks, ground cavities, rodent burrows, and even in human buildings (Bullock 1929, Housse 1945, Barros 1950, Johnson 1967). According to Barros (1950), they usurp nests of Dark-bellied Cinclodes (Cinclodes patagonicus), and according to Goodall et al. (1957), they use hollows probably made by Chilean Flickers (Colaptes pitius). In Aucó we have seen Austral Pygmy-Owls perching outside tree hollows apparently made by Striped Woodpeckers (Picoides lignarius). According to Housse (1945), the clutch size is 3–4 eggs, with an incubation period of 15 to 17 days. Other clutch sizes reported are 3–4 (Bullock 1929), and 3–5 (Goodall et al. 1957, Johnson 1967). Sample sizes were not reported in these studies.

Activity.—Most authors in Chile and Argentina agree that G. nanum is active (i.e., hunting) day and night (Bullock 1929, Housse 1945, Barros 1950, Johnson 1967, Venegas and Jory 1979, Narosky and Yzurieta 1987).

Vocalization.—The Austral Pygmy-Owl vocalizes during the evening and night, and not infrequently during the day (Housse 1945, Barros 1950). According to the latter author, the voice of the male differs from that of the female, and Humphrey et al. (1970) reported that the male responds to voice imitation, unlike the female. In Tierra del Fuego, the Austral Pygmy-Owl vocalizes at night, especially shortly after nightfall in late spring; but vocalizations can be heard intermittently throughout the night (Vuilleumier pers. comm.). Goodall et al. (1957) recognized two types of vocalizations, a hunting call and a mating call. We are familiar only with the latter call: the “song” is a series of short whistles repeated in very rapid succession (mean = 2.9 whistles/sec ± 0.35 [SD], N = 10 “songs” with durations from 8 to 22 sec each, and number of notes from 26 to 66). Our description agrees with that in Burton (1973:204) for G. brasillianum, whose call is depicted as “huj huj huj huj huj ... in series of 11–33 notes, each one with an upward inflection, uttered at a rate of about 5–6 notes every 2 seconds.” The number of serial notes that we detected is considerably higher, however.

Behavior.—Glaucidium nanum does not avoid man’s presence, and it is often mobbed by passerines (Housse 1945, Barros 1950, Johnson 1967 pers. obs.). In Nothofagus forests of Magallanes Region (F. Vuilleumier pers. comm.), playbacks of the Austral Pygmy-Owl elicited aggressive responses from the Thorn-tailed Rayadito (Aphrastura spinicauda). The Austral Pygmy-Owl is a solitary hunter that stalks prey from perches day-
round (Barros 1950). It attacks small birds caught in mist nets, and either gets itself caught or destroys part of the net (pers. obs.). We captured one Austral Pygmy-Owl at night, using a live cricetid rodent as bait in a Bal-Chatri trap.

Diet. — All accounts so far available are qualitative. However, all authors (e.g., Housse 1945, Barros 1950, Johnson 1967) concur that the species preys primarily on birds: Plain-mantled Tit-spine-tail (*Leptasthenura aegithaloides*), White-crested Elaenia (*Elaenia albiceps*), Common Diuca-Finch (*Diuca diuca*), Austral Blackbird (*Curaeus curaeus*), Austral Thrush (*Turdus falklandii*), Moustached Turca (*Pteroptochos megapodius*), Chilean Tinamou juvenile (*Nothoprocta perdicaria*), Eared Dove (*Zenaida auriculata*), as well as Rock Doves (*Columba livia*), Domestic Fowl (*Gallus domesticus*), and caged canaries (*Emberiza serin*), have been frequently cited as prey. Humphrey et al. (1970) examined five stomachs from Tierra del Fuego and found four with birds and one with a small rodent. Small mammals such as Fence degu rat (*Octodon degus*), domestic rats, and bats, as well as insects have been reported as secondary prey. An interesting feature that has been reported is that, when eating birds and mammals, Austral Pygmy-Owls start with the head, sometimes eating only the brains (Housse 1945, Barros 1950, Vigil 1973).

Quantitative food habits. — We report here the first quantitative information on the food habits of *G. nanum*, based on observations in our study site at Aucó. Remains deposited under plucking places indicate that Austral Pygmy-Owls pluck only wing and tail feathers of avian prey; occasionally, we found a whole wing dropped on the ravine floor. 284 unbroken pellets had a length of 28.8 ± 5.5 mm (x ± SD) and a width of 12.5 ± 1.4 mm. By number, its most frequent prey appeared to be insects, particularly nocturnal tenebrionid beetles (Table 2). However, the biomass contributed by insects was clearly smaller than that represented by avian and mammalian prey. Among the former, Austral Pygmy-Owls preyed on a wide variety of diurnal birds, ranging in size from juvenile tinamous to hummingbirds. Of 37 species of potential avian prey in Aucó, 22 (59%) were found among the actual prey taken by the owls (Table 2). Of nine species of potential mammalian prey in the locality, six were actually taken (67%). Judging from the sizes and incidence of the different small mammals in their diet (Table 2), their biomass contribution is the greatest.

Our results are at variance with previous reports; the Austral Pygmy-Owl in Aucó may be better depicted as a small-mammal eater that secondarily preys on birds. Perhaps because mobbing by passerines is so apparent, and remains of avian prey so easy to detect, earlier authors may have overestimated its predation on birds. However, we suspect that our
## Table 2

**Percent of Prey Taken (by Number and with Their Respective Weights) by Austral Pygmy-Owls in Auco, North-Central Chile**

<table>
<thead>
<tr>
<th>Prey</th>
<th>Weight (g)</th>
<th>Percent by no.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mammals</strong></td>
<td>(31.7)$^c$</td>
<td></td>
</tr>
<tr>
<td>Bennett’s chinchilla rat (<em>Abrocoma bennettii</em>)$^b$</td>
<td>80.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Olivaceous field mouse (<em>Akodon olivaceus</em>)</td>
<td>32.3</td>
<td>7.4</td>
</tr>
<tr>
<td>Unidentified field mouse (<em>Akodon sp.</em>)</td>
<td>—</td>
<td>0.4</td>
</tr>
<tr>
<td>Llaca mouse opossum (<em>Marmosa elegans</em>)</td>
<td>22.6</td>
<td>2.4</td>
</tr>
<tr>
<td>Fence degu rat (<em>Octodon degus</em>)$^b$</td>
<td>80.0</td>
<td>3.6</td>
</tr>
<tr>
<td>Long-tailed rice rat (<em>Oryzomys longicaudatus</em>)</td>
<td>24.4</td>
<td>1.3</td>
</tr>
<tr>
<td>Darwin’s leaf-eared mouse (<em>Phyllotis darwini</em>)</td>
<td>58.2</td>
<td>3.3</td>
</tr>
<tr>
<td>Cricetidae: unidentified</td>
<td>—</td>
<td>12.2</td>
</tr>
<tr>
<td>Octodontidae: unidentified</td>
<td>—</td>
<td>0.3</td>
</tr>
<tr>
<td>Rodentia: unidentified</td>
<td>—</td>
<td>0.5</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
<td>(14.0)</td>
<td></td>
</tr>
<tr>
<td>Chilean Tinamou (<em>Nothoprocta perdicaria</em>)$^b$</td>
<td>160.0</td>
<td>0.3</td>
</tr>
<tr>
<td>California Quail (<em>Callipepla californica</em>)</td>
<td>64.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Eared Dove (<em>Zenaida auriculata</em>)</td>
<td>137.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Green-backed Firecrown (<em>Sephanoides galeritus</em>)</td>
<td>5.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Striped Woodpecker (<em>Picoides lignarius</em>)</td>
<td>39.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Crag Chilia (<em>Chilia melanura</em>)</td>
<td>40.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Plain-mantled Tit-spine-tail (<em>Leptasthenura aethaloides</em>)</td>
<td>10.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Furnariidae: unidentified</td>
<td>—</td>
<td>0.4</td>
</tr>
<tr>
<td>Moustached Turca (<em>Pteroptochos megapodius</em>)</td>
<td>119.0</td>
<td>0.1</td>
</tr>
<tr>
<td>White-throated Tapaculo (<em>Scelorchilus albicollis</em>)</td>
<td>60.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Rhinocryptidae: unidentified</td>
<td>—</td>
<td>0.1</td>
</tr>
<tr>
<td>Fire-eyed Diucon (<em>Pyrope pyrope</em>)</td>
<td>38.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Tufted Tit-tyrant (<em>Anairetes parulus</em>)</td>
<td>7.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Patagonian Tyrant (<em>Colorhamphus parvirostris</em>)</td>
<td>8.5</td>
<td>0.1</td>
</tr>
<tr>
<td>House Wren (<em>Trogodytes aedon</em>)</td>
<td>10.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Austral Thrush (<em>Turdus falklandii</em>)</td>
<td>94.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Chilean Mockingbird (<em>Mimus therca</em>)</td>
<td>66.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Austral Blackbird (<em>Curaeus cauraeus</em>)</td>
<td>90.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Red-breasted Meadowlark (<em>Sturnella loyca</em>)</td>
<td>112.6</td>
<td>0.1</td>
</tr>
<tr>
<td>Icteridae: Unidentified</td>
<td>—</td>
<td>0.1</td>
</tr>
<tr>
<td>Rufous-collared Sparrow (<em>Zonotrichia capensis</em>)</td>
<td>19.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Gray-headed Sierra-Finch (<em>Phrygilus gayi</em>)</td>
<td>20.0</td>
<td>0.2</td>
</tr>
<tr>
<td>Mourning Sierra-Finch (<em>Phrygilus fruticeti</em>)</td>
<td>31.5</td>
<td>1.7</td>
</tr>
<tr>
<td>Band-tailed Sierra-Finch (<em>Phrygilus alaudinus</em>)</td>
<td>18.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Common Diuca-Finch (<em>Diuca diuca</em>)</td>
<td>31.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Fringillidae: unidentified</td>
<td>—</td>
<td>0.9</td>
</tr>
<tr>
<td>Passeriformes: unidentified</td>
<td>—</td>
<td>5.6</td>
</tr>
<tr>
<td>Bird: unidentified</td>
<td>—</td>
<td>0.5</td>
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</table>
### Table 2
**Continued**

<table>
<thead>
<tr>
<th>Prey</th>
<th>Weight (g)</th>
<th>Percent by no.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reptiles</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified lizard (<em>Liolaemus sp.</em>)</td>
<td>2.5</td>
<td>1.4</td>
</tr>
<tr>
<td>Rough-scaled lizard (<em>Liolaemus nitidus</em>)</td>
<td>15.0</td>
<td>0.3</td>
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<tr>
<td>Long-tailed snake (<em>Philodryas chamissonis</em>)</td>
<td>70.0</td>
<td>0.5</td>
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<tr>
<td><strong>Insects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Buprestidae: unidentified adult</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Bronze wood-boring beetle (<em>Ectinogonia buqueti</em>)</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>Curculionidae: unidentified adult</td>
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</tr>
<tr>
<td>Black snout-beetle (<em>Rhyephenes sp.</em>)</td>
<td>0.1</td>
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</tr>
<tr>
<td>Tenebrionidae: unidentified adult</td>
<td>9.2</td>
<td></td>
</tr>
<tr>
<td>Giant darkling-beetle (<em>Gyriosomus sp.</em>)</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Rounded darkling-beetle (<em>Praocis sp.</em>)</td>
<td>8.3</td>
<td></td>
</tr>
<tr>
<td>Elongated darkling-beetle (<em>Nycterinus sp.</em>)</td>
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<td></td>
</tr>
<tr>
<td>Scarabaeidae: unidentified adult</td>
<td>7.2</td>
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<td>Bostrichidae: unidentified adult</td>
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<td></td>
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<tr>
<td>Carabidae: unidentified adult</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Elateridae: unidentified larva</td>
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<td></td>
</tr>
<tr>
<td>Elateridae: unidentified adult</td>
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<td></td>
</tr>
<tr>
<td>Coleoptera: unidentified larva</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Coleoptera: unidentified adult</td>
<td>3.5</td>
<td></td>
</tr>
<tr>
<td>Lepidoptera: unidentified larva</td>
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<td></td>
</tr>
<tr>
<td>Hymenoptera: unidentified adult</td>
<td>2.4</td>
<td></td>
</tr>
<tr>
<td>Field ant (<em>Camponotus sp.</em>)</td>
<td>3.3</td>
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</tr>
<tr>
<td>Gryllidae: unidentified adult</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>Cicadidae: unidentified adult</td>
<td>4.0</td>
<td></td>
</tr>
<tr>
<td>Orthoptera: unidentified adult</td>
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<tr>
<td>Odonata: unidentified adult</td>
<td>0.1</td>
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<tr>
<td>Neuroptera: unidentified adult</td>
<td>0.1</td>
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</tr>
<tr>
<td>Insect: unidentified adult</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td><strong>Arachnids</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aranea: unidentified adult</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Scorpionidae: unidentified adult</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td><strong>Total prey</strong></td>
<td>780</td>
<td></td>
</tr>
<tr>
<td><strong>Total pellets</strong></td>
<td>311</td>
<td></td>
</tr>
<tr>
<td><strong>Total prey remains</strong></td>
<td>110</td>
<td></td>
</tr>
</tbody>
</table>

*After Meserve et al. (1987).*

*Juveniles.*

*Figures in parentheses are subtotals by class.*
results actually reflect the mouse outbreak that occurred in the winter of 1987 and continued throughout the winter 1988 (Unpubl. data). Austral Pygmy-Owls may have opportunistically exploited the surplus of rodents, thus relieving normal predation levels upon birds.

Whether avian prey are killed during their daylight activities or at their nightly roosting places is difficult to establish. Among mammalian prey, Austral Pygmy-Owls took mainly species with crepuscular and nocturnal habits (pers. obs.). Reptiles and arachnids made up a small part of the owls' prey base. Given that the lizards and snakes detected in the diet are all known to be strictly diurnal, the above findings indicate that the owls are able to hunt both day and night.

Some of the avian and mammalian prey reported in Table 2 are substantially larger than *G. nanum* (Table 1). The powerful feet and talons characteristic of this otherwise small owl probably allow it to easily kill large prey. Based on weight data reported in Table 2, it is possible to compute the geometric mean weight of vertebrate prey (Jaksić and Carothers 1985) in the diet of Austral Pygmy-Owls = 34.2 ± 2.3 g (± SD; N = 209). Prey weight relative to owl weight amounts then to about 45%. This figure is the largest reported for owls by Jaksić and Carothers (1985) and confirms ornithological common knowledge that these little owls prey on rather large prey.

**ACKNOWLEDGMENTS**

We are grateful to G. Soto for granting permits to work in Aucó's CONAF National Reserve, and to C. Noton for making recommendations about field work in the Reserve. R. P. Schlatter kindly provided some owl and prey weight data. We are grateful to all the curators and collection managers who answered our queries; their names are listed in Appendix I. Special thanks are due to Sadie Coats for supplying measurements from museums which we did not know had specimens of *G. nanum*. We are also grateful to J. P. Myers, B. D. Patterson, D. A. Schlitter, and R. Zink, for acting as conduits. The reviews of R. J. Clark, P. S. Humphrey, and F. Vuilleumier are duly appreciated. This research was funded directly by grants DIUC 09487 and INT 8802054, and indirectly by CONAF/WWF 1297 and FONDECYT 116187.

**LITERATURE CITED**


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APPENDIX I
MUSEUM SPECIMENS EXAMINED

The following museums/curators/collections managers were contacted and the number of specimens reported by them is indicated as sample sizes: Academy of Natural Sciences, Philadelphia (M. Robbins, N = 1); American Museum of Natural History, New York (F. Vuilleumier/S. Coats, N = 26); Carnegie Museum of Natural History, Pittsburgh (K. C. Parkes, N = 6); Centro Regional de Investigaciones Científicas y Técnicas, Mendoza (L. Marone, N = 0); Centro de Zoología Aplicada, Córdoba (M. Nores, N = 0); Field Museum of Natural History, Chicago (D. Willard, N = 35); Florida State Museum, Gainesville (T. Webber, N = 0); Instituto de la Patagonia, Punta Arenas (courtesy of F. Vuilleumier/S. Coats, N = 6); Instituto de Zoología, Universidad Austral, Valdivia (R. P. Schlatter, N = 4); Instituto Miguel Lillo, Tucumán (R. Báquez, N = 11); Los Angeles County Museum, Los Angeles (courtesy of S. Coats, N = 19); Museo de Zoología, Universidad de Concepción, Concepción (N = 12); Museo Nacional de Historia Natural, Santiago (J. C. Torres, N = 21); Museum of Comparative Zoology, Harvard University, Cambridge (R. A. Paynter, N = 18); Museum of Natural History, University of Kansas, Lawrence (P. S. Humphrey/P. C. Rasmussen, N = 1); Museum of Natural Science, Louisiana State University, Baton Rouge (J. V. Remsen/S. W. Cardiff, N = 12); Museum of Vertebrate Zoology, University of California, Berkeley (N. K. Johnson, N = 6); National Museum of Natural History, Washington, D.C. (J. P. Angle, N = 8); Western Foundation of Vertebrate Zoology (L. F. Kiff, N = 9).
NEW AND NOTEWORTHY RECORDS OF BIRDS FROM THE EASTERN YUCATÁN PENINSULA

ARTURO LOPEZ ORNAT,1 JAMES F. LYNCH,2 AND BARBARA MACKINNON DE MONTES3

ABSTRACT.—Thirteen species of birds are recorded for the first time from Mexico’s Yucatán Peninsula, and significant new distributional information within the peninsula is reported for 56 additional species. The distributional records reported here fall into three major categories: (1) northward extensions into semi-evergreen forest of species previously known to occur in more humid tropical forest, (2) mainland records of species normally restricted (or nearly so) to offshore islands, and (3) miscellaneous new records of uncommon species. Received 17 June 1988, accepted 1 Dec. 1988.

The avifauna of Mexico’s Yucatán Peninsula has been studied in a series of reports (Peters 1913; Griscom 1926a, b; Traylor 1941) that culminated in the classic monograph by Paynter (1955a). The latter author listed 429 bird species from the peninsula, including the surrounding ocean and offshore islands. Later publications (Paynter 1955b, Storer 1961, Klaas 1968, Parkes 1970, Gatz et al. 1985, Scott et al. 1985) have increased the species list slightly (to 437 species). Over the three decades since Paynter’s studies, construction of new roads and airfields has increased the accessibility of the eastern portion of the region where relatively little ornithological work had been done previously. The present paper summarizes significant new distributional data that we and our colleagues have gathered in the eastern Yucatán Peninsula during the course of ongoing studies of migratory and resident bird communities.

STUDY AREA

The Yucatán Peninsula is a large (240,000 km²), essentially flat sedimentary shelf that juts northward into the Gulf of Mexico and Caribbean Sea from the igneous tectonic core of Central America. The physiographic limits of the peninsula include all of the Mexican states of Yucatán, Quintana Roo, and Campeche (parts of Chiapas and Tabasco are also included according to some definitions), the Petén region of northern Guatemala, and the entire nation of Belize. The present study concerns only the Mexican portion of the peninsula, particularly Quintana Roo and adjacent portions of the state of Yucatán. Lundell (1934), Paynter (1955a), and Lee (1980) contain descriptions of the geology, physiography, climate, and vegetation of the Yucatán Peninsula. Lynch et al. (1985) present a generalized vegetation map that is based on satellite imagery. For present purposes, we summarize only the major features of vegetation and climate that might influence bird distribution.

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2 Smithsonian Environmental Research Center, Edgewater, Maryland 21037 USA. (Author to whom reprint requests should be made.)
3 Robalo 30 SM-3, Cancun 77500, Quintana Roo, Mexico.
Annual precipitation tends to increase from NW to SE, with extreme values ranging from ca 450 mm on the NW coast of the state of Yucatán to ca 4000 mm in southern Belize (Russell 1964, Garcia 1965). Within the Mexican portion of the peninsula, maximum annual rainfall (1500–2000 mm) occurs in southernmost Quintana Roo and adjacent Campeche. Rainfall in the northern half of the peninsula is strongly seasonal, and surface water there is restricted to sinkholes, seasonal pools, and a few scattered lakes. Marshes and lagoons are scattered around the perimeters of the Yucatán. One such wetland is located within the 528,000 ha Sian Ka’an Biosphere Reserve on the Caribbean coast of central Quintana Roo. A narrow, discontinuous zone of dune vegetation flanks much of the Yucatán coast. Despite its limited area, this vegetation type has considerable biogeographic significance, both to plants (Moreno-Casasola and Espejel 1986, Espejel 1987) and to birds (see below).

The NW–SE gradient in the Yucatán rainfall and edaphic conditions is paralleled by corresponding zonation in the natural vegetation, although patterns are complicated by the effects of long-term human settlement in the region. In an effort to adopt a simple vegetation classification that could be used by ornithologists, Paynter (1955a) applied the term “rain forest” to the native forest of the entire eastern and southern portions of the Yucatán. Similarly, some large-scale vegetation maps (Leopold 1950, Rzedowski 1983) also lump the sub-humid forests of central and northern Quintana Roo with the much wetter forests to the south. However, annual rainfall in Quintana Roo is both too low and too seasonal to support even tropical wet forest, much less rain forest as these vegetation types conventionally are defined. Thus, according to the Holdridge scheme of vegetation classification (Holdridge et al. 1971), the climate of northern and central Quintana Roo supports Dry Tropical Forest (Thien et al. 1982). Elsewhere in the Mexican portion of the Yucatán, climax vegetation ranges from low thorn scrub on the northern coast, through a series of moderate-height deciduous, semi-deciduous, and semi-evergreen forest types in most of the area, to tall semi-evergreen forest in limited areas of southern Quintana Roo and adjacent Campeche (Miranda 1958, Fig. 1). Tropical evergreen forest occurs still farther south in sections of eastern Belize that receive more than ca 3500 mm of annual precipitation (Wright et al. 1959, Russell 1964).

The main biogeographic questions addressed in the present paper are the extent to which: (1) bird species typically associated with lowland wet forest in Middle America penetrate the drier, more seasonal forests of the northern Yucatán, and (2) species normally considered to occur only on offshore islands also occur on the Yucatán mainland.

METHODS

Distributional data reported here were gathered over the period 1974–1988. Lopez-Ornat and MacKinnon de Montes have resided in Quintana Roo since 1981 and 1974, respectively. Lynch has visited the peninsula some 15 times since 1979, mostly during October–March when many Nearctic migrants are present. Lopez-Ornat and Lynch have conducted mist-netting studies at 20 sites in northern and central Quintana Roo in habitats that represent a wide range of natural and disturbed vegetation types. Eight sites were clustered within 15 km of the coastal village of Puerto Morelos, in northeastern Quintana Roo (7182 net-h); the remaining 12 sites were in the Sian Ka’an Biosphere Reserve in east-central Quintana Roo (15,174 net-hrs). Lynch and associates have performed more than 1000 point counts (Lynch et al. 1985) of birds in Quintana Roo, Yucatán, Campeche, northern Belize, and the Petén region of northern Guatemala. Additional distributional data, particularly for aquatic species, have been obtained from surveys of coastal areas and exploratory trips throughout the Yucatán.

We realize the potential pitfalls of faunistic studies based on sight records (e.g., Austin et
al. 1981), and recognize that even specimen-based distributional records can be unreliable if not accompanied by adequate documentation (e.g., Parkes 1970). We rigorously excluded questionable identifications from the present report, and note that most of the records reported below are based either on mist-netted birds or on repeated sightings by more than one qualified observer. In addition, we have photographed many of the species in question. Copies of field notes documenting our sight records are available upon request from the authors.

The following account is restricted to species that are either: (1) new to the entire Mexican portion of the Yucatán Peninsula (indicated by an asterisk), (2) state records for Quintana Roo or Yucatán, (3) insular forms rarely or never previously reported from the mainland of the peninsula, or (4) widespread but rare forms for which there were three or fewer published records for the Mexican portion of the peninsula (Campeche, Quintana Roo, Yucatán). We have included accounts of breeding activity for a few uncommon species. For the purposes of this paper, we have not considered undocumented listings in popular field guides or checklists (e.g., Blake 1953, Peterson and Chalif 1973, MacKinnon de Montes 1986) to constitute verified records of species occurrences in the study region.


SPECIES ACCOUNTS

Red-footed Booby (Sula sula).—This booby breeds on scattered islands off the coast of Belize and elsewhere in the Caribbean. The only previous record for the Mexican portion of the Yucatán Peninsula is a specimen collected near Chetumal in southern Quintana Roo (Paynter 1955a). In May 1984, AL identified a Red-footed Booby that had been captured by a local fisherman at Puerto Morelos in NE Quintana Roo. In June 1985, AL photographed another individual that was perched along the shore at Puerto Morelos. There is an unconfirmed record of breeding by this species on Arecife Alacran off the northern coast of Yucatán state (C. C. Lockwood, in litt. to BM).

American White Pelican (Pelecanus erythrorhynchos).—Paynter (1955a) cites a sight record of several individuals of this Nearctic migrant from the extreme NW coast of the state of Yucatán. We (SH, AL, JL—photo, BM, EM) have observed flocks of as many as 200 American White Pelicans on every winter visit we have made to the lagoons between Río Lagartos and Las Coloradas on the NE coast of Yucatán (February 1982, 1983, 1986, 1988). The species has been observed during winter on one or more occasions at the following additional coastal localities: between Progreso and Dzidzantun, Yucatán (JL), and Isla Holbox, Quintana Roo (SH, BM). The American White Pelican is clearly a regular winter visitor to the northern coast of the peninsula, and small numbers of birds have been observed as late as 24 June at Las Coloradas (BM).
Least Bittern (*Ixobrychus exilis*).—Previous Yucatán records were a specimen taken on Banco Chinchorro, off the southern coast of Quintana Roo (Paynter 1955a), and a photographic record and several sightings from Coba in the central part of the state (BM; Scott et al. 1985). AL has observed the species at Vigia Chico, in the Sian Ka’an reserve (May 1983), and at Puerto Morelos (January 1984), both in Quintana Roo. The two birds were observed as they crossed the road in areas of *Cladium* marsh. In February 1987, AL netted a Least Bittern in a stand of black mangrove (*Avicennia*) scrub within the Sian Ka’an reserve.

Bare-throated Tiger-Heron (*Tigrisoma mexicanum*).—Paynter (1955a) encountered this species at one locality in southernmost Quintana Roo and noted Griscom’s (1926a) earlier breeding record from the coast of central Quintana Roo. We have found tiger-herons to be widely distributed throughout the coastal region of the state in mangroves, seasonally flooded low forest, and along the margins of pools, inlets, and beaches. Quintana Roo: Mahahual (RG, DN), 40 km W of Mahahual (JL, WR), Sian Ka’an reserve (AL, BM—photo, DN), Tulum (JL), Akumal (AL), Xcaret (JL), Punta Celiz (JL), Puerto Morelos (AL), Isla Cancun (BM), 15 km N of Cancun (AL, JL), Chiquila (SH). A nest containing two eggs was found in red mangrove (*Rhizophora*) scrub at the Sian Ka’an reserve on 22 March 1986 (AL—photo); and a nest with two downy young was found in a *Rhizophora* tree in Laguna Nichupte, behind Isla Cancun, on 18 July 1979 (BM—photo).

Jabiru (*Jabiru mycteria*).—This rare stork is known to breed in Belize and in the extensive marshes of the Tabasco lowlands, but Paynter’s (1955a) sight record from extreme southern Quintana Roo is the only published record of the species for the Mexican portion of the Yucatán Peninsula. We (AL, JL) have observed one to two individuals on 14 separate occasions within the Sian Ka’an reserve in east-central Quintana Roo. Extreme dates are 25 November and 22 March. A pair was attending a nest from 13 January 1987 to 19 February 1987 when the birds abandoned the nest and two eggs (AL—photo). The species also was sighted 2 km W of Francisco Villa, Quintana Roo in January 1984 and December 1985 (SH).

Fulvous Whistling-Duck (*Dendrocygna bicolor*)*.—The first peninsula records for this resident species are sightings on 22 January 1984 and 1 April 1984 (possibly the same individual) at Isla Cancun, Quintana Roo (BM—photo).

Northern Shoveler (*Anas clypeata*).—This species is known to overwinter in small numbers on the coast of Yucatán state, but there is only a single previous record for Quintana Roo (Paynter 1955a). In February 1984, JL observed one shoveler in a temporary pond, just W of Tulum,
and several individuals in the extensive marshes 40 km W of Mahahual; both localities are in east-central Quintana Roo.

Hooded Merganser (Lophodytes cucullatus)*.—The first record for this Nearctic migrant on the peninsula is a female observed by AL 2 December 1983 2 km W of Puerto Morelos in NE Quintana Roo. The bird, which was watched at close range for several minutes, was swimming in a seasonal pool at the edge of a small clearing surrounded by semi-evergreen forest.

Masked Duck (Oxyura dominica).—The only published record of this secretive species for the Yucatán Peninsula is a specimen from southern Campeche (Storer 1961). In January 1984, JL photographed a live female Masked Duck that had been captured by a local boy in the coastal lagoon just W of Puerto Morelos, Quintana Roo.

Lesser Yellow-headed Vulture (Cathartes burrovianus).—At the time of Paynter’s (1955a) monograph, the Yellow-headed Vulture was not clearly distinguished from the much more widespread and common Turkey Vulture (C. aura) in southern Mexico. Klaas (1968) reported one specimen from the SW coast of Campeche, but there are no other published records for the peninsula. We have positively identified Lesser Yellow-headed Vultures (perched or low-flying birds observed through binoculars at close range) at a number of coastal localities and in areas of savannah in all months between September and April. Quintana Roo: Boca Paila, within the Sian Ka’an reserve (AL, JL, BM), marshes 40 km W of Mahahual (RG, JL, DN), Puerto Morelos (AL, JL), 10 km S of Cancun (BM), Cancun (BM), 12 km N of Cancun (AL, JL), Isla Contoy (BM), Isla Holbox (SH); Yucatán: 12 km E of Las Coloradas (AL, JL), Río Lagartos (SH, AL, JL), and Celestun (SH, BM).

Black-shouldered Kite (Elanus caeruleus).—Paynter (1955b) did not observe this species and considered it to be “extremely rare on the peninsula.” He reported one specimen from southern Quintana Roo, and there are several records from Campeche. We have observed the species at scattered sites throughout the study area, always in areas of grass or other low vegetation. Quintana Roo: Road between Chetumal and La Unión (SH), several points along road between Chetumal and Xpujil, Campeche (SH, BM), 10 km S of Bacalar (JL), 36 km W of Mahahual (BM), Sian Ka’an reserve (RG, JL, DN), Isla Cancun (BM); Yucatán: 10 km E of Kanasin (BM); Campeche: and several points along road between Escarcega and Candelaria (JL). The range of the species is expanding globally, and its spread in the peninsula has no doubt been aided by the proliferation of cattle pastures over the past few decades.

White-tailed Hawk (Buteo albicaudatus).—Paynter (1955a) listed three records of this species from the state of Yucatán, and Storer (1961) re-
ported a specimen from Campeche. We have observed the White-tailed Hawk at four localities in Quintana Roo: 2 km W of Francisco, Villa (SH, BM), Sian Ka’an reserve (AL—photo, RG, DN), 6 km W of Puerto Morelos (JL, EM), and Cancun (BM). One of two individuals seen at the Sian Ka’an reserve was eating a Green-backed Heron (*Bororhoides striatus*).

Zone-tailed Hawk (*Buteo albonotatus*).—We have observed this species, which has not previously been recorded from the peninsula, at five localities. Quintana Roo: 10 km S of Puerto Morelos (February 1986 and February 1987—JL), Cancun (February 1986—BM), Isla Cancun (February 1987—BM); Yucatán: Chichén Itzá (November 1984, January 1987—SH—photo), and Celestún (February 1987—SH). The species probably is a winter visitor.

Black-and-white Hawk-Eagle (*Spizastur melanoleucus*).—Paynter (1955a) did not observe this species and reported only an 1879 record from Tizimín, Yucatán. We have observed this hawk-eagle at two localities in Quintana Roo: 10 km W of Puerto Morelos (JL, EM), and Puerto Morelos (AL). The latter specimen, which was killed by a car, was preserved as a mounted specimen by a local resident.

Black Hawk-Eagle (*Spizaetus tyrannus*).—Paynter (1955a) recorded one specimen from Campeche and one from southern Quintana Roo. We have observed the species at three localities in central and northern Quintana Roo: road between Felipe Carillo Puerto and Vigia Chico (RG, SH, DN), Puerto Morelos (SH), and 5 km S of Cancun (JL).

Collared Forest-Falcon (*Micrastur semitorquatus*).—Paynter did not observe this species, and it has been known on the Peninsula only from specimens collected near Chichén Itzá, (Yucatán), Puerto Morelos, (Quintana Roo), and in southern Campeche (Traylor 1941, Paynter 1955a, Storer 1961). We have found this forest-falcon to be widely distributed in both semi-deciduous and semi-evergreen forest throughout the peninsula. It readily responds to imitations or tape-recorded playbacks of its call, and has been mist-netted several times. Quintana Roo: 10 km W of Felipe Carillo Puerto (JL, EM), Sian Ka’an reserve (SH), 4 km NW of Tulum (JL, EM), 4 km SW of Coba (JL), 20 km S of Playa del Carmen (JL), 4 km N of Playa del Carmen (JL, BM), 10 km W of Puerto Morelos (JL, EM), 7 km S of Puerto Morelos (AL, JL), Puerto Morelos (SH, JL); Yucatán: 6 km E of Xcalacocoop (JL, EM), Uxmal (JL, EM), Sayil (SH), and 20 km SE of Uxmal (JL, EM).

Merlin (*Falco columbarius*).—This Nearctic migrant had previously been observed on Isla Mujeres, Isla Cozumel, and Cayo Culebra Quintana Roo, but the only mainland records cited by Paynter (1955a) were two specimens from the north-central coast of Yucatán state. We have observed Merlins at both coastal and insular localities. Quintana Roo: 16
km S of Boca Paila (RG, AL, JL, DN); Sian Ka’an reserve (RG, DN), Akumal (JL); Puerto Morelos (AL, JL), Isla Cancun (BM); Yucatán: lagoon between Río Lagartos and Las Coloradas (AL, JL), Arrecife Alacran (BM), and Uxmal (SH). Extreme dates are 1 October and 1 June.

Peregrine Falcon (*Falco peregrinus*).—Paynter (1955a) obtained one specimen from SW of Campeche, and cited an earlier record from Banco Chinchorro, in SE Quintana Roo. We have observed the species at 8 additional localities. Quintana Roo: Sian Ka’an reserve (six observations—RG, AL, DN), Isla Cancun (BM), Puerto Juarez (BM), Isla Holbox (SH); Yucatán: Las Coloradas (SH, AL, JL), Río Lagartos (AL, JL), Celestún (SH); Chinchorro and Campeche: Isla Perez (SH). Extreme dates are 23 October and 26 April.

Black-throated Bobwhite (*Colinus nigrocularis*).—This quail is abundant in the dry secondary vegetation of Yucatán and Campeche, but Paynter (1955a) reported only one sight record from the western border of Quintana Roo. We have observed the species in central and northern Quintana Roo: Sian Ka’an reserve (RG, DN), Felipe Carillo Puerto (SH), and 9 km N of Playa del Carmen (JL). Like the Black-shouldered Kite, this species probably has benefited from increased ranching in Quintana Roo.

Sungrebe (*Heliornis fulica*).—Previously reported only from southernmost Quintana Roo (Traylor 1941), BM observed this species 27 January 1985 on Lago Coba in the central part of the state.

Lesser Golden-Plover (*Pluvialis dominica*).—The first peninsula records for this Nearctic migrant are as follows (all in Quintana Roo): road between Limones and Mahahual (DN), Vigia Grande, in the Sian Ka’an reserve (AL), Puerto Morelos (AL), Isla Cancun (BM). The species, which in the Yucatán is greatly outnumbered by the Black-bellied Plover (*P. squatarola*), has been observed in October, March, and April.

Snowy Plover (*Charadrius alexandrinus*).—Paynter (1955a) reported this normally migratory plover from several localities on the coast of Yucatán state. During winter, we have observed it on numerous occasions along the Quintana Roo coast, sometimes in flocks of as many as 100 individuals: Boca Paila (RG, SH, AL, JL, DN), Puerto Morelos (AL, JL), Isla Cancun (BM), and Isla Holbox (SH). The species is known to breed along the northeastern coast of Mexico and in the West Indies (A.O.U. 1983), and the fact that it occurs at all seasons at Isla Cancun (BM) and Boca Paila (SH, AL) suggests that there may also be a small resident population on the peninsula.

Semipalmated Plover (*Charadrius semipalmatus*).—Paynter (1955a) considered this species a rare winter visitor. He observed Semipalmated Plovers only on Isla Cozumel and Isla Mujeres and cited an earlier record
for the central coast of Quintana Roo. There are no published records for Yucatán. We (AL, JL, EM) have observed this species in the winters of three different years (1982, 1983, 1988) at Río Lagartos, Yucatán. Additional localities in Yucatán: Telchac Puerto (BM), Progreso (SH), Celestún (SH); Quintana Roo localities (all coastal): Xcalak (RG, DN), Boca Paila (RG, AL, JL, DN), Vigia Grande (AL), Tulum (RG, JL, DN), Puerto Morelos (AL, JL), Isla Cancun (BM), and Isla Holbox (SH). Extreme dates are 17 September and 22 May.

American Avocet (*Recurvirostra americana*).—This migratory species has not previously been reported from the peninsula. In January 1983, JL observed approximately 30 avocets in the coastal lagoon between Progreso and Telchac Puerto, Yucatán; a month later JL observed 25–30 avocets (possibly the same group) between Río Lagartos and Las Coloradas, Yucatán, and 10 were seen at Río Lagartos in March 1988 (DN). In all cases avocets were associated with Black-necked Stilts (*Himantopus mexicanus*).

Whimbrel (*Numenius phaeopus*).—This transient migratory species has not previously been reported from the peninsula, but we have found that it occurs regularly along the eastern and northern coasts. Quintana Roo: Vigia Chico (DN), Playa del Carmen (JL), Puerto Morelos (JL), Isla Cancun (BM—photo), Isla Holbox (SH); Yucatán: Río Lagartos (AL, JL, EM), Las Coloradas (AL, JL), and Celestún (SH). Sightings have been made in all months between October and April.

Marbled Godwit (*Limosa fedoa*).—Paynter (1955a) considered this species to be an "extremely rare" migrant on the peninsula. He observed it only at Santa Clara, Yucatán, and cited earlier records from Isla Cozumel. We have observed the species on several separate occasions between December and February at two localities. Quintana Roo: Isla Cancun (BM); Yucatán: Río Lagartos (RG, AL, JL, EM, DN).

Stilt Sandpiper (*Calidris himantopus*).—The first published reports for this Nearctic migrant on the peninsula are sightings on 7 April 1978 (BM) at Isla Cancun, Quintana Roo, and 25 January 1987 (SH) and 9 April 1988 (AL, JL) at the salt evaporating ponds near Las Coloradas, Yucatán. On the latter occasion, 200–250 Stilt Sandpipers were feeding in small flocks associated with large numbers of other shorebirds, including Greater Flamingo (*Phoenicopterus ruber*), Lesser Yellowlegs (*Tringa flavipes*), Western Sandpiper (*Calidris mauri*), Least Sandpiper (*C. minuilla*), Semipalmated Sandpiper (*C. pusilla*), and Ruddy Turnstone (*Arenaria interpres*). About half of the April birds had partially or completely molted into breeding plumage. The January record may seem somewhat surprising, as the species is thought normally to overwinter in temperate South America (A.O.U. 1983). However, S. N. G. Howell has informed
us (In litt.) that he has observed the species between November and January in Nayarit, Jalisco, Colima, Michoacan, Distrito Federal, Mexico, Tlaxcala, Veracruz, Tabasco, Campeche, Yucatán, Oaxaca, and Chiapas.

Common Snipe (Gallinago gallinago).—Paynter (1955a) reported this species from two localities in Yucatán state, and Storer (1961) recorded specimens from one locality in Campeche. We have observed the Common Snipe at four localities in Quintana Roo: 40 km W of Mahahual (JL), Tulum (RG), Coba (BM), and Isla Cancun (BM). At the latter locality, the species has been recorded in August, November, December, and January.

American Woodcock (Scolopax minor)*. —Although the American Ornithologists’ Union (1983) mentions the Yucatán as within the distribution of this Nearctic migratory species, the first specific published records for the peninsula are from Quintana Roo: Cancun (18 December 1986—BM), and Isla Cancun (20 February 1987—BM).

Bonaparte’s Gull (Larus philadelphia)*. —Apart from a questionable sight record that Paynter (1955a) dismissed as a misidentification of the locally common Laughing Gull (L. atricilla), Bonaparte’s Gull has not previously been reported from the Mexican portion of the peninsula. On 28 and 30 December 1983, AL observed an individual of this species standing next to a shallow pool 0.5 km inland from the beach at Puerto Morelos in NE Quintana Roo. The bird, which was in winter plumage, was identified by the following combination of characteristics: noticeably smaller and paler than a Laughing Gull, legs and feet red, tail white, extensive white patch on the distal portion of the wing, and a black spot behind the eye. The bird appeared following a period of cool, cloudy weather and northerly winds.

Ring-billed Gull (Larus delawarensis)*. —The first peninsula records for this species are as follows: Quintana Roo: Isla Cancun (five sightings in 1977 and 1978—BM), and Cancun (SH); Yucatán: Río Lagartos (DN), Progreso (AL, JL), Celestun (SH). Extreme dates are 10 October and 25 July. Ring-billed Gulls are uncommon but regular winter visitors to the northern coast.

Caspian Tern (Sterna caspia).—Paynter did not observe this species, and reported only one previous sight record from Isla Cozumel, Quintana Roo. We observed the species in the winters of 1982, 1986, 1987 and 1988 at Río Lagartos, Yucatán (RG, AL, JL, DN); localities for Quintana Roo: Boca Paila (SH, JL), and Isla Holbox (SH). In most cases, the species was associated with the much commoner Royal Tern (S. maxima). Caspian Terns are regular winter visitors to the coasts of the peninsula, and one individual has been observed at Boca Paila in summer (July 1988—SH).
Least Tern (*Sterna antillarum*).—Paynter (1955a) reported this species from two localities along the coast of Yucatán state and suggested that it might prove to be a breeding resident. In May 1985 and June 1986, AL observed small breeding colonies (5–15 pairs) of Least Terns along the Quintana Roo coast at Boca Paila and on two small cays in Bahía de la Ascensión, all in the Sian Ka’an reserve (photo). BM has observed breeding by this species at Isla Cancun in June of several summers. The species arrives at Cancun by the third week of April and is gone by the third week of September (BM).

Black Tern (*Chlidonias niger*).—The only previous records for the Mexican portion of the peninsula are from the coast of Yucatán state (Paynter 1955a). The species is a regular transient and non-breeding summer visitor to the northeastern coast of Quintana Roo: Sian Ka’an reserve (SH, AL), Isla Cancun (BM), Isla Mujeres (BM), and Isla Holbox (SH).

Pale-vented Pigeon (*Columba cayennensis*).—Paynter did not see this pigeon, and the only records for the Mexican portion of the peninsula are from southern Campeche (Traylor 1941). We have observed the species on several occasions in low, seasonally flooded woodland at the Sian Ka’an reserve, Quintana Roo (SH, AL, DN), and along the road between Limones and Mahahual (SH).

White-crowned Pigeon (*Columba leucocephala*).—The only previous peninsula records for this Caribbean species are from Isla Cozumel and Cayo Culebra, Quintana Roo, and a single specimen from the Quintana Roo mainland (Paynter 1955a). We have observed up to 40 White-crowned Pigeons at a time on several cays in Bahía de la Ascensión within the Sian Ka’an reserve (SH, AL—photo), and at three localities on the mainland of Quintana Roo: Sian Ka’an reserve (SH, AL), Tulum Pueblo (SH), and Puerto Morelos (JL). Additional insular records for Quintana Roo: Isla Cancun (BM), Isla Mujeres (JL), and Isla Contoy (BM). The breeding season on the cays is July and August, during which period birds fly back and forth daily to the mainland to feed. The species appears to vacate the cays between September and May (AL).

Mourning Dove (*Zenaida macroura*).—This migratory dove has been reported previously from Yucatán and Campeche, but the sole Quintana Roo record is from Isla Cozumel (Paynter 1955a). We have observed Mourning Doves at four localities in Quintana Roo: between Chunyaxche and Chumphon (RG), Puerto Morelos (AL), Isla Cancun (BM), and Puerto Juárez (BM). Extreme dates are 3 October and 16 March.

Short-billed Pigeon (*Columba nigrirostris*).—This pigeon, which is widely distributed in the humid lowlands of Middle America, was not seen by Paynter (1955a), who reported one earlier specimen from southern Quin-
tana Roo. JL and his field assistants have mist-netted this species on three occasions in the vicinity of Puerto Morelos, in northern Quintana Roo (photo), and we have one sight record from Isla Cancun (BM).

Ruddy Quail-Dove (*Geotrygon montana*).—This dove is widespread in humid lowland forests of Central America and South America, but it was encountered by Paynter (1955a) only in the wet forests of Campeche and extreme southern Quintana Roo. Paynter mentions an 1893 specimen ("probably accidental") from northern Yucatán, and Klaas (1968) collected a specimen between X-Can and Nuevo X-Can, in NE Yucatán. JL has observed the species throughout Quintana Roo as far north as Puerto Morelos, where several specimens have been mist-netted (photo).

Black-billed Cuckoo (*Coccyzus erythropthalmus*).—This Nearctic migrant was previously known on the peninsula from a century-old record from Isla Cozumel (Paynter 1955a) and a mist-netted specimen from northern Yucatán (Rogers et al. 1986). In September 1979, the car being driven by JL and EM struck and killed a Black-billed Cuckoo just E of Chichén Itzá, Yucatán (photo). A second individual was mist-netted in Puerto Morelos, Quintana Roo in February 1985 (AL—photo).

Striped Cuckoo (*Tapera naevia*).—The only previous record for the peninsula was Paynter’s (1955a) report of a specimen from southernmost Quintana Roo. In July 1985 AL observed a singing individual of this species in seasonally flooded low forest in the Sian Ka’an reserve. In January 1986, a Striped Cuckoo (probably the same individual or its mate) was mist-netted by AL at the same locality.

Burrowing Owl (*Speotyto cunicularia*).—The only previous peninsula records are from northern Yucatán (Paynter 1955a) and southern Campeche (Storer 1961). On 12 September 1979, BM observed a Burrowing Owl on Isla Cancun, Quintana Roo.

Little Hermit (*Phaethornis longuemareus*).—Paynter (1955a) saw the species at one locality in southern Quintana Roo and reported an earlier record from southern Campeche. In addition to sighting this hummingbird at several localities in southernmost Quintana Roo, we have seen it 10 km N of Felipe Carillo Puerto (JL, EM), Puerto Morelos (JL), and on the western outskirts of Cancun (JL).

White-necked Puffbird (*Bucco macrorhynchos*).—This species was previously known from the humid forest of southern Quintana Roo and Campeche (Paynter 1955a). We have observed it at the following localities in central and northern Quintana Roo: 20 km S of Felipe Carillo Puerto (JL, EM), Sian Ka’an reserve (AL, RG, DN), 5 km NE of Felipe Carillo Puerto (found dead—SH), 10 km N of Chunyaxche (BM), Playa del Carmen (road-killed specimen—JL, EM), and Puerto Morelos (RG, SH). All sightings have been in semi-evergreen forest.
Yellow-bellied Sapsucker (*Sphyrapicus varius*).—This winter visitor has been recorded twice previously from Yucatán state and once from coastal Quintana Roo (Paynter 1955a). We have observed the species at three localities. Quintana Roo: 8 km S of Puerto Morelos (two individuals mist-netted—JL), Isla Cancun (BM), Isla Mujeres (BM); and Yucatán: Uxmal (BM). Extreme dates are 23 October and 8 March.

Barred Woodcreeper (*Dendrocolaptes certhia*).—Previously known only from southernmost Quintana Roo and adjacent Campeche (Paynter 1955a, Storer 1961), this woodcreeper has been observed or mist-netted at the following localities in central and northern Quintana Roo: 5–10 km NE of Felipe Carillo Puerto (SH), Sian Ka’an reserve (RG, AL, DN), several locations within 10 km of Puerto Morelos (JL), and 14 km S of Cancun (BM).

Caribbean Elaenia (*Elaenia martinica*).—This small flycatcher is widespread throughout the Caribbean islands, including those off the Quintana Roo coast (Paynter 1955a), but it has not previously been recorded from the mainland of the peninsula. Between February 1984 and February 1985, JL mist-netted more than 30 Caribbean Elaenias in a brushy old-field 8 km S of Puerto Morelos, Quintana Roo (photo). Several individuals have been netted in similar habitat in the Sian Ka’an reserve (AL). Additional sight records on the Quintana Roo coast: Bacalar (BM), Boca Paila (RG, DN), El Meco (BM), 8 km NE of Felipe Carillo Puerto (SH), Puerto Morelos (SH), Isla Cancun (BM), 34 km W of Cancun (BM). The species has not been noted on the mainland during summer, suggesting that it may be a winter migrant that breeds on offshore islands. At the locality south of Puerto Morelos and in the Sian Ka’an reserve, the Caribbean Elaenia occurred with overwintering Least Flycatchers (*Empidonax minimus*), as well as the resident Greenish Elaenia (*Myiopagis viridicata*) and Yellow-bellied Elaenia (*Elaenia flavogaster*).

Sepia-capped Flycatcher (*Leptopogon amaurocephalus*).—This rainforest flycatcher has not previously been reported from the Mexican portion of the Yucatán, although it occurs in Belize (Russell 1964). We have observed the species at two localities in southern and northern Quintana Roo: 15 km S of San José along the road to Tomas Garrido (JL), and 1 km S of Puerto Morelos (RG).

Stub-tailed Spadebill (*Platyrinchus cancrominus*).—Paynter (1955a) found this species to be common in southern Quintana Roo but did not encounter it north of Tabi in the central portion of the state. Traylor (1941) and Storer (1961) reported specimens from Campeche. We have found this spadebill to be abundant throughout Quintana Roo, north almost to Chiquilá. Numerous individuals have been mist-netted at Puerto Morelos (JL) and in the Sian Ka’an reserve (RG, AL, JL, EM, DN).
The species occurs in semi-evergreen forest and seasonally flooded low woodland.

Vermilion Flycatcher (*Pyrocephalus rubinus*).—This flycatcher, which is common in the dry coastal scrub of northern Yucatán state (Paynter 1955a) and has been taken in southern Campeche (Storer 1961), has not previously been reported from Quintana Roo. In February 1983, JL observed a male Vermilion Flycatcher in an area of dry savannah within the Sian Ka’an reserve.

Acadian Flycatcher (*Empidonax virescens*).—This Nearctic migrant overwinters from Nicaragua southward (A.O.U. 1983). Paynter (1955a) cited two earlier, questionable records for the Yucatán, neither of which was supported by specimens. In early October 1985, AL mist-netted 27 Acadian Flycatchers in the Sian Ka’an reserve. All were captured in areas of low, seasonally flooded woodland or savannah. One study skin was preserved. In March 1986, WR observed an Acadian Flycatcher and heard its song in the Sian Ka’an reserve.

Yellow-bellied Flycatcher (*Empidonax flaviventris*).—Paynter (1955a) and Storer (1961) reported specimens from southern Campeche, and Rogers et al. (1986) mist-netted two individuals in northern Yucatán. In October 1985, AL netted a Yellow-bellied Flycatcher in the Sian Ka’an reserve. The species was observed 8 km NE of Felipe Carillo Puerto, Quintana Roo, in February 1987 (SH) and at X-Can, Yucatán in February 1984 (SH).

Fork-tailed Flycatcher (*Tyrannus savana*).—Paynter (1955a) recorded this species at one site in southernmost Quintana Roo. In February 1984, AL observed an individual in an area of *Cladium* savannah in the Sian Ka’an reserve.

Veery (*Catharus fuscescens*).—This Nearctic migrant overwinters in South America, and the only previous mainland record for the peninsula is a specimen from Yucatán (Paynter 1955a). We have mist-netted Veerys during fall migration at two locations in Quintana Roo: Sian Ka’an reserve (AL) and 7 km S of Puerto Morelos (JL). The species has been observed at Coba (RG) and Cancun (BM).

Gray-cheeked Thrush (*C. minimus*).—This Nearctic migrant has previously been known from one mainland record (Campeche) and one specimen from Isla Cozumel, Quintana Roo (Paynter 1955a). We mist-netted five individuals on the mainland of northern Quintana Roo during spring and fall of 1985 and 1986: Sian Ka’an reserve (AL) and 7 km S of Puerto Morelos (AL, JL).

Swainson’s Thrush (*C. ustulatus*).—This migratory species was previously known from two records in Yucatán and two in Campeche (Paynter
1955a, Storer 1961, Rogers et al. 1986). We have mist-netted eight individuals and observed several others between October and March at four localities in Quintana Roo: Coba (BM), 7 km S of Puerto Morelos (JL), Sian Ka’an reserve (RG, AL, DN), and Cancun (BM). These records lend support to Paynter’s (1955a) suggestion that small numbers of Swainson’s Thrushes may overwinter on the peninsula.

Golden-winged Warbler (*Vermivora chrysoptera*).—This uncommon warbler had been recorded on several offshore cays during fall migration (Paynter 1953, 1955a), but, except for an unverified 1886 report, previously was not known to overwinter on the peninsula. We have observed the species at three mainland localities. Quintana Roo: Tulum (February—AL), Puerto Morelos (October—JL); and Yucatán: Chichén Itzá (February—JL).

Orange-crowned Warbler (*V. celata*).—The only previous records of this Nearctic migrant for the peninsula are two specimens mist-netted by Parkes (1970) along the coast of Yucatán state. We have three records for Quintana Roo: Sian Ka’an reserve (AL—one mist-netted), Akumal (BM), and Isla Cancun (BM).

Nashville Warbler (*V. ruficapilla*).—Except for a doubtful record from Campeche (Paynter 1955a), the first records of this migratory species for the peninsula are as follows: one individual observed at close range by JL and EM on Isla Contoy, Quintana Roo, 11 February 1983; one observed by SH on Isla Perez, Campeche in October 1984.

Cape May Warbler (*Dendroica tigrina*).—This Nearctic migrant overwinters on islands in the northern Caribbean, and the only two previous mainland records for the peninsula are from northern Yucatán and southernmost Quintana Roo (Paynter 1955a). In addition to observing the species on Isla Contoy (JL, EM), Isla Cancun (BM), and Isla Holbox (SH), we have recorded it during fall and winter at several coastal localities in Quintana Roo: Bacalar (JL, EM), Mahahual (JL), Puerto Morelos (JL, EM), and Cancun (BM). At the latter locality, as many as 15 individuals have been observed in a single day. The species is also widely distributed on the islands off the coast of Campeche (SH).

Black-throated Blue Warbler (*D. caerulescens*).—Like the previous species, the main winter range of this migratory warbler comprises the larger islands of the northern Caribbean. The only Yucatán record reported by Paynter (1955a) is from Isla Cozumel. S. N. G. Howell has also observed the species on Isla Holbox, Quintana Roo, and Isla Perez, Campeche. JL has observed and mist-netted the species several times during fall and winter on the mainland in the vicinity of Puerto Morelos, Quintana Roo, where it is an uncommon, but regular, winter visitor. Other
mainland localities include the Sian Ka’an reserve, Quintana Roo (SH), and X-Can, Yucatán (SH). The species has been seen in all months between October and February.

Swainson’s Warbler (*Lymnothlypis swainsonii*). — The only records cited by Paynter (1955a) for this uncommon Nearctic migrant are from two localities in southernmost Quintana Roo and one in southern Campeche. We have observed or mist-netted Swainson’s Warblers on numerous occasions between October and February within a 10-km radius of Puerto Morelos, Quintana Roo (RG, JL, EM), and in or near the Sian Ka’an reserve (10 individuals mist-netted and several observed in October, January, February, and April—SH, AL). Gilberto Chavez-Leon (pers. comm.) has netted several individuals farther south, at San Felipe Bacalar, and we have observed it several times on Isla Cozumel (SH, JL, EM).

Kentucky Warbler (*Oporornis formosus*). — Paynter (1955a) encountered this Nearctic migrant only in southernmost Quintana Roo and Campeche and considered the species to be uncommon and restricted to wetter forest. Rogers et al. (1986) mist-netted two fall migrants and one winter bird in Yucatán state. Although Kentucky Warblers are more abundant in Belize and southern Quintana Roo than in the drier forest farther north, we have found the species to be widespread and reasonably common in the semi-evergreen forest of central and northern Quintana Roo, where we have mist-netted dozens of individuals. Kentucky Warblers do seem to avoid the semi-deciduous woodland of the northwestern peninsula, and we have observed the species at only one locality in the state of Yucatán. Selected localities in Quintana Roo: 18 km S of San Jose along the road to Tomas Garrido, Kohunlich ruins, 2 km N of La Unión San Felipe Bacalar, 5 km E of Limones, Senor, 22 km S of Felipe Carillo Puerto, 5 km W of Felipe Carillo Puerto, Sian Ka’an reserve, Coba, 10 km NW of Tulum, 2 km S of Playa del Carmen, Punta Celiz, 7 km S of Puerto Morelos (photo), 1 km S of Puerto Morelos, Vallarta, 4 km W of Cancun, 12 km N of Kantunilkin, Isla Cozumel; and Yucatán: 17 km E of Xcalacoco. Extreme dates are 25 August and 14 April.

Wilson’s Warbler (*Wilsonia pusilla*). — Although this Nearctic migrant is common in the wet forest of southern Belize and northern Chiapas (Russell 1964, JL—pers. obs.), the only previous report for the Mexican portion of the peninsula is a sight record by W. H. Buskirk (*fide* Parkes 1970) from the northern coast of Yucatán state. On 22 January 1978, a black-capped individual of this species was seen at Cancun (BM). On 21 February 1985, a black-capped individual was observed closely 7 km S of Puerto Morelos (JL). Both localities are in NE Quintana Roo.

Golden-crowned Warbler (*Basileuterus culicivorus*). — This uncommon resident was observed by Paynter (1955a) only in southernmost Quintana
Roo, and Storer (1961) recorded one specimen from southern Campeche.
We have observed it during fall and winter at scattered locations through-
out Quintana Roo in areas of semi-evergreen forest: 3 km N of La Unión
(JL, EM), 40 km S of San Jose along the road to Tomas Garrido (JL,
EM), 28 km S of Felipe Carillo Puerto (JL, EM), Sian Ka’an reserve (RG,
SH, DN), 10 km N of Felipe Carillo Puerto (JL, EM), and Vallarta (JL).
Several individuals have been mist-netted at the latter locality.

Bananquit (Coereba flaveola).—The species is widespread on the Ca-
ribbean islands, and is common in some parts of mainland Mexico and
Central America. The only previous records for the peninsula are from
offshore islands (Cozumel, Holbox, Cayo Culebra) and a single specimen
collected at Isla Cancun (Paynter 1955a). We were therefore surprised to
discover that the species is extremely abundant at all seasons in the coastal
scrub of central Quintana Roo between Boca Paila and Punta Allen, where
hundreds of individuals have been mist-netted (AL, JL—photo). Bana-
naquits are far less common elsewhere but have been observed or mist-
netted at the following mainland localities in Quintana Roo: Tulum (JL),
7 km S of Puerto Morelos (JL), 5 km W of Puerto Morelos (JL), Cancun
(BM—nesting), 34 km W of Cancun (BM). Mainland birds are referable
to the white-throated race (C. f. caboti), which was previously considered
to be endemic to the islands off the coast of Quintana Roo.

Black-throated Shrike-Authanager (Lanio aurantius).—This uncommon
resident species has been recorded from southernmost Quintana Roo and
adjacent Campeche (Paynter 1955a, Storer 1961). In the winters of 1983
and 1986 we observed single individuals of the species near Puerto Mol-
relos, Quintana Roo (JL, EM).

Bobolink (Dolichonyx oryzivorus).—Paynter (1955a) reported Bobo-
links from Isla Cozumel and one locality in Yucatán state. In 1987, flocks
of this migratory species were observed on 23 April, 27–28 April, and 1
May along the Caribbean coast of Quintana Roo. The species has also
been observed along the Quintana Roo coast during fall migration (Oc-
tober, November). Localities in Quintana Roo: Chunyaxche (AL), Ak-
mal (AL), Puerto Morelos (AL), and Isla Cancun (BM).

DISCUSSION

Of the 69 species discussed here, 13 are new to the Mexican portion of
the Yucatán Peninsula, 31 are state records for Quintana Roo, and 11
are state records for Yucatán. Perhaps because much of our field work
has taken place in the winter months, Nearctic migrants make up a dis-
proportionately large fraction (36/69 = 52%) of the species reported.

Our observations confirm Paynter’s (1955a) prediction that many of
the species he observed only in the humid portions of southern Quintana
Roo and Campeche would eventually be discovered to inhabit northern areas of what he called “rain forest.” Seventeen of the species discussed above exemplify this distributional pattern. Nevertheless, we suggest that use of the term “rain forest” for strongly seasonal semi-evergreen vegetation that generally receives less than 1200 mm of annual precipitation is inappropriate and obscures the fact that many species of birds that are widely distributed in true rain forest and tropical wet forest throughout Middle America do, in fact, avoid the zone of drier semi-evergreen forest in central and northern Quintana Roo (Griscom 1926a, Paynter 1955a). In addition, even those species that we have shown to occur farther north in the peninsula than was previously known tend to be more abundant in the humid forests to the south, based on the results of point counts (JL, unpubl. data). Thus, some bird species respond differently to evergreen vs semi-evergreen forest, and we should reflect these distinctions in our classification of vegetation.

We suspect that only a few species have expanded their ranges in the Yucatán Peninsula since Paynter’s (1955a) survey was completed. Exceptional cases include the Black-shouldered Kite and the Black-throated Bobwhite, both open-country forms that have followed the spread of cattle ranching into Quintana Roo. Most of our other records probably reflect the greater accessibility of the peninsula to observers in recent years. There are, however, a few species (e.g., Collared Forest-Falcon, White-throated Spadebill, Kentucky Warbler) that are presently fairly common in the semi-evergreen forest of central and northern Quintana Roo, yet were not seen there by Paynter or earlier investigators.

Our data indicate that five species of land birds whose Yucatán distribution was previously thought to be restricted (or nearly so) to offshore islands actually occur regularly along the Caribbean coast of Quintana Roo. The Bananaquit and Caribbean Elaenia maintain large mainland populations, at least during fall, winter, and spring. Although there are no positive indications of breeding for either species in the area of the central coast where they are most numerous, it seems likely that both are resident on the mainland. The White-crowned Pigeon, Black-throated Blue Warbler and Cape May Warbler are not as common along the Quintana Roo coast, but nevertheless are regular winter visitants. For such species, mainland coastal scrub and adjacent low, seasonal tropical forest probably appear structurally similar to corresponding vegetation on the larger Caribbean islands. Certainly, there are well-documented floristic similarities between the coastal flora of the Yucatán coast and that in the Caribbean islands (Moreno-C. and Espejel 1986, Espejel 1987). The fact that this narrow and fragile coastal community occurs in the same zone
where touristic development is rapidly expanding in Quintana Roo should be of great concern to conservationists.

ACKNOWLEDGMENTS

We take this opportunity to thank the following people who ably assisted us in our field work, or allowed us to cite their observations: E. Balinsky, O. Barrera, E. Cabrera, M. Berlanga, L. Greenberg, R. Greenberg, J. Harms, S. Howell, B. Jones, E. Ley, W. Mayher, E. Morton, D. Niven, M. Van der Voort, and D. Whigham. Steve N. G. Howell was especially generous in sharing his numerous records, and carefully read the manuscript. Our research was encouraged by Alfredo Careaga and Enrique Carillo, former directors of the Centro de Investigaciones de Quintana Roo. We gratefully acknowledge the financial support of the World Wildlife Fund-U.S. and the Smithsonian Institution, and logistical support by the Amigos de Sian Ka'an.

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PHYLOGENETIC RELATIONSHIPS AND INCIPIENT FLIGHTLESSNESS OF THE EXTINCT AUCKLAND ISLANDS Merganser

Bradley C. Livezey

Abstract.—Phylogenetic relationships and evidence for pectoral reduction in the extinct Auckland Islands Merganser (Mergus australis) were investigated using a plumage-based phylogenetic analysis of the six Recent species of merganser and morphometric comparisons of study skins and skeletal specimens. The hypothesized phylogeny indicates that M. australis diverged from the other Mergus immediately after the Hooded Merganser (Lophodytes cucullatus) and is a member of a basal grade of comparatively small, southern hemisphere mergansers; the Brazilian Merganser (M. octosetaceus) branched next and is the sister-group to the larger, more derived, northern hemisphere species of Mergus. M. australis was unique in its natal and adult plumage characters, including the sexually monochromatic plumage of adults. Morphometric analyses revealed that M. australis was the smallest member of its genus but possessed the longest bills and relatively short wings and tails. Based on regression estimates of body mass and wing area for M. australis, the species had estimated wingloadings which exceeded those for other Mergini and approach the threshold of flightlessness hypothesized by Meunier (1951). Skeletal comparisons confirmed that M. australis had exceptionally long bills, and this also revealed that the species possessed relatively short wing elements and scapulae, as well as sterna characterized by shallow carinae and small caudal widths. These morphological characteristics, hypothesized phylogenetic relationships, and ecological information for M. australis are compared to the typical correlates of insularity in waterfowl listed by Weller (1980), and the evolutionary implications of these characteristics are considered. Received 26 May 1988, accepted 1 Nov. 1988.

The mergansers (Lophodytes cucullatus and five species of Mergus) are highly derived members of the sea ducks (Mergini), most closely related to the Smew (Mergellus albellus) and goldeneyes (Bucephala spp.) (Livezey 1986). Mergansers are capable divers and are largely piscivorous, but unlike several other genera of the Mergini (e.g., Somateria, Melanitta, and Clangula), are strictly foot-propelled divers, i.e., strokes of the feet provide the sole propulsion at submergence and for underwater locomotion (Townsend 1909; Kelso 1922; Brooks 1945; Humphrey 1957, 1958). Most mergansers, like other Mergini, are limited in distribution to the northern hemisphere, show striking sexual dichromatism, and are migratory (Delacour 1959; Johnsgard 1965, 1978).

The Auckland Islands Merganser (Mergus australis) was one of two Recent species of merganser with southern-hemisphere distributions (the

1 Museum of Natural History, Univ. of Kansas, Lawrence, Kansas 66045.
other being the Brazilian Merganser [\textit{M. octosetaceus}]), being limited, at least in historical times, to the Auckland Islands (50°S, 165°E), a small group of islands located 330 km south of the South Island of New Zealand (Phillips 1925, Delacour 1959, Williams 1964, Greenway 1967, Kear and Scarlett 1970, Weller 1980). Subfossil specimens of \textit{Mergus}, mensurally comparable to \textit{M. australis}, have been found as well on the main islands of New Zealand (Kear and Scarlett 1970). Extirpated during the first decade of the twentieth century, this insular species is represented in museum collections by some 26 skins (including downy young), three virtually complete skeletons, some additional skeletal parts, and one carcass preserved in alcohol (Kear and Scarlett 1970). In addition to its southern-hemisphere insular distribution, the Auckland Islands Merganser has been noted for its small size, lack of sexual dichromatism, relatively long bill, and unusual plumage pattern of its downy young (Mathews and Feredale 1913, Humphrey 1955, Kear and Scarlett 1970, Weller 1980).

The Auckland Islands Merganser was not, as claimed by Luther (1967), flightless; individuals were observed in flight by Hutton and Ranfurly (\textit{fide} Kear and Scarlett 1970). The notion that \textit{M. australis} was flightless may have originated with the mistaken inclusion of \textit{M. australis} as a synonym of the Auckland Islands Flightless Teal (\textit{Anas aucklandica}) by Gray (1844). Based on a study of skeletal measurements, however, Humphrey (1955) concluded that the humerus of \textit{M. australis} showed evidence of reduction in length. Humphrey further inferred from proportions of wing elements that the species also showed reduction of the ulna and manus.

The unusual distribution and morphology of \textit{M. australis}, particularly the evidence of wing reduction, prompted its inclusion in an ongoing study of flightlessness in diving birds. In this paper I propose a phylogenetic hypothesis for the six Recent species of mergansers using published descriptions of natal and adult plumages. This analysis is followed by morphometric comparisons of external and skeletal measurements to determine interspecific patterns of size, shape, and sexual dimorphism within the group and to examine in greater detail the evidence for reduction of the pectoral limb in \textit{M. australis} and the possibility that the species was evolving toward flightlessness.

\textbf{MATERIAL AND METHODS}

\textit{Phylogenetic characters}.—Characters of natal and adult plumages, as well as colors of soft parts, were taken from illustrations and text in Partridge (1956), Delacour (1959), Kear and Scarlett (1970), and Bartmann (1988). Kear and Scarlett (1970) pointed out several errors in the illustration of a downy \textit{M. australis} in Delacour (1959). Characters used in the phylogenetic analysis were those that varied within the in-group (\textit{Lophodytes} and \textit{Mergus}) and for which polarities (primitive states) could be determined by comparison with its sister
genera, *Bucephala* and *Mergellus* (Lieversey 1986). I endeavored to reduce all character complexes to binary characters (i.e., having but a primitive and a single derived state), those for which this was not possible were analyzed as unordered. Autapomorphies (derived character states unique to a single terminal taxon) were included in the analysis because such differences have been considered of taxonomic value in traditional, phenic classifications (e.g., Humphrey 1955, Delacour 1959, Johnsgard 1961a, Kear and Scarlett 1970). The tree was constructed using the criterion of parsimony (Wiley 1981). It was hoped that phylogenetic relationships inferred from plumage characters would be effectively independent of the morphometric patterns that were investigated. In addition to the plumage characters, I attempted to include courtship behaviors (Johnsgard 1960, 1961a, b, 1965) and syringeal morphology (Humphrey 1955) in the analyses, but was unsuccessful because of uncertain homologies, polarities, continuous variation (in syringeal bullae), and missing data for crucial species (e.g., *M. australis* and *M. octosetaceus*).

**Specimens and morphometric data.**—Mensural data from 15 skins of (*fully grown*) *M. australis* were collected by me or provided by colleagues. Where possible, I also made counts of the primary remiges in *M. australis*. I measured 10 skins of adults of each sex of the Hooded Merganser (*Lophodytes cucullatus*), Red-breasted Merganser (*M. serrator*), and Common Merganser (*M. merganser*); smaller samples of skins of the Brazilian Merganser (*N = 5* males, *5 females*) and the Chinese Merganser (*M. squamatus*; *N = 8, 6*) were available for measurement. Measurements taken on skins were as follows: total body length; length of exposed culmen on midline; nail width; length of the chord of the unstraightened wing; length of the tail, measured medially; length of the tarsus on anterior surface; and length of the middle toe, excluding nail. Total lengths were measured only on properly prepared study skins (i.e., realistically extended, unmounted skins), had coefficients of variation (s/ mean) comparable to those for other external variables, and their means were used, in part, for estimates of body size of *M. australis*, *M. octosetaceus*, and *M. squamatus*—for which published records of body mass were not available. Specifically, body masses were estimated using external “body lengths” (mean total lengths minus the mean lengths of culmen and tail), which were independent of interspecific variation in relative lengths of bills and appendages. Together with estimates of wing area based on wing length, these estimated body masses were used to infer the approximate wing-loadings of the three species of *Mergus* lacking these data. Wing areas, where available, were measured as described by Raikow (1973), and wing-loadings for species (g of mean body mass divided by cm² of mean total wing area) were calculated as recommended by Clark (1971). Additional data on body masses and wing areas of mergansers and other Mergini were taken from Müllenhoff (1885), Magnan (1912, 1922), Poole (1938), Meunier (1959), Dement’ev and Gladkov (1967), Raikow (1973), Madge and Burn (1988), and P. S. Humphrey (unpubl. data). Three virtually complete skeletons and a few disassociated skeletal elements of *M. australis* were available for study. I sought to measure 15 skeletons of each sex of the other mergansers, although only one complete skeleton of *M. squamatus* and a partial skeleton of *M. octosetaceus* were available. Thirty-three skeletal variables were used in the comparisons, most of which were described in Lieversey and Humphrey (1984, 1986) and Lieversey (1988, 1989). Several nontraditional measurements require definition, however: LWM’s of limb elements refer to “least widths at the midpoints” of shafts; LMW of the tarsometatarsus is the “lateromedial width” of the shaft (at midpoint); and length of digit-III (middle toe) is the sum of lengths of the three proximal phalanges of the digit. All skeletal measurements were made with dial calipers to within 0.1 mm.

**Statistical analyses.**—Simple measurements of skins and skeletons were compared using two-way analysis of variance (ANOVA); missing data resulted in slight variations in sample sizes in univariate analyses. Wing-loadings were log-transformed for tests with ANOVA.
Significances of differences (and associated P-values) based on correlated data were judged using the Bonferroni method of simultaneous inference (Milliken and Johnson 1984). Intraalar proportions of skeletal wing elements were calculated as lengths of the single elements divided by skeletal wing length (sum of the lengths of the humerus, ulna, carpometacarpus, and the two phalanges of the major digit); arcsines of square roots of proportions were used in ANOVA (Sokal and Rohlf 1981).

Allometry of wing areas with body mass, in which both variables include error (model II; Sokal and Rohlf 1981), was investigated through "geometric mean" regressions or central trend lines (Ricker 1984) of log-transformed species means. The slopes of regressions using log-transformed means are estimates of the "allometric coefficients" (b) and reflect interspecific scaling between the variables (Gould 1966); in this application the slope reflects scaling of wing area (and wing-loading) with body size.

Stepwise multivariate analysis of variance (MANOVA; see appendix 23 in Dixon 1985) was used to test for interspecific, intersexual, and species-sex interactive differences in mean vectors of external and skeletal measurements; summary statistics (Wilks' lambda and F-statistics) were based on backstep-selected subsets (P < 0.05) of the variables submitted (Jennrich and Sampson 1985). Canonical analysis (CA), a technique which defines mutually orthogonal multivariate axes that maximally separate predefined groups (relative to their pooled within-group covariances), was used to explore multivariate differences among species and sexes (Pimentel 1979). CAs also were used to isolate the multivariate differences between *M. australis* and the other species (referred to as "canonical contrasts"). Importance of interspecific and intersexual differences on the canonical variates (CVs) was tested through two-way ANOVAs of scores on these CVs (referred to as "ANOVA of scores"). For MANOVA and CA only, external and skeletal data sets were subjected to a missing-data program (Frane 1985) in which measurements missing for reasons of deformity or bilateral breakage (for specimens lacking a small minority of data) were estimated using separate stepwise regressions on specimens grouped by species; these estimates permitted the inclusion of 99 skins and 91 skeletons in MANOVAs and CAs and comprised only 1.0% and 2.0% of the sets, respectively. Both data sets were log-transformed for CA and MANOVA (Jolicoeur 1963).

Statistical programs employed are part of the 1987 version of the Biomedical Computer Programs (BMDP; Dixon 1985), performed on an IBM computer at the University of Kansas.

**PHYLOGENETIC ANALYSIS**

Based on published descriptions and illustrations, I defined 11 characters of natal plumages and 11 of adult plumages of mergansers (Table 1). Four of the latter included two derived states (characters 16, 17, 18, 20), of which the first three involved the unique plumage aspect of *M. australis*. The problematic black-and-orange bill of *M. australis* was coded as a unique character state (15c); the tree depicted remains most parsimonious if bill color of *M. australis* is treated instead as a (partial) reversal from an orange bill (15b). Both *M. australis* and *M. octosetaceus* lack significant sexual dichromatism (character 16), but these conditions are not homologous (illustrated in Delacour 1959, Scott 1972). In *M. australis*, plumages of both sexes closely resemble females and juveniles of *Mergus* generally, and monochromatism of this species evidently is the result of the loss of the distinctive alternate plumage of males. This plumage condition rendered several characters (17-19) not comparable in this species (Appendix I). In contrast, the plumage pattern shared by the sexes of *M. octosetaceus* differs significantly from the rest of the genus and, although not as striking as those for adult males of most other mergansers, is not juvenal-like and is evidently uniquely derived.

Although complicated by these few instances of multiple and/or noncomparable states
(Appendix 1), the 22 plumage characters formed the basis for a phylogenetic tree for the Recent mergansers (Fig. 1) of high consistency (consistency index = 1.0). The sister-group relationship of Lophodytes with Mergus, supported by osteological comparisons in Livezey (1986), was corroborated by three plumage characters of downy young (Table 1, Fig. 1). M. australis emerged as the second branch in the basal grade of mergansers and was characterized by four autapomorphies. Based on characters of its natal plumages, M. octosetaceus was the next branch to diverge in Mergus, and this neotropical species possessed four autapomorphies of the adult plumage (Fig. 1). The presence of a pale suborbital stripe in the natal plumage (character 4b) is shown as a synapomorphy uniting M. octosetaceus with the three remaining species (Fig. 1); this stripe was shown as conspicuous in M. octosetaceus by Partridge (1956) and Delacour (1959), but it was not indicated in photographs included by Bartmann (1988). If the latter state is taken as representative, then the change in character 4 supports the monophyly of only M. serrator, M. squamatus, and M. merganser, but the topology shown (Fig. 1) is unchanged. The sister clade of M. octosetaceus comprised the more “typical” mergansers of the northern hemisphere; of these three species, M. serrator and M. squamatus appear to be closest relatives (Fig. 1), although this relationship is supported by only one synapomorphy, and the topology for these three species conservatively might be considered a trichotomy. Based on this preliminary analysis, M. australis represents an early but uniquely derived branch in the merganser clade and, although comparable in grade to M. octosetaceus, the two southern-hemisphere species are not closest relatives.

MORPHOMETRIC COMPARISONS

Univariate comparisons of external measurements.—A substantial range of body size and a diversity of shape was indicated by comparisons of skin characters of mergansers. Total length of the body, probably the best directly measurable “size” measure which is independent of wing size and available for all species, differed significantly among species ($F = 35.75; \text{df} = 5, 84; P < 0.0001$) and ranked L. cucullatus as the smallest, followed (in order of increasing size) by M. australis, M. octosetaceus, M. serrator, M. squamatus, and M. merganser (Table 2); males were larger than females within species ($F = 10.43; \text{df} = 1, 84; P < 0.005$). Available mean body masses—617 g (N = 97) for L. cucullatus, 984 g (79) for M. serrator, and 1382 g (197) for M. merganser—confirmed these size rankings. “Body lengths” (total lengths minus lengths of culmen and tail) mirrored these interspecific ($F = 27.35; \text{df} = 5, 83; P < 0.0001$) and intersexual differences ($F = 5.68; \text{df} = 1, 83; P < 0.05$). Regressions of mean body masses on mean “body length” (log-transformed data, N = 3, $r = 0.988$) provided rough estimates of body mass for the remaining three species: M. australis, 898 g; M. octosetaceus, 983 g; and M. squamatus, 1234 g. Comparison of actual and estimated body masses with the phylogenetic tree (Fig. 1) indicates that the merganser clade is characterized by a strong evolutionary trend toward increased body size.

Tarsus length differed significantly among species ($F = 195.40; \text{df} = 5, 87; P < 0.0001$) and between the sexes ($F = 157.61; \text{df} = 1, 87; P < 0.0001$), and conformed closely with body length in interspecific rankings
Table 1  
Characters and Character States Used in Phylogenetic Tree Depicted in Fig. 1

<table>
<thead>
<tr>
<th>Group</th>
<th>Character</th>
<th>Statesa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natal plumage</td>
<td>(1) Breast band</td>
<td>a = present; b = absent</td>
</tr>
<tr>
<td></td>
<td>(2) Flank spots</td>
<td>a = confined by dark; b = open ventrally</td>
</tr>
<tr>
<td></td>
<td>(3) Head color</td>
<td>a = gray; b = reddish brown</td>
</tr>
<tr>
<td></td>
<td>(4) Subocular stripe</td>
<td>a = absent; b = present</td>
</tr>
<tr>
<td></td>
<td>(5) Distal forewing</td>
<td>a = dark; b = white</td>
</tr>
<tr>
<td></td>
<td>(6) Cheek patch</td>
<td>a = large, above gape; b = small, ventral to gape</td>
</tr>
<tr>
<td></td>
<td>(7) White back spots</td>
<td>a = present; b = absent</td>
</tr>
<tr>
<td></td>
<td>(8) White preorbital spots</td>
<td>a = absent; b = present</td>
</tr>
<tr>
<td></td>
<td>(9) Breast color</td>
<td>a = gray or white; b = tawny washed</td>
</tr>
<tr>
<td></td>
<td>(10) Dorsal spotting</td>
<td>a = distinct; b = vestigial</td>
</tr>
<tr>
<td></td>
<td>(11) Chestnut subocular spot</td>
<td>a = none; b = present</td>
</tr>
<tr>
<td>Adult plumage (definitive alternate)</td>
<td>(12) Chin</td>
<td>a = dark; b = whitish</td>
</tr>
<tr>
<td></td>
<td>(13) Breast (males)</td>
<td>a = white; b = dark red</td>
</tr>
<tr>
<td></td>
<td>(14) Dark nape stripe (males)</td>
<td>a = absent; b = present</td>
</tr>
<tr>
<td></td>
<td>(15) Bill colorb</td>
<td>a = grayish; b = orange; c = orange with culmen and nail black</td>
</tr>
<tr>
<td></td>
<td>(16) Sexual dichromatismb</td>
<td>a = present; b = absent, males like females; c = absent, unique plumage</td>
</tr>
<tr>
<td></td>
<td>(17) Background color of sides, flanks (males)b</td>
<td>a = white; b = red; c = gray</td>
</tr>
<tr>
<td></td>
<td>(18) Barring of sides (males)b</td>
<td>a = black; b = white; c = none</td>
</tr>
<tr>
<td></td>
<td>(19) Barring of sides</td>
<td>a = linear vermiculations; b = scalloping</td>
</tr>
<tr>
<td></td>
<td>(20) Crestb</td>
<td>a = 1-parted, from crown; b = emerges continuously from crown to occiput; c = 2-parted</td>
</tr>
<tr>
<td></td>
<td>(21) Crest</td>
<td>a = present in both sexes; b = absent in males</td>
</tr>
<tr>
<td></td>
<td>(22) Ventral barring</td>
<td>a = absent; b = present</td>
</tr>
</tbody>
</table>

*Primitive state = a, derived states b–c.  
* Analyzed as unordered.

(Table 2); middle-toe lengths (not tabulated) mirrored tarsus lengths in interspecific and intersexual differences. Culmen length, however, deviated markedly from this pattern. M. australis, one of the smallest species overall, had the largest culmen lengths, followed by M. serrator, the approximately equal M. merganser and M. squamatus, M. octosetaceus, and the much shorter-billed L. cucullatus (Table 2); both interspecific \((F = 131.29; \text{df} = 5, 87; \text{P} < 0.0001)\) and intersexual differences \((F = 58.99; \text{P} < 0.0001)\).
Fig. 1. Phylogenetic tree for Recent mergansers (Lophodytes and Mergus). Characters (numbers) and states (letters) are defined in Table 1 and compiled in the Appendix; black rectangles indicate skeletal synapomorphies described in Livezey (1986).

df = 1, 87; P < 0.0001) in culmen length were significant. Nail width (not tabulated) also differed significantly among species (F = 15.19; df = 5, 85; P < 0.0001) and sexes (F = 26.28; df = 1, 85; P < 0.0001); this variable tended to follow body length in interspecific rankings, except that M. australis and especially L. cucullatus had large nail widths relative to their body size.

Wing lengths showed substantial interspecific (F = 376.44; df = 5, 87; P < 0.0001) and intersexual variation (F = 123.78; df = 1, 87; P < 0.0001), and although means tended to follow total body length in interspecific rankings, M. australis had disproportionately short wings (Table 2); body lengths of M. australis averaged 67 mm longer than those of L. cucullatus, but wing lengths of the former averaged 8 mm shorter. All specimens of M. australis retained the full complement of primary remiges and other mergansers (10 functional plus 1 reduced). Tail lengths also varied significantly among species (F = 58.90; df = 5, 86; P < 0.0001), and paralleled wing lengths in interspecific differences; M. australis had disproportionately short tails (Table 2).

Wing-loadings of the Mergini. — Wing areas were available for all species
<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>N</th>
<th>Total length</th>
<th>Culmen length</th>
<th>Wing length</th>
<th>Tail length</th>
<th>Tarsus length</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lophodytes cucullatus</em></td>
<td>M</td>
<td>10</td>
<td>424 ± 25</td>
<td>40.7 ± 1.2</td>
<td>193.9 ± 4.2</td>
<td>90.6 ± 5.1</td>
<td>33.6 ± 1.6</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>10</td>
<td>405 ± 18</td>
<td>39.0 ± 2.1</td>
<td>183.2 ± 3.4</td>
<td>85.7 ± 5.5</td>
<td>32.2 ± 1.1</td>
</tr>
<tr>
<td><em>Mergus australis</em></td>
<td>M</td>
<td>9</td>
<td>488 ± 63</td>
<td>59.6 ± 3.8</td>
<td>185.1 ± 5.2</td>
<td>69.6 ± 4.9</td>
<td>43.4 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>6</td>
<td>475 ± 54</td>
<td>55.0 ± 2.8</td>
<td>175.2 ± 3.5</td>
<td>72.2 ± 2.1</td>
<td>40.5 ± 1.2</td>
</tr>
<tr>
<td><em>M. octosetaceus</em></td>
<td>M</td>
<td>5</td>
<td>540 ± 55</td>
<td>51.6 ± 1.5</td>
<td>200.2 ± 4.4</td>
<td>93.6 ± 6.6</td>
<td>44.4 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>5</td>
<td>480 ± 31</td>
<td>48.6 ± 0.9</td>
<td>193.0 ± 3.9</td>
<td>85.0 ± 10.7</td>
<td>40.8 ± 2.2</td>
</tr>
<tr>
<td><em>M. serrator</em></td>
<td>M</td>
<td>10</td>
<td>524 ± 45</td>
<td>58.1 ± 1.5</td>
<td>236.3 ± 9.0</td>
<td>78.0 ± 6.1</td>
<td>46.6 ± 1.6</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>10</td>
<td>506 ± 41</td>
<td>54.4 ± 2.6</td>
<td>216.8 ± 9.1</td>
<td>70.7 ± 6.0</td>
<td>45.1 ± 2.8</td>
</tr>
<tr>
<td><em>M. squamatus</em></td>
<td>M</td>
<td>8</td>
<td>564 ± 61</td>
<td>55.6 ± 1.4</td>
<td>249.0 ± 6.5</td>
<td>98.5 ± 5.3</td>
<td>46.8 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>6</td>
<td>570 ± 53</td>
<td>50.5 ± 2.0</td>
<td>235.5 ± 11.9</td>
<td>94.0 ± 5.8</td>
<td>45.7 ± 2.3</td>
</tr>
<tr>
<td><em>M. merganser</em></td>
<td>M</td>
<td>10</td>
<td>624 ± 40</td>
<td>55.5 ± 3.6</td>
<td>266.9 ± 5.5</td>
<td>104.2 ± 8.1</td>
<td>51.9 ± 1.7</td>
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<tr>
<td></td>
<td>F</td>
<td>10</td>
<td>541 ± 33</td>
<td>50.6 ± 2.3</td>
<td>239.0 ± 3.5</td>
<td>92.0 ± 3.5</td>
<td>46.7 ± 1.3</td>
</tr>
</tbody>
</table>

*Sample sizes for total length were 3, 4.*
Fig. 2. Logarithmic plot of mean wing areas on mean body masses for extant Mergini; mergansers shown as squares, other species as circles. Regression equation (geometric-mean fit) excludes three estimated points for *Mergus* (hollow squares); slope given ±2 standard errors.

...of sea duck except the extinct Labrador Duck (*Camptorhynchus labradorius*) and three species of *Mergus*, including *M. australis*. For the latter, wing areas were estimated using a regression of mean wing areas on mean wing lengths for the three species of merganser for which both data were available (N = 3, log-transformed data, r = 0.999). These estimates were 371 cm² for *M. australis*, 450 cm² for *M. octosetaceus*, and 722 cm² for *M. squamatus*; together with the corresponding estimates for body mass (detailed above), rough estimates of wing-loadings (g·cm⁻²) were 2.42, 2.18, and 1.71, respectively. The estimates for *M. octosetaceus* and especially *M. australis* were high relative to those for other *Mergus* (unweighted mean of species = 1.67, 2 species, N = 4 wing areas), *Lophodytes* (1.50, 1 species, N = 6), *Mergellus* (1.52, 1 species, N = 3), *Bucephala* (1.50, 3 species, N = 20), *Clangula* (1.76, 1 species, N = 5), *Melanitta* (1.62, 3 species, N = 18), *Histrionicus* (1.32, 1 species, N = 8), *Somateria* (1.93, 3 species, N = 6), and *Polysticta* (1.68, 1 species, N = 1).

A logarithmic plot of mean wing areas and body masses of 16 extant...
Mergini revealed a strong allometric relationship between the variables (Fig. 2), one which was not significantly different \((P > 0.05)\) from that preserving geometric similarity (slope relating an area with mass expected to be 0.67; Gould 1966). The estimated points for the three Mergus lacking data were plotted but were not included in the regression. The pronounced negative deviation of *M. australis* (Euclidean distance from line = 0.35) and *M. octosetaceus* (distance = 0.25) from the tribal line reflects their relatively heavy wing-loadings (Fig. 2). The clarity of the allometric relationship indicates that wing-loadings were largely a function of body mass (with the possible exception of the two austral Mergus); there was little clustering of congeners, including most mergansers.

**Canonical analysis of external measurements.** — A CA of external measurements produced significant dispersion of species-sex groups (Wilks' lambda = 0.0002; df = 6, 11, 87; \(P < 0.001\)). Stepwise MANOVAs revealed that these multivariate differences involved significant interspecific (Wilks' lambda = 0.11; df = 3, 1, 87; \(P < 0.001\)) and intersexual (Wilks' lambda = 0.38; df = 2, 1, 87; \(P < 0.001\)) effects. The first three canonical variates together accounted for over 95% of the total intergroup dispersion and included those dimensions in which *M. australis* differed from the other taxa.

The first canonical variate (CV-I) encapsulated roughly two-thirds of the total intergroup dispersion in external measurements (Table 3, Fig.
Table 3
Standardized Coefficients and Summary Statistics for Canonical Variates of External Measurements Separating Species and Sexes of Mergansers

<table>
<thead>
<tr>
<th>Character</th>
<th>All-group analysis</th>
<th>Contrast of \textit{Mergus australis}</th>
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<tr>
<td></td>
<td>CV-I</td>
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</tr>
<tr>
<td>Total length</td>
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</tr>
<tr>
<td>Culmen length</td>
<td>0.16</td>
<td>-0.77</td>
</tr>
<tr>
<td>Nail width</td>
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<td>Wing length</td>
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<td>0.55</td>
</tr>
<tr>
<td>Tail length</td>
<td>0.11</td>
<td>0.23</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>-0.39</td>
<td>-0.41</td>
</tr>
<tr>
<td>Middle-toe length</td>
<td>0.02</td>
<td>-0.10</td>
</tr>
<tr>
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<td>13.0</td>
</tr>
<tr>
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<td>25.3</td>
</tr>
<tr>
<td>Canonical $R$</td>
<td>0.99</td>
<td>0.96</td>
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</table>

3) and involved both interspecific ($F = 572.43; \text{df} = 5, 87; P < 0.0001$) and intersexual differences ($F = 90.50; \text{df} = 1, 87; P < 0.0001$; ANOVA of scores). Canonical coefficients indicate that CV-I primarily contrasted lengths of the wing and tarsus with nail width (Table 3); positions of species and sexes on this axis shows that CV-I is strongly inversely correlated with overall body size (Fig. 3). Large \textit{M}. \textit{merganser} had the lowest scores on CV-I, followed closely by \textit{M}. \textit{squamatus} and \textit{M}. \textit{serrator}, and ultimately the high-scoring \textit{M}. \textit{octosetaceus}, \textit{M}. \textit{australis}, and \textit{L}. \textit{cucullatus}; males had lower scores than females in all species (Fig. 3).

CV-II described a strikingly different multivariate axis, one involving strong interspecific ($F = 215.83; \text{df} = 5, 87; P < 0.0001$) and less pronounced intersexual differences ($F = 7.46; \text{df} = 1, 87; P < 0.01$; ANOVA of scores). This variate contrasted lengths of the culmen and tarsus with the lengths of the wing and tail (Table 3). \textit{M}. \textit{australis} had the lowest scores on CV-II, indicating that this species had long bills and tarsi relative to their wing and tail lengths. \textit{L}. \textit{cucullatus} had opposite proportions, and the remaining \textit{Mergus} had intermediate scores; males tended to have slightly lower scores than females within species (Fig. 3).

The third canonical variate (CV-III) for external measurements incorporated both interspecific ($F = 27.96; \text{df} = 5, 87; P < 0.0001$) and intersexual differences ($F = 39.20; \text{df} = 1, 87; P < 0.0001$; ANOVA of scores). CV-III contrasted wing length with other measurements, especially nail width, tail length, and middle-toe length (Table 3). \textit{M}. \textit{serrator} had comparatively low scores on this axis, indicating that this species had
long wings relative to their tail lengths, nail widths, and (to a lesser degree) other external measurements (Fig. 3). The high scores of *M. merganser* and *M. octosetaceus* reflected their opposite proportions, and other species were intermediate on this axis; males exceeded females in all species on CV-III.

A canonical contrast between *M. australis* and the other species using external measurements provided good separation of the insular form from other mergansers (*F* = 382.30; df = 3, 85; *P* < 0.0001). Canonical coefficients show that this contrast primarily contrasted wing length with culmen length and nail width (Table 3). Positions of species-sex groups along the contrast indicate that the axis was oriented diagonally with respect to canonical variates I and II and that *M. australis* was distinguished most clearly by its relatively short wings (Fig. 3).

**Univariate comparisons of skeletal measurements.**—With few exceptions, means of skeletal measurements followed overall body size (total length or body mass) in interspecific rankings (Table 4); *M. squamatus* (not tabulated), represented by a single skeleton, was intermediate between *M. serrator* and *M. merganser* in skeletal measurements. As in external measurements, males exceeded (*P* ≤ 0.01) females in skeletal dimensions (Table 4). Several skeletal measurements, however, deviated from the general interspecific size rankings: bill length, scapula length, sternal caudal width, and sternal carina depth (Table 4). Skeletal bill lengths of *M. australis* were disproportionately large, exceeding those of the generally larger *M. serrator*, *M. squamatus*, and *M. merganser*. Scapula lengths, sternal caudal widths, and sternal carina lengths of *M. australis*, however, were the smallest of all the species compared, including *L. cucullatus* (Table 4).

**Intra-alar skeletal proportions.**—Mean skeletal wing lengths differed among species (*F* = 748.48; df = 3, 70; *P* < 0.0001) and between sexes (*F* = 59.06; df = 1, 70; *P* < 0.0001) and followed interspecific rankings in body size (\(\bar{x} \pm s, n\)): *L. cucullatus* (191.5 ± 6.4, 24), *M. australis* (194.6 ± 6.3, 3), *M. serrator* (245.9 ± 9.9, 25), *M. squamatus* (250.6, 1), and *M. merganser* (268.6 ± 15.8, 26). However, the proportions of skeletal wing length contributed by constituent elements differed (ANOVA of transformed proportions) among species, many of these differences being attributed to the unusual proportions of *M. australis* and, to a lesser degree, overall size; intersexual differences in proportions were not significant in any element (*P* > 0.10). Humeral proportions differed among species (*F* = 17.14; df = 4, 74; *P* < 0.0001), constituted an average of 35.7% of skeletal wing length in *M. australis*, but accounted for only 34.1–34.9% of the wing in the other species compared. Ulnar proportions increased with overall size of species (*F* = 14.65; df = 4, 74; *P* < 0.0001), ranging
<table>
<thead>
<tr>
<th>Character</th>
<th>L. cucullatus</th>
<th>M. australis</th>
<th>M. serrator</th>
<th>M. merganser</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Bill length</td>
<td>45.6 ± 1.5</td>
<td>42.9 ± 1.5</td>
<td>65.6</td>
<td>61.3 ± 1.8</td>
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<tr>
<td>(14)</td>
<td>(15)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Humerus length</td>
<td>67.8 ± 1.1</td>
<td>64.9 ± 1.3</td>
<td>72.1</td>
<td>68.3 ± 0.7</td>
</tr>
<tr>
<td>(15)</td>
<td>(14)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Ulna length</td>
<td>55.5 ± 1.3</td>
<td>53.1 ± 1.2</td>
<td>57.7</td>
<td>54.8 ± 0.3</td>
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<tr>
<td>(14)</td>
<td>(14)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
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<td>Carpometacarpus length</td>
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<td>39.2 ± 1.2</td>
<td>40.7</td>
<td>38.7 ± 0.1</td>
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<td>(15)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Digit-II, Ph. 1 length</td>
<td>17.2 ± 0.5</td>
<td>16.3 ± 0.6</td>
<td>16.2</td>
<td>15.5 ± 0.1</td>
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<tr>
<td>(15)</td>
<td>(15)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Ph. 2 length</td>
<td>14.5 ± 1.0</td>
<td>13.5 ± 0.9</td>
<td>15.1</td>
<td>13.8 ± 0.3</td>
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<tr>
<td>(12)</td>
<td>(14)</td>
<td>(1)</td>
<td>(2)</td>
<td>(15)</td>
</tr>
<tr>
<td>Femur length</td>
<td>40.3 ± 0.8</td>
<td>37.8 ± 1.0</td>
<td>45.5</td>
<td>42.8 ± 0.4</td>
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<tr>
<td>(15)</td>
<td>(14)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Tibiotarsus length</td>
<td>65.4 ± 1.2</td>
<td>62.0 ± 1.6</td>
<td>—</td>
<td>77.3 ± 0.5</td>
</tr>
<tr>
<td>(15)</td>
<td>(15)</td>
<td>(0)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Scapula length</td>
<td>59.4 ± 1.8</td>
<td>55.8 ± 1.3</td>
<td>58.6 ± 4.4</td>
<td>56.0 ± 0.5</td>
</tr>
<tr>
<td>(15)</td>
<td>(15)</td>
<td>(2)</td>
<td>(2)</td>
<td>(15)</td>
</tr>
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<td>Sternum carina length</td>
<td>83.8 ± 2.5</td>
<td>78.2 ± 2.0</td>
<td>89.4</td>
<td>82.8 ± 0.8</td>
</tr>
<tr>
<td>(15)</td>
<td>(15)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
<tr>
<td>Caudal width</td>
<td>51.2 ± 2.0</td>
<td>49.3 ± 1.7</td>
<td>49.4</td>
<td>46.6 ± 0.7</td>
</tr>
<tr>
<td>(15)</td>
<td>(15)</td>
<td>(1)</td>
<td>(2)</td>
<td>(15)</td>
</tr>
<tr>
<td>Carina depth</td>
<td>22.1 ± 0.8</td>
<td>20.4 ± 0.8</td>
<td>19.4</td>
<td>18.1 ± 0.5</td>
</tr>
<tr>
<td>(15)</td>
<td>(15)</td>
<td>(1)</td>
<td>(2)</td>
<td>(16)</td>
</tr>
</tbody>
</table>
from 28.4% in *L. cucullatus* to 29.0% in *M. merganser*. Intra-alar proportions of the carpometacarpus (*F* = 21.19; df = 4, 74; *P* < 0.0001) and proximal (first) phalanx of digit-II (*F* = 14.65; df = 4, 74; *P* < 0.0001) opposed those of the humerus, being smaller in *M. australis* (20.2% and 8.1%, respectively) than in the other species (20.4–20.9% and 8.5–8.7%, respectively). The distal (second) phalanx of digit-II had equal (*F* = 0.07; df = 4, 74; *P* > 0.95) proportions in all species (7.3%).

**Canonical analysis of complete skeletons.**—Suites of 33 skeletal measurements provided the basis for powerful separation of the eight species-sex groups available (Wilks’ lambda = 0.0002; df = 10, 7, 83; *P* < 0.001); the single skeleton of *M. squamatus* was plotted on the axes based on the other three species. Stepwise MANOVAs documented significant interspecific (Wilks’ lambda = 0.053; df = 13, 1, 83; *P* < 0.001) and intersexual differences (Wilks’ lambda = 0.29; df = 5, 1, 83; *P* < 0.001) in these 33-dimensional comparisons. The first three canonical variates accounted for over 95% of the total intergroup variation in skeletons (Table 5). The first canonical variate (CV-I) displayed significant interspecific (*F* = 5079.52; df = 3, 83; *P* < 0.0001) and intersexual differences (*F* = 46.70; df = 1, 83; *P* < 0.0001; ANOVA of scores) but primarily discriminated *Lophodytes* from *Mergus*; *M. australis* was slightly more similar to *Lophodytes* than its congeners on this axis (Fig. 4). Canonical coefficients for CV-I indicate that *Lophodytes* differed from other mergansers on a complex size-shape axis involving relative proportions of the skull, among elements within the wing and leg, and among dimensions of the pectoral and pelvic girdles (Table 5). Notable proportionalities of *Lophodytes* indicated by the coefficients were: skulls characterized by relatively short bills and long, deep crania; wings with relatively short ulnae and radii; and legs with relatively large femora. Within each species, males and slightly lower scores than females on CV-I (Fig. 4).

CV-II for complete skeletons accounted for an additional 7% of the total intergroup dispersion and included both interspecific (*F* = 346.83; df = 37.41; *P* < 0.0001) and intersexual differences (*F* = 37.41; df = 1, 83; *P* < 0.0001; ANOVA of scores). Mean scores (Fig. 4) indicate that CV-II, together with CV-III (discussed below) primarily discriminated *M. australis* from the other groups (including *Lophodytes*). Because of the small sample available for *M. australis*, interpretation of multivariate differences between *M. australis* and other mergansers must be conservative. Coefficients for CV-II (Table 5), together with the low scores of *M. australis*, primarily indicate that the species was characterized by relatively long bills, relatively short mid-wing elements, legs with relatively robust proximal elements and long tarsometatarsi, and sterna with shallow carinae.
<table>
<thead>
<tr>
<th>Character</th>
<th>CV-I</th>
<th>CV-II</th>
<th>CV-III</th>
<th>CV of M. australis</th>
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</thead>
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<td>-0.65</td>
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<tr>
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</tbody>
</table>
The third axis (CV-III) for complete skeletons also incorporated significant interspecific ($F = 227.47; \text{df} = 3, 83; P < 0.0001$) and intersexual differences ($F = 126.26; \text{df} = 1, 83; P < 0.0001$; ANOVA of scores) but mostly represented residual differences between *M. australis* and other species not accounted for by CV-II; CV-III also provided a lesser discrimination of *M. serrator* (Fig. 4). Coefficients for CV-III, together with the high scores of *M. australis*, reflected the small size of most wing elements relative to the lengths of the femur, coracoid, furcula, and interacetabular width (Table 5).

The fourth canonical variate (not tabulated) accounted for another 3.2% of the intergroup variance but served largely to separate further *M. serrator* from its congeners ($F = 73.03; \text{df} = 3, 83; P < 0.0001$) and to discriminate sexes ($F = 97.04; \text{df} = 1, 83; P < 0.0001$) within species (ANOVA of scores). The remaining three variates for complete skeletons together incorporated less than 1% of the total dispersion, contributed mostly to intersexual discrimination, and are not considered further.

The distinctive skeletal proportions of *M. australis* were summarized in a canonical contrast between this species and the other species, which
maximally distinguished *M. australis* from all other groups independently of other interspecific differences and all intersexual differences (*F* = 51.00; df = 15, 69; *P* < 0.001). Mean scores of species and coefficients of variables for the axis showed the contrast to be largely a linear combination of CV-II and CV-III in the all-group analysis, with a lesser contribution from CV-I (Fig. 4). The coefficients for the contrast (Table 5) and the low scores of *M. australis* on this axis primarily reflected the following relative proportions: long bills; wing bones generally small, specifically the humerus, carpometacarpus, and proximal phalanx of the major digit; proximal and distal leg elements disproportionately long; and sterna with relatively shallow carinae and small caudal widths.

**Canonical analysis of sternal measurements.** — A separate CA of the five sternal measurements permitted the plotting of the single specimen of *M. octosetaceus* and a closer examination of this important and relatively complex part of the pectoral girdle. The analysis documented significant differences among groups (Wilks' lambda = 0.003; df = 5, 7, 81; *P* < 0.001), and included both interspecific (Wilks' lambda = 0.39; df = 5, 1, 81; *P* < 0.001) and intersexual differences (Wilks' lambda = 0.38; df = 2, 1, 81; *P* < 0.001). Interspecific differences were significant on each of the first three variates (*F* = 895.73, 64.28, and 30.71, respectively; df = 3, 81; *P* < 0.0001), but sexual differences were limited to the first variate (*F* = 134.95; df = 1, 81; *P* < 0.00001; ANOVA of scores).

Coefficients of CV-I for sterna were of the same sign, suggesting that the axis essentially reflected "sternal size" (Table 6); differences in magnitude among coefficients, however, show that this was not isometric size and that widths contributed little to this axis. CV-I primarily separated

<table>
<thead>
<tr>
<th>Character</th>
<th>All-group analysis</th>
<th>CV-I</th>
<th>CV-II</th>
<th>CV-III</th>
<th>Contrast of <em>M. australis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Carina length</td>
<td>-0.45</td>
<td>-0.40</td>
<td>-1.06</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td>Basin length</td>
<td>-0.23</td>
<td>-0.29</td>
<td>1.04</td>
<td>-0.27</td>
<td></td>
</tr>
<tr>
<td>Least width</td>
<td>-0.12</td>
<td>-0.39</td>
<td>-0.54</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td>Caudal width</td>
<td>-0.01</td>
<td>0.22</td>
<td>0.90</td>
<td>-0.43</td>
<td></td>
</tr>
<tr>
<td>Carina depth</td>
<td>-0.49</td>
<td>0.90</td>
<td>0.11</td>
<td>-0.92</td>
<td></td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>38.6</td>
<td>2.5</td>
<td>1.3</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td>Variance (%)</td>
<td>90.6</td>
<td>5.9</td>
<td>3.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canonical <em>R</em></td>
<td>0.99</td>
<td>0.85</td>
<td>0.76</td>
<td>0.87</td>
<td></td>
</tr>
</tbody>
</table>
the three smaller, "primitive" species (L. cucullatus, M. australis, and M. octosetaceus) from the larger, more derived species and distinguished sexes within species (Fig. 5). The two austral species were poorly represented, however, and multivariate inferences must be made conservatively. CV-II clearly separated M. australis and M. octosetaceus from the other mergansers (Fig. 5); coefficients indicate that the former were characterized by sterna with relatively shallow carinae and small caudal widths (Table 6). CV-III provided further separation between M. australis and other mergansers, including M. octosetaceus (Fig. 5), and primarily reflected the small differences between lengths of the carina and basin and between the two sternal widths in M. australis (Table 6). A canonical contrast of M. australis (Wilks' lambda = 0.24; df = 3, 1, 81; \( P < 0.001 \)) summarized these sternal differences, and combined the reduced carina depth with the "squarish" ventral and lateral aspects of the sterna of M. australis indicated in CV-III of the all-group CA (Table 6, Fig. 5).

**DISCUSSION**

**Phylogenetic and biogeographic inferences.** — The evolutionary tree proposed (Fig. 1) differs from previous hypotheses concerning M. australis; earlier workers either considered the relationships of M. australis to be unresolved (Johnsgard 1961a) or suggested that M. australis was an isolated relative of an extant northern-hemisphere congener, most probably M. squamatus or M. merganser (Humphrey 1955, Johnsgard 1965, Kear and Scarlett 1970, Weller 1980). The tree presented in this paper also
suggests several unexpected historical patterns. First, there is a pronounced trend toward increasing body size, and the relatively small size of *M. australis* is apparently the direct result of phylogeny rather than a secondary (derived) decrease in size. Second, *M. australis* and *M. octosetaceus* are representatives of an early grade of mergansers limited to the southern hemisphere. Although *Mergus* is known from subfossil remains on the mainland of New Zealand, the phylogenetic relationship of these to *M. australis* is not known. It should be noted that a comparatively long (82-mm) subfossil humerus from South Island, New Zealand, attributed by Kear and Scarlett (1970) to a possibly larger congener of *M. australis*, was reidentified by Olson (1977) as that of a coot (*Fulica*). Third, morphological similarities between *M. australis* and *M. octosetaceus* are the result of shared primitive characters (symplesiomorphies; e.g., head color of downy young) or convergence (homoplasies; e.g., sexual monochromatism), and do not reflect close relationship. Fourth, many of the unique plumage characters of *M. australis* are uniquely derived (autapomorphies) and, although not useful for determining relationships, are informative regarding the evolutionary characteristics of this peculiar insular form.

*Morphometrics of mergansers.*—Mergansers, like all sea ducks, are typical power-fliers, using rapid wing beats in normal flight (Meinertzhagen 1955) and being characterized by moderately high wing-loadings and comparatively pointed wings with reduced slotting between remiges (Rainbow 1973; Greenewalt 1962; Livezey and Humphrey 1986, this study). A direct relationship between wing-loading and body size in the Mergini (Fig. 2), a simple outcome of the more rapid increases in mass (a three-dimensional variable) than wing area (a two-dimensional variable), generally produces the greatest wing-loadings in the largest species. A similar allometry of wing area with body mass pertains to birds generally (Poole 1938, Hartman 1961, Greenewalt 1962). Projected estimates for *M. australis* and *M. octosetaceus*, however, suggest that these species possess(ed) wing-loadings comparatively high for the Mergini (Fig. 2). The estimated wing-loading for *M. australis*, roughly 2.4 g·cm⁻², is especially high (even allowing for possible over-estimation) and approximates the threshold of flightlessness (2.5 g·cm⁻²) hypothesized by Meunier (1951). The estimate for *M. australis* is comparable to the wing-loadings of Flying Steamer-Ducks (*Tachyeres patachonicus*), a species in which flight is heavy in most individuals and impossible for the heaviest males in some marine populations (Humphrey and Livezey 1982). Consequently, it is noteworthy that the *M. australis* observed in flight by Lord Ranfurly was, based on its vocalizations, a female (Kear and Scarlett 1970). I suspect that the heaviest males of *M. australis*, if not permanently flightless, were able to take flight only when aided by the lift provided by a strong head-wind.
(presumably common in the Aucklands), and with substantial room for take-off (on water) or from a decline (on land).

Statistical comparisons of external measurements not only confirmed the comparatively small size and relatively short wings of *M. australis* but revealed that the species possessed relatively short tails and exceptionally long bills (Tables 2, 3; Fig. 3). A significant portion of the morphometric differences among mergansers, however, was related to phylogeny in that *L. cucullatus*, *M. australis*, and *M. octosetaceus* were more similar (sympleiomorphically) to each other than to other *Mergus* on the most important axis of variation (CV-I, Fig. 3). *M. octosetaceus* was most similar to *M. australis* in its external dimensions (Fig. 3). *M. octosetaceus* is specialized for life along fast-flowing tropical rivers (Partridge 1956), and *M. australis* is believed to have inhabited primarily riverine habitats in the Auckland Islands (Delacour 1959, Kear and Scarlett 1970). Therefore, although the riverine habitats of *M. octosetaceus* and *M. australis* differed greatly in ecological characteristics, morphometric similarity between the austral species of *Mergus* may reflect, in part, convergence associated with similar feeding habits.

Analyses of skeletal measurements confirmed the long bills and relatively short wing elements of *M. australis* as well as a diversity of other, less obvious differences in proportions (Tables 4, 5; Fig. 4). Absolute length of the wing skeleton in *M. australis* was very similar to that in *L. cucullatus*; lengths of the manus (carpometacarpus and major digit) were equal in the two species, indicating that the shorter external wing lengths of *M. australis* result from a roughly 8-mm shortening of the primary remiges. *M. australis* also was characterized by disproportionately short mid-wing elements and relatively weakly keeled, caudally flared sterna (Table 6; Figs. 4, 5). Disproportionately short mid-wing elements and (particularly) reduced sternal carinae are typical of most flight-impaired and flightless species of carinate birds, including those of grebes (Podicipedidae; Livezey 1989), steamer-ducks (Anatidae, *Tachyeres*; Livezey and Humphrey 1986), and rails (Rallidae; Olson 1973). Although not represented by a complete skeleton, *M. octosetaceus* was most similar to *M. australis* in sternal conformation (Fig. 5); given the more typical sterna of *L. cucullatus* and the remaining *Mergus*, the similarity between the two austral species is evidently convergent.

**Paedomorphosis in M. australis.**—Paedomorphosis, “... retention of ancestral juvenile characters in the descendant adult phase ...” (McNamara 1986), is the result of the alteration of developmental patterns; a frequently cited form of such heterochrony is neoteny, the retardation of the growth of a body part relative to general developmental state (Gould 1977). Neoteny of the pectoral girdle has been inferred as the ontogenetic
basis for the “degenerate” conditions of sterna and wing elements of a number of flightless birds (Lowe 1928, Olson 1973, Diamond 1981, James and Olson 1983) as well as the more subtle changes in skeletal proportions of flightless steamer-ducks (Livezey and Humphrey 1986). The wing skeleton and sternum, and the short primary remiges of M. australis, could be characterized similarly. Both sexes of M. australis have adult plumages that closely resemble that of juveniles of mergansers generally, and juvenile plumages of Mergus can be presumed to be primitive. Therefore, by definition, the adult plumage of male M. australis also is paedomorphic; perhaps the condition might be more precisely termed “paedochromatic.” Whether this plumage change is the result of neoteny is not known, but such a developmental mechanism may underlie the reduced sexual dichromatism characteristic of many insular populations of anatids (Lack 1970, Weller 1980).

**Morphological and ecological correlates of insularity in M. australis.**—Weller (1980) described a number of unusual phenotypic features, averred to represent adaptive changes from the ancestral condition, which tend to characterize insular waterfowl: (1) reduced mobility, sometimes flightlessness; (2) reduced body size; (3) reduced sexual dichromatism; (4) development of white eye-rings; (5) comparatively dark natal plumages; (6) exceptional tameness of adults; (7) niche expansion, often to include marine habitats; (8) relaxed seasonality of nesting; (9) long-term pairbonds; (10) small clutch size; and (11) large egg size. Of these, four clearly characterized M. australis—reduced flight capacity, reduced sexual dichromatism, dark natal plumages, and tameness (the last based on a virtual lack of escape behavior observed by early collectors). The small size of M. australis conforms with the general pattern among insular ducks, but it appears to have been the result of phylogeny (i.e., the species represents a branch from the early grade of smaller mergansers; Fig. 1) instead of representing a decrease in size from a larger “continental” ancestor. The small size of M. australis is notable, however, in that increased body size is typical of avian lineages undergoing the loss of flight (Pennycuick 1975).

Two other correlates of insularity—increased utilization of marine habitat and long-term pairbonds—find weak support in M. australis. Although it is believed to have been primarily reliant on freshwater rivers, M. australis were observed on salt water near river mouths, and specimens have contained marine organisms (Kear and Scarlett 1970); given that most mergansers have largely freshwater habitats (the sole exception being M. serrator), this evidence suggests a comparatively broad, presumably derived, feeding niche. The disproportionately long bills of M. australis also may provide evidence of a diversified, more marine diet; for example, M. serrator, a comparatively marine species of moderate size, has a longer
bill than the larger freshwater *M. merganser* (Table 2). Existence of long-term pair bonds in *M. australis* is suggested by the presence of both adults with broods and the observation of paired adults from October to (perhaps) July (Kear and Scarlett 1970). The development of a white eye-ring clearly does not apply to *M. australis*, and the remaining three correlates—relaxed nesting schedule, decreased clutch size, and increased egg size—cannot be evaluated for *M. australis* because of lack of information.

**Significance of flight impairment in *M. australis*.—** It appears likely that adults and especially the downy young of *M. australis* were vulnerable, even prior to the arrival of humans, to a variety of avian and subaquatic predators, including Skuas (*Catharacta skua*), Peregrine Falcons (*Falco peregrinus*), predaceous fish, eels, and sea lions (Kear and Scarlett 1970). Although the introduction of exotic predators to the Auckland Islands, notably cats and pigs, posed a significant threat to the endemic birds of the Auckland Islands (Kear and Scarlett 1970), the reduced flight capacity of *M. australis* cannot be considered an evolutionary “response” to a lack of predators. Reduced predation pressure is invoked frequently in discussions of flightlessness in insular birds (e.g., Snow 1966; Weller 1975, 1980); paradoxically, concealment from predators is proposed by some to explain, at least in part, the reduced sexual dichromatism and dark natal plumages of some of these same species (Sibley 1957, Kear and Scarlett 1970, Lack 1970, Weller 1980). It appears that the evolutionary reduction or loss of flight capacity in *M. australis*, a species which did not use its wings in diving, reflects instead the developmentally economical reduction of the pectoral apparatus rendered of decreased selective importance in environments permitting year-round habitation.

**ACKNOWLEDGMENTS**

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LITERATURE CITED


LOWE, P. R. 1928. A description of Atlantisia rogersi, the diminutive and flightless rail of Inaccessible Island (southern Atlantic), with some notes on flightless rails. Ibis 70:99–131.


ERRATUM

In “Song repertoires and the singing behavior of male Northern Cardinals” by Gary Ritchison (Wilson Bull. 100:583–603), the penultimate sentence in paragraph 2 on page 597 should read “Groschupf (1985) reported that male Five-striped Sparrows (Amphiza quin-questriata) used more complex songs in intersexual contexts.”
## APPENDIX I

**Character Matrix for 22 Morphological Characters of Lophodytes and Mergus**

| Species              | Character*       | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
|----------------------|------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|    |
| Outgroups\(^b\)      |                  | a | a | a | a | a | a | a | a | a | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |    |    |
| *L. cucullatus*      |                  | a | b | a | a | a | a | a | a | a | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | b  | a  | a  | a  |    |    |
| *M. australis*       |                  | b | b | a | a | b\(^c\) | b | a\(^d\) | a | b | b | b | a | a | a | c | b | — | — | — | a  | a  |    |    |    |
| *M. octosetaceus*    |                  | b | b | a | b\(^c\) | b | a | b | a | a | a | a | a | a | c | c | b | a | a | a | b  |    |    |    |    |
| *M. serrator*        |                  | b | b | b | b | b | a | b | a | a | a | b | b | b | a | a | a | a | c | a |    |    |    |    |    |
| *M. squamatus*       |                  | b | b | b | b | b | a | b | a | a | a | b | a | b | b | a | a | a | a | b  | c  | a  |    |    |    |
| *M. merganser*       |                  | b | b | b | b | b | b | b | a | a | a | b | a | a | a | b | a | a | a | a | c  | — | c | b | a  |    |

* States described in Table 1; dash indicates that state not comparable and treated as "missing" (see text).

\(^b\) *Bucephala* spp., *Mergellus albellus*.

\(^c\) Weakly developed, possibly intermediate.

\(^d\) Vestigial.
POPULATION TRENDS IN SOME FLORIDA BAY WADING BIRDS

GEORGE V. N. POWELL,¹ ROBIN D. BJORK,¹ JOHN C. OGDEN,² RICHARD T. PAUL,³ A. HARRIETT POWELL,¹ AND WILLIAM B. ROBERTSON, JR.²

ABSTRACT.—Roseate spoonbills (Ajaia ajaja), Reddish Egrets (Egretta rufescens), and Great White Herons (Ardea herodias occidentalis) have unique subpopulations that are largely restricted to Florida Bay. All three species are believed to have had relatively large populations in Florida Bay, but the birds were virtually extirpated from the area between the late 1800s and the mid-1930s by human harvesting for food and feathers. After the birds were protected, they reestablished small populations that initially grew quickly. The Great White Heron population in Florida Bay increased from a low of about 20 individuals after the 1935 hurricane to a population of 800–900 resident adults in the early 1960s. As many as 400 additional birds (juveniles and possibly seasonal migrants) were present in winter censuses. The population remained at about that level through the 1960s, after recovering from a 20–40% decrease caused by a 1960 hurricane. After 1968, the population was surveyed only once, in 1984, when about the same number of birds were censused. The Reddish Egret recovered more slowly from total extirpation around 1935 to an estimated 200–250 adults in the late 1970s. Casual observations in the 1980s suggest the population has remained at about that level. Roseate Spoonbills showed an exponential recovery from just a few individuals up to a maximum of 2400 breeding birds by 1978–79. Subsequent censuses (1984–1986) revealed only about 800–900 nesting adults.

The virtual absence of pre-1880s data precludes comparing present populations with those of the pristine environment. However, the most recently surveyed population of each of these species seems to be at a lower density than was historically present. The recent decline in the spoonbill population and low reproductive success of the Great White Heron population are causes for concern about the future of the populations. These findings point out the importance of continued monitoring and analysis of population trends. Received 11 March 1988, accepted 26 Nov. 1988.

Florida Bay supports one of the most species-rich piscivorous avifaunas in North America. The most diverse group, the Ciconiiformes (long-legged wading birds), is represented by 14 species (Table 1). In this paper, we review population data for three wading bird species, Roseate Spoonbill (Ajaia ajaja) Reddish Egret (Egretta rufescens), and the white phase of the Great Blue Heron, the Great White Heron (Ardea herodias occidentalis), that are closely associated with the Florida Bay ecosystem. All three species are dependent on the bay and associated euryhaline habitats (here-

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after we lump the euryhaline, mangrove-dominated habitats as part of the Florida Bay ecosystem) for nest sites and foraging substrate. In the eastern United States, about 50% of the Great White Herons and Reddish Egrets and 90% of the Roseate Spoonbills nest within Florida Bay. Because of their small, geographically restricted populations, and their high trophic positions in relatively complex food webs, these species are likely to be particularly vulnerable to habitat changes in south Florida.

The environmental sensitivity of wading birds, coupled with the relative ease with which they can be counted, has resulted in their being proposed as biological indicators of habitat quality (Custer and Osborn 1977, Powell and Powell 1986). The three species we have selected to analyze should function well as indicators because all have small populations that are concentrated in relatively few breeding colonies. These characteristics make them likely to respond quickly to environmental changes in a measurable fashion.

Our objectives were to determine population changes for adults of each species and to provide ecological interpretation of identified trends.

METHODS

The Great White Heron exists in Florida Bay in what is currently recognized as two distinct color morphs, the typical “blue” form, Great Blue Heron, and an all white form, Great White Heron. While the color morphs coexist throughout the bay, the Great White Heron has been the focus of attention because the south Florida coastal ecosystem appears
to be the epicenter of its distribution; Florida Bay supports roughly half of the entire Florida population. The other 50% are distributed predominantly south in the lower keys (Robertson unpubl. data), with a few breeding records north along the east coast to Biscayne Bay and along the Gulf coast to Tampa (Robertson 1978a). We have limited our comments to the white morph because there are insufficient data to analyze population trends of the blue morph.

Great White Herons were surveyed from fixed-wing aircraft flown in an irregular grid designed to cover all islands and shallow mud banks in the bay. The large size and white color of this heron make individuals highly visible from low level (150–400 m) reconnaissance. Aerial counts were assumed to record the entire population, however, the accuracy of the surveys has never been tested. Potential sources of error include: difficulty in distinguishing between Great White Herons and Great Egrets {Casmerodius albus} in large breeding colonies, overlap or voids in coverage of extensive mud banks in the western bay, and difficulty in locating diurnally resting birds on mangrove islands in the eastern bay. The presence of large fledglings that were generally indistinguishable from adults made it impossible to determine population size during the protracted breeding season. Aerial counts (up to three in one year) were made intermittently between 1935 and 1968 and again in 1984 (Appendix I). Aerial surveys of the Great White Herons were estimates of the total population.

Reddish Egrets are difficult to detect from the air, so population estimates of this species have been based primarily on ground counts. Population estimates prior to 1977 were rough estimates based on partial nest counts and the number of birds observed foraging on banks. For two nesting seasons beginning in 1977–78, one of us (RTP) attempted to make complete counts of breeding Reddish Egrets in Florida Bay. Because the nesting season is protracted and Reddish Egrets may nest solitarily, a variety of methods were used to locate nesting pairs: previously known sites were checked repeatedly throughout the year, foraging adults with brightly colored soft parts (indicating breeding condition) were followed back to breeding sites, and vocalizations from begging young were used to identify islands with active nests. Furthermore, because adults were not individually recognizable, it was necessary to adjust the number of nests found to account for the possibility of multiple nesting attempts. Toward this end, two population values were generated: one based on the total number of nests observed, and a second controlling for duplication, based on the number of nests that successfully produced young. As mentioned, the first value is likely an overestimate because it includes renestings; the second is likely to underestimate by assuming that all pairs are successful.

Beginning in the 1930s, the number of spoonbill breeding pairs generally was determined by one of two methods. Both methods derive population estimates of breeding birds only and do not include the nonbreeding portion of the population. During most years, ground counts of active nests were made (Appendix II). In contrast to the Reddish Egrets, spoonbills nest in compact colonies and have a highly synchronous nesting season. Therefore, the ground counts produce highly accurate measures of the breeding population based on single annual censuses. Post-breeding censuses were made immediately after the last young had fledged to avoid inclusion of second nest attempts and minimize the loss of nests through stick thievery by later nesting wading birds. Nesting attempts that occurred two to three months after the initial breeding effort were assumed to be second attempts. For several years, primarily in the 1960s and early 1970s, the spoonbill population in the bay was estimated by aerial reconnaissance (Appendix II). Spoonbills nesting in dense mangroves are difficult to accurately detect from the air, however, so these counts must be considered as rough approximations of population size.

The survey techniques used for each species produced somewhat different results because
for the Great White Heron all individuals were counted, while Roseate Spoonbill estimates were derived exclusively from nest counts, and Reddish Egret estimates were derived from a combination of both. For the latter two species, it is not known what percent of each population is reproductively active during a given year.

RESULTS

Overview.—Insufficient data are available to estimate wading bird populations that existed in Florida Bay prior to human influence on the system. Audubon reported that during his travels in relatively pristine Florida Bay in 1832 that at Sandy Key there were “flocks of birds that covered the shelly beaches” and “the air was darkened by whistling wings” (Proby 1974). Beyond these superlatives, the only insight Audubon provided regarding population sizes was through his reports of numbers of birds he saw in groups or the numbers he was able to shoot at one site. The next available reports date from the late 1800s when more quantitatively oriented ornithologists began to visit south Florida (Maynard 1881, Scott 1889, 1891). By that time, however, the millinery trade had focused on bird feathers as a source of adornment, and wading bird populations were devastated by plume hunters. Even after the plume hunting was largely terminated in 1912, Florida Bay colonies continued to be disrupted by local inhabitants and commercial sponge fishermen who collected eggs and nestlings for food (Sprunt 1935). Due to the early and persistent history of exploitation, there are no known sources from which to quantify pristine wading bird populations in Florida Bay. Consequently, for each of the three target species, we can only point to indicators of population size prior to man’s influence.

Great White Heron.—Quantitative records of the Great White Heron population prior to human disturbance are nonexistent, with Audubon again providing the only information that allows us to speculate on population size. Though Audubon gave no estimate of the Ardea population, his reference to Great White Heron flocks indicates that the species was abundant in the bay. Audubon (Proby 1974) reported flocks “sometimes a hundred or more being seen together” to be a regular occurrence on the flats. For the next 100 years after Audubon’s visit to the keys, data on Ardea populations in Florida Bay are limited primarily to nest records on isolated bay keys (Scott 1890, Bent 1926, Holt 1928). These data, plus the aggregation of records from a large series of clutches collected by Court in 1925, indicate the existence of a relatively large population at that time. Court collected at least 29 Great White Heron clutches from Palm Key and estimated there were 15 additional nests present on Oyster and Clive keys in western Florida Bay. Holt and Sutton (1926) reported Great White Herons were “common on the keys and mud banks off Flamingo” in
Fig. 1. Population growth of Great White Heron (Ardea herodias occidentalis) in Florida Bay. Data were collected from fixed-wing aircraft by three different observers (see Appendix I). Round points are summer censuses, X's mark winter censuses. Line is fitted to censuses through summer 1960 (Y = 28.6 + 32.7X).

1924. It is known, however, that as the human population grew in the mainline keys and areas adjacent to Florida Bay, the use of Ardea as a food source by humans had a major impact on the population (Holt 1928, Sprunt 1935). Sprunt (1935) made the first systematic survey of the entire bay and recorded only 56 individuals (Fig. 1, Appendix I; the area between the Florida mainland and Key West had 211 individuals). Sprunt concluded that this was the entire population for the area. However, it is unlikely that his 3.25-h survey could have canvassed all relevant habitat, as aerial surveys made at similar flight speeds by one of us (WBR) in the 1960s required about 50 h to cover the same area thoroughly. In any case, on the basis of his surveys, Sprunt predicted the Great White Heron would be extirpated within five years due to harvesting of nestlings for food. In the fall of 1935, the bay population was further reduced by a major hurricane that passed across the upper keys and Florida Bay. A month after the hurricane, Sprunt (1935) again surveyed the population and found only 20 Great White Herons in Florida Bay and 146 birds throughout the species' range as far west as Key West. In April 1936, Sprunt again flew the transects and recorded 39 Great White Herons in the bay (Sprunt 1936a). The next aerial survey in October 1936 recorded 86 birds (Sprunt 1936b). Sprunt (1937, 1939b) made aerial surveys of the population in September 1937 and January 1939, each of which revealed a continuing recovery of the population (Fig. 1).
Extensive surveys of the *Ardea* population were again made by one of us from 1959 through 1968 (Fig. 1; WBR, in 1958 through 1967; JCO in 1967, 1968). In 1959 and summer of 1960, WBR counted between 809 and 898 Great White Herons in Florida Bay. In August, 1960, a second major hurricane (Donna) passed across the upper keys and Florida Bay (Gentry 1974). This storm had a large impact on the *Ardea* population, as had the hurricane in 1935. A survey two months after the hurricane yielded 30–40% fewer Great White Herons in the bay than had been present the previous two years (Fig. 1). It is not known what portion of that decline resulted from mortality as opposed to relocation. However, more than 100 Great White Heron carcasses were found in limited searches of storm racks on keys in the bay and along the south shore of the mainland after the hurricane (WBR unpubl. data). This large number of carcasses indicates that much of the population reduction was the result of storm-induced mortality. The path of the hurricane had its greatest impact within the bay, and presumably bird mortality was primarily in that area. Therefore, the portion of the Great White Heron population that was located in the lower keys (estimated to be about half of the total) would have been largely unaffected, and storm-induced mortality might have been as much as 20% of the total population. Two years after the 1960 hurricane, the Florida Bay Great White Heron population had recovered to at least 90% of the pre-hurricane level. Continued surveys through the 1960s indicated a stabilization of the population at between 800–900 birds in summer and 1200–1400 birds in winter (Fig. 1). After 1968, the Great White Heron population was not surveyed again until the winter of 1984 by WBR, when 1509 birds were counted in the Bay. That count was similar to winter counts made in the 1960s (Fig. 1).

**Reddish Egret.**—Historically, Reddish Egrets nested in coastal colonies north to Clearwater Harbor, Pinellas Co., and probably North Anclote Key, Pasco Co., on the Gulf Coast, and were particularly abundant in Tampa Bay and Charlotte Harbor. On the Atlantic Coast, they were found at Pelican Island in the Indian River and possibly at Cape Canaveral, Brevard Co., but were not reported from other localities and may have been relatively uncommon. They were also widely distributed in Florida Bay and probably the lower keys (Audubon 1843, Maynard 1881).

Indications of Reddish Egret abundance in pristine Florida Bay are limited to anecdotal reports. When Audubon visited Florida Bay in 1832, he was told that “though still plentiful, this species was much more so when the keys were first settled” (Audubon 1843). He reported seeing as many as “twenty or thirty, sometimes as many as a hundred” foraging on shallow flats (Audubon 1843). Audubon found Reddish Egrets easy to collect, killing 12 in less than half an hour at one colony (possibly one
of the Peterson or Buchanan Keys; see Audubon 1843). He also reported watching another hunter take 28 in an hour. In 1872, Maynard (1881) found white-morph Reddish Egrets abundant among the “interior keys” of Card Sound, an area he termed the “stronghold” of the “species” (“Ardea pealii” or Peale’s Egret, then considered distinct from “A. rufescens,” the Reddish Egret). On the inhabited “outer keys,” Maynard found “Peale’s Egrets” “not uncommon” and the dark phase nearly absent. While Audubon’s and Maynard’s data are not sufficient to estimate the Reddish Egret population in the bay, they do indicate the presence of a substantially larger population than at present.

In the two decades following 1890, Reddish Egrets declined sharply in Florida, but are known to have persisted in Florida Bay at least until 1908. Scott (1889) still considered the species locally common in Florida, an opinion supported by Jamison (1891) who found about 60 nests in a small heronry in Pine Island Sound (Lee County) in 1891. However, one year later Scott (1892) reports it rare in the Caloosahatchee region. In March 1902, Howe and King (1902) found only two Reddish Egrets (near “Tavanier Bank, Bay of Florida,” probably the area now referred to as Upper Cross Bank) in a two-day trip in Florida Bay, and noted that this species still suffered from plume hunting. Bent and Job spent two weeks in April–May 1903 searching Florida Bay and Cape Sable for nesting herons with Audubon wardens Guy Bradley and William Burton. In separate accounts, Bent (1926) reported only scattered individuals, and Job (1905) noted that “several” birds flushed from one key—possibly Porjoe Key. Broadhead (1910) described Reddish Egrets as “not uncommon” at Upper Matecumbe Key in the spring of 1906, where he saw two birds “brought in.” Chapman (1908) found six Reddish Egrets foraging at the head of Snake Bight (possibly Garfield Bight incorrectly identified) near Flamingo on 29 March 1908. In contrast to these estimates of a very low Reddish Egret population, Guy Bradley, chief Audubon warden for the area, estimated in 1904 that 300 Reddish Egrets survived, from Key West to Florida Bay and north along the Gulf Coast to Chokoloskee (Allen 1954, 1955). However, no details of Bradley’s report have survived, so the basis for this estimate is unknown.

Soon after 1908, Reddish Egrets apparently disappeared entirely from Florida Bay and the rest of Florida (Howell 1932; Allen 1954, 1955). The species was not reported again from Florida Bay until 23 April 1937, when two birds in non-breeding plumage were found at Upper Matecumbe Key (Davis 1937). The following year a nest was discovered at Bottlepoint (now called Bottle) Key (Desmond 1939). For the next few years, the known population in Florida Bay was 4–5 birds (Fig. 2, Sprunt 1938, Poor 1941, Stimson 1942). During this time the species was limited to
Fig. 2. Population growth of Reddish Egret (*Egretta rufescens*) in Florida Bay following recovery from probable extirpation in 1930s. Equation for line $Y = -12.1 + 6.0X$.

eastern Florida Bay, notably Bottle, Low, Stake and Manatee keys. Reddish Egrets also returned to the lower keys, with 2–5 birds reported near Key West in 1939–40 (Greene 1946). By 1944, Reddish Egrets had increased to perhaps 50 birds in eastern Florida Bay, with 38 recorded at one (unnamed) key (Baker 1944). The population continued to increase through the 1950s; Allen (1954, 1955) estimated 150 birds in Florida Bay and the keys in 1954 (Fig. 2). In 1959, Allen estimated that the Reddish Egret population was not over 200 individuals (Palmer 1962). Based on current distribution, we estimate the bay population would have been between 150 and 175 birds.

Reddish Egrets were not censused again until the mid-1970s, when the entire Florida population was roughly estimated to be about 300 individuals, with most nesting occurring in Florida Bay (Robertson and Kushlan 1974, Robertson 1978b). In 1977–78, 168 nest were located on 17 different keys (Table 2). Seventy-four of those nests were successful. The large number of failed nesting attempts and a nine-month breeding season makes it likely that renesting was wide-spread and that the Reddish Egret population was substantially lower than 168 pairs. At the same time, some pairs were probably unable to produce young throughout the season in spite of multiple nesting attempts. Therefore, a population estimate based on the 74 successful pairs would be a low estimate. On the basis of these considerations, we suggest a range of 100–125 pairs or 200–250 adults as a breeding population estimate for that year (Fig. 2). Repro-
Table 2
Number of Nesting Attempts by Reddish Egrets in Florida Bay in 1977–78 and 1978–79

<table>
<thead>
<tr>
<th>Key</th>
<th>1977–78</th>
<th>1978–79</th>
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<tbody>
<tr>
<td>Frank</td>
<td>54</td>
<td>32</td>
</tr>
<tr>
<td>Tern</td>
<td>38</td>
<td>39</td>
</tr>
<tr>
<td>Porjoe</td>
<td>28</td>
<td>25</td>
</tr>
<tr>
<td>Foxtrot/Bob Allen</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>Buchanan</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Manatee</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Bottle</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Cowpens</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Sandy</td>
<td>3</td>
<td>ND</td>
</tr>
<tr>
<td>Oyster</td>
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<td>ND*</td>
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<td>Peterson</td>
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<td>1</td>
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<td>Butternut</td>
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<td>1</td>
<td>ND</td>
</tr>
<tr>
<td>C. Jimmie</td>
<td>ND</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>169</td>
<td>135</td>
</tr>
</tbody>
</table>

*ND = no data, status of colony unknown.

Productive data from the following season support that conclusion. In 1978–79, only 135 nesting attempts were recorded (Table 2), but nest success was generally high (RTP unpubl. data). Therefore, fewer second nesting attempts would have been expected, and most of the 135 nesting attempts probably represented different pairs.

There have been no attempts to survey the Reddish Egret population since 1980. Casual observation of active nests in the 1980s indicate that the major breeding sites in the eastern bay (Tern, Porjoe, and Buchanan keys) are still active.

Roseate Spoonbill. — Reports from travelers and naturalists in the mid-1880s indicated that a large spoonbill population existed in south Florida (summarized in Allen 1942). Major spoonbill colonies prior to 1850 included coastal colonies at Indian Key in Tampa Bay, Marquesas Keys, Boca Grande Key, and Pelican Island in the Indian River, and inland colonies at Alligator Lake, Cuthbert Lake, Corkscrew rookery, Okaloacoochee Slough, 17 Mile Swamp, Lake Poinsett (Allen 1942), and the Big Cypress (Sprunt 1939a). Scott (1889) reported that spoonbills had once
"bred in enormous rookeries" around Cape Romano and that large numbers of birds were present in that region as late as 1880. Further indication of colony size is evidenced by Bryant's (1859) report of a plume hunter killing sixty spoonbills in a day at Pelican Island. Historical records documenting spoonbill abundance in Florida Bay are even more limited than for the rest of the state. Audubon refers to spoonbills breeding among the Florida Keys (in Allen 1942) and foraging along the mangrove edges of Sandy Key during his trip through the keys in 1832 (Audubon 1960). During the last half of the 1800s, and continuing through the early 1900s, the spoonbill population was greatly reduced. Although prohibition of plume hunting and protection of nesting colonies began in the early 1900s, the decline continued until, by the early 1930s, fewer than 200 pairs were thought to nest in Florida. These birds nested sporadically in small numbers (6-10 pairs) in mixed species colonies at Cuthbert Lake, Lane River, Shark River, and Charlotte Harbor (Allen 1942) and in one larger colony located at Bottle Key in eastern Florida Bay (Grimes and Sprunt 1936). By 1935, continued human predation on adults and eggs had probably eliminated all colonies except the Bottle Key colony which had been reduced to 15 pairs (Allen 1963) (Fig. 3). By 1941, it was thought to be the only remaining active colony in Florida (Fig. 3; Allen 1942).

After 1940, the next account of spoonbills breeding in Florida was by J. C. Watson of the U.S. Fish and Wildlife Service. Watson estimated 100 breeding pairs and up to 10 colonies in the Bay during the 1948-49

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**Fig. 3.** Population growth of Roseate Spoonbill (*Ajaia ajaja*) in Florida Bay. Simple points are total number of nests counted on ground visits to colonies; encircled points are estimates derived from aerial counts which are relatively inaccurate. Equation for line during growth period (up to 1978-79) \[ Y = 13.22 \times \exp(0.099X). \]
season (Allen 1963). Allen resumed his spoonbill surveys in Florida Bay in 1950 and found larger numbers of nesting birds and a greater number of active colonies, compared to his surveys in the 1930s, but fewer than estimated by Watson (Appendices II–IV).

Approximately every 10 years from 1955 through 1978, the nesting population doubled (Fig. 3). In the 1978–79 season there was a dramatic increase in the number of breeding spoonbills (based on nest counts) over the previous two years, with the population reaching 1254 breeding pairs (Fig. 3). During 1978–79, nesting also occurred at two sites in the mangrove fringe adjacent to the bay, Madeira Rookery and Lane River. Spoonbill nesting had been noted only once for each of these colonies since the 1940s: 6 nests at Madeira Rookery in 1967 (unpubl. data, ENP), 3 nests at Lane River in 1975 (Ogden 1975). In 1978–79, these 2 colonies had an additional 115 pairs of spoonbills. These nests were initiated in spring, 3–4 months later than the highly synchronous bay colonies and may have been renesting. For this reason, we have not included them in the total nesting population estimate. No information is available for five years subsequent to 1978–79, but by 1984 when population surveys were reinitiated, the nesting population was 64% smaller than the peak 1978–79 level (Fig. 3). Subsequent surveys in 1985, 1986, and 1987 revealed a breeding population similar to levels in 1984 (Fig. 3).

DISCUSSION

During the first third of this century, Florida Bay wading bird populations went through an extreme bottleneck period (Weins 1977). One species, the Greater Flamingo (Phoenicopterus ruber) that was represented by a nonbreeding population of up to several thousand individuals disappeared from the area and has never become reestablished. The three species we analyzed were similarly pushed to the brink of extirpation or possibly were temporarily extirpated during this same period. In each case, however, when the exploitation was terminated, the population recovered.

The history of exploitation and recovery for these bay species differs from that of adjacent, more interior wading bird populations (i.e., White Ibis [Eudocimus albus], Snowy Egrets [Egretta thula], and Great Egrets). Protection was achieved for the latter species by 1915. Their population responded with rapid growth so that by the 1930s their combined population was estimated to be greater than a million birds (Robertson and Kushlan 1974). In contrast, the Great White Heron, Reddish Egret, and Roseate Spoonbill were still being heavily exploited as a food resource throughout the 1930s (Sprunt 1935). This delay in the implementation of protection for these species is significant in that it precluded their
becoming reestablished while south Florida was still relatively unaltered by human development. By the end of the 1940s, when Florida Bay species began to recover, south Florida hydrology had been seriously disrupted (Anonymous 1950). The delay in recovery of the Florida Bay populations is also significant in that it means there are no population data for these species from a period that can be considered as representative of relatively pristine conditions. Thus, while a relatively firm basis for comparison exists to assess current status of interior wading bird populations no equivalent data exist for the three Florida Bay populations. Consequently, we can only speculate about the population sizes of these species before human interference.

The populations of these three species did not begin to recover at least until the late 1930s, and in the case of the Reddish Egret, recovery probably was predicated on recolonization from outside the state. With cessation of major human disruption of colonies, the populations of all three species increased relatively rapidly. If Sprunt’s initial surveys adequately reflect the population, the Great White Heron population had the greatest rate of recovery, with a calculated increase of 30–40 birds per year between 1936 and 1960 (Fig. 1). More likely, Sprunt’s estimates were actually low and initial recovery was slower, but still robust. The Reddish Egret and Roseate Spoonbill, which were both recovering from even smaller populations, initially increased at a slower rate (Figs. 2 and 3). The spoonbill population curve was ultimately exponential, with increases of over 150 birds per year by the late 1970s. As with the Great White Heron, the results was a near doubling of the population every decade between 1940 and the late 1970s. The Reddish Egret appears to have continued a linear growth rate up until the late 1970s, though the paucity of data makes that conclusion tentative.

For at least two of these species, the population recoveries have not continued into the present. In the mid-1980s, when spoonbills were surveyed after a hiatus of five years, the population was only one-third as large as the actual nest count compiled in 1978–79. The largest colony, Tern Key, had declined to one-fourth its previously recorded maximum (Appendix II). Interpretation of the spoonbill population data is made difficult by the gap in surveys between 1979 and 1984. The population peak of about 2500 adult birds (1254 pairs) was recorded for only a single year (1978–79). Five years later, when the spoonbills were next surveyed, only 900 (450 pairs) birds nested in the Bay. We do not know whether the 1978–79 peak represents a single year and whether the subsequent decline occurred in a single year or was spread out over five years.

Based on the 1978–79 population size, subsequent surveys indicate that a major population decline occurred during the early 1980s. This decline
presumably resulted from some combination of low reproductive success, a high mortality rate, or emigration of juveniles and adults between 1979–84. The estimated mortality rate of 20% per year calculated for some adult wading bird species by Henny (1972) would be sufficient to explain the population decline if reproduction failed for a period of several years. We have no information available to suggest that adult mortality would have been greater during those years. In both 1977–78 and 1978–79, reproductive success was very low with 0.06 fledglings per nest produced in 1977–78 (Robertson 1978b), and 0.45 in 1978–79 (Robertson 1979). As suggested by Roberston (1979), almost complete nesting failure in 1977–78 and 1978–79 would result in major year-class gaps. Because spoonbill maturity is reached in three years (Allen 1942), reduced recruitment of new adults into the breeding population would be expected in the early 1980s. Therefore, the observed population decline in the early 1980s conforms with these predictions.

It is too early to determine whether the spoonbill population has again stabilized, but surveys in 1984–1987 show a consistent number of breeding birds. Low reproductive success has also been noted during the 1980s: 1982–83 = 0.06 young/nest, 1983–84 = 0.5 young/nest, 1986–87 = 0.06 young/nest (Powell, unpubl. data). Again, with some year-classes nearly missing, we expect a further decline in the spoonbill breeding population.

As with the Roseate Spoonbill, gaps in the Great White Heron data make conclusions about the population trends tenuous. The heron data present an additional difficulty due to a 40–50% yearly variation in population estimates. This within-year variation appears to be a seasonal phenomenon, with populations being up to 50 percent larger in winter (Appendix I). Large nestlings and fledglings are indistinguishable from adults in aerial surveys, and probably account for much of the variability. These young leave the bay within two months of fledging from winter nests (Powell and Bjork, unpubl. data) so they would be absent from summer, fall, and, to varying degrees, spring surveys. In view of our inability to distinguish reliably between adults and juveniles, we have chosen to use the summer adult population as the base population for the species. Great White Herons reached this base level of about 900 birds by 1960. The population suffered a major decline during Hurricane Donna in 1960, but recovered to the pre-hurricane level within two years. For the rest of the decade, the population remained at about 900 adult birds. The winter surveys increased slightly throughout the decade (Fig. 1), but the 20% difference between the survey extremes probably reflects a combination of sampling error and differences in reproductive success rather than changes in the adult population.

The existence of only a single survey after 1968 makes conclusions
about the current status of the population largely speculative. The 1984 survey was made in January and February when there were large numbers of nestlings and recent fledglings particularly at colonies along the eastern fringe of the bay. While the number of birds recorded in winter 1984 was up to 10 percent higher than comparable surveys in the 1960s, we do not consider that difference indicative of a significant change in the population. Our conclusion is that the Great White Heron population was the same size in 1984 as it was two decades before.

As with the Roseate Spoonbill, we attribute the absence of continued population growth to low reproductive success and a low rate of recruitment. A three-year analysis of reproduction by Great White Herons in the early 1980s (Powell and Powell 1986) indicated that only 24% of nests produced young and productivity of only 0.5 young fledged per nest attempt in natural colonies (N = 97 nests). This productivity is well below the 1.91 young per nest that Henny (1972) calculated to be necessary to sustain Great Blue Heron populations. Though the method Henny used to derive that value is flawed (Anderson et al. 1981), it is likely an approximation of required productivity. The magnitude of spread between Florida Bay productivity and Henny's value is probably indicative of real differences. However, Henny's data were obtained from birds banded in the northeastern U.S. where life expectancies may be substantially shorter than those of a non-migratory, sub-tropical population. At this point, we have no measures of adult survival rate and therefore cannot estimate the level of recruitment that would be necessary to maintain a stable population in the bay. It should be noted, however, that a majority of the Great White Heron productivity during the early 1980s came from more productive nests of food-supplemented birds (mean young/nest, Powell and Powell 1986). This raises the possibility that stability of the Great White Heron population is dependent on supplemental feeding by humans.

Through a food addition experiment, Powell and Powell (1986) identified insufficient food as the major cause for low Great White Heron productivity. They also compared their current data with measures of reproductive parameters collected in 1923 (Holt 1928) and found (comparing distributions by chi square) that both clutch size and productivity were significantly greater in 1923. These findings are corroborated by a comparison of clutch size data for Great White Herons nesting between 1889 and 1925 and those nesting between 1981 and 1984. Prior to 1925, clutches averaged 3.41 ± 0.58, N = 112 (Powell unpubl. data) which was significantly larger than the average clutch size produced by naturally foraging herons in the 1980s (\( \bar{x} = 3.0 \pm 0.53; N = 57; \chi^2 = 33, P < 0.01 \)). There was no significant difference between the number of eggs laid by
Great White Herons prior to 1925 and supplemented birds in the 1980s ($\bar{x} = 3.59 \pm .79$, N = 32, $P > 0.01$). The clutch data from nests prior to 1926 are primarily from several large series collected by E. Court, H. J. Hoyt, and E. Holt, so they are probably an unbiased representation of clutch size.

The Reddish Egret is by far the least abundant of the three species and also has the weakest data set for deriving a population growth curve. After their return to the bay in 1937, the Reddish Egret population appears to have grown at least through the 1950s and possibly the 1960s. In the mid-to late 1970s, the population appears to have remained stable. Because the population was not monitored between the mid-1950s and mid-1970s, we cannot determine if the population stabilized, increased gradually, or peaked and declined during the 1960s and early 1970s. The absence of data beyond the 1979–80 breeding season makes it impossible to project a current population trend. Casual observations in the 1980s indicate that the major colonies are still active, but no recent attempts have been made to evaluate reproductive success or population size.

The apparent instability of the Roseate Spoonbill and Great White Heron populations is probably ultimately related to human manipulation of south Florida hydrology. Recent evidence obtained from the analysis of coral in Florida Bay indicates that, prior to 1915, twice as much freshwater reached the bay as post-1930 (Smith et al. 1988). Reduced freshwater input would be expected to have major impacts on the ecosystem as a habitat for piscivorous wading birds. A reduced freshwater runoff would alter sheet flow and the resultant hydropattern of associated euryhaline marshes, which has major impacts on the availability of food resources for the three species. Great White Heron juveniles, Roseate Spoonbills and, to a lesser extent, Reddish Egrets, must have access to fish and invertebrates concentrated in shallow pools and ponds by cyclic flooding and drying of euryhaline wetlands. A reduction of freshwater runoff would also affect fish and invertebrate communities through resulting increases in salinity. A strong positive correlation exists between high runoff years and high recruitment by sport fishes (Tilmant, in press) and pink shrimp (*Penaeus duorarum*) (Browder 1985). These species, and others, are dependent on low salinities during larval and post-larval stages (Robblee pers. comm.; Rutherford et al., in press). Schmidt (1979) reported the occurrence of salinities along the northern mangrove-seagrass ectone in the bay that were high enough to be fatal to most euryhaline species of fish. These high salinities would have been moderated by historic hydropatterns that maintained a higher water table in upland areas (Tabb 1967, Sculley 1986).

Another human impact on the ecosystem that negatively affected wad-
ing bird populations was modification of foraging habitat for commercial and residential land development along the mainline keys. Historically, these high marsh areas were the principal foraging habitat for spoonbills (Sprunt pers. comm.). Transitional wetlands on the mainline keys are also important as alternative foraging habitats for Reddish Egrets when storm-induced high water levels prevent them from using most bank habitats in the bay (Powell 1987).

The aggregate of low reproductive success manifested as a consistent high rate of nestling starvation and nest failure in Great White Herons and the high frequency of complete colony failure in Roseate Spoonbills indicate that these populations are at best marginal under current habitat conditions. The recent decline in the spoonbill population may indicate submarginal habitat quality for that species. The heavy dependence of Great White Herons on supplemented food for successful reproduction points to an unstable population for that species, as well.

In view of the inadequacy of presently available data, we recommend monitoring all three species to determine their population trends under current water management conditions. Furthermore, any future manipulation of water release schedules should include an analysis of impacts on these species. The three species forage in different habitats with little overlap in either prey type or capture technique. An analysis of carbon isotope ratios of tissues from nestling Great White Herons indicates that the population is dependent on a seagrass-derived food chain, while Roseate Spoonbills show a mangrove-based dependency (Sternberg and Powell, unpubl. data). These differences underscore the need for a diverse research program that analyzes the interrelationships of freshwater input, productivity of the estuary, and wading bird foraging ecology.

ACKNOWLEDGMENTS

We have attempted to summarize several decades of census data which could not have been collected without the assistance of many individuals including: Sonny Bass, Harris Chustz, Pat Healy, Barbara Patty, Nancy Paul, Alexander Sprunt IV, Kevan Sunderland, Martha Van der Voort. Special thanks to Lorraine Breen for beginning the process of analyzing the Roseate Spoonbill data, to Alexander Sprunt IV for providing invaluable insights into Florida Bay wading bird populations, and particularly to Nancy Paul for assisting with the preparation of the manuscript. We also thank R. Michael Erwin, Thomas W. Custer, Kathleen G. Beal, and Peter Frederick for reviewing an earlier draft of this manuscript.

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**APPENDIX I**

**GREAT WHITE HERON SURVEYS**

<table>
<thead>
<tr>
<th>Date</th>
<th>Survey time (h)</th>
<th>Coverage</th>
<th>Estimated population</th>
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<tbody>
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<td>3.25 FL Bay &amp; lower keys</td>
<td>56 155</td>
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<td>Sprunt</td>
<td>Oct. 1935</td>
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<td>20 126</td>
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</tr>
<tr>
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<tr>
<td>Robertson</td>
<td>Oct.–Nov. 1959</td>
<td>NA FL Bay</td>
<td>1172</td>
</tr>
<tr>
<td>Robertson</td>
<td>Jan.–Feb. 1960</td>
<td>NA FL Bay</td>
<td>1361</td>
</tr>
<tr>
<td>Robertson</td>
<td>May 1960</td>
<td>NA FL Bay</td>
<td>898</td>
</tr>
<tr>
<td>Robertson</td>
<td>Sept.–Oct. 1960</td>
<td>NA FL Bay</td>
<td>546</td>
</tr>
<tr>
<td>Robertson</td>
<td>Aug. 1962</td>
<td>22 FL Bay</td>
<td>818</td>
</tr>
<tr>
<td>Robertson</td>
<td>Sept. 1963</td>
<td>NA FL Bay</td>
<td>844</td>
</tr>
<tr>
<td>Robertson</td>
<td>Feb.–Mar. 1965</td>
<td>NA FL Bay</td>
<td>1382</td>
</tr>
<tr>
<td>Robertson</td>
<td>Nov. 1965</td>
<td>15 FL Bay</td>
<td>1430</td>
</tr>
<tr>
<td>Robertson</td>
<td>Apr. 1967</td>
<td>NA FL Bay</td>
<td>903</td>
</tr>
<tr>
<td>Ogden</td>
<td>July 1967</td>
<td>NA FL Bay</td>
<td>914</td>
</tr>
<tr>
<td>Ogden</td>
<td>Apr. 1968</td>
<td>NA FL Bay</td>
<td>897</td>
</tr>
<tr>
<td>Robertson</td>
<td>Jan.–Feb. 1984</td>
<td>NA FL Bay</td>
<td>1508</td>
</tr>
</tbody>
</table>

* NA = not available.
## Appendix II

### Total Number of Roseate Spoonbill Colonies and Nests per Year

<table>
<thead>
<tr>
<th>Year</th>
<th>Total colonies</th>
<th>Total nests</th>
<th>Total nests*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1935-36</td>
<td>1</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>1936-37</td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>1937-38</td>
<td>1</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>1938-39</td>
<td>1</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>1939-40</td>
<td>2</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>1948-49</td>
<td>10</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>1950-51</td>
<td>7</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>1951-52</td>
<td>8</td>
<td>80</td>
<td>81</td>
</tr>
<tr>
<td>1952-53</td>
<td>5</td>
<td>66</td>
<td>60</td>
</tr>
<tr>
<td>1953-54</td>
<td>3</td>
<td>81</td>
<td>101</td>
</tr>
<tr>
<td>1954-55</td>
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<td>174</td>
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</tr>
<tr>
<td>1955-56</td>
<td>8</td>
<td>214</td>
<td></td>
</tr>
<tr>
<td>1956-57</td>
<td>6</td>
<td>183</td>
<td>148</td>
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<tr>
<td>1957-58</td>
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<td>92</td>
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</tr>
<tr>
<td>1958-59</td>
<td>6</td>
<td>145</td>
<td>110</td>
</tr>
<tr>
<td>1959-60</td>
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<td>119</td>
<td>117</td>
</tr>
<tr>
<td>1960-61</td>
<td>5</td>
<td>125</td>
<td></td>
</tr>
<tr>
<td>1961-62</td>
<td>4</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td>1962-63</td>
<td>9</td>
<td>266</td>
<td></td>
</tr>
<tr>
<td>1966-67</td>
<td>8</td>
<td>368</td>
<td></td>
</tr>
<tr>
<td>1968-69</td>
<td>6</td>
<td>272</td>
<td></td>
</tr>
<tr>
<td>1969-70</td>
<td>7</td>
<td>255</td>
<td></td>
</tr>
<tr>
<td>1975-76</td>
<td>11</td>
<td>802</td>
<td></td>
</tr>
<tr>
<td>1977-78</td>
<td>16</td>
<td>619</td>
<td></td>
</tr>
<tr>
<td>1978-79</td>
<td>18</td>
<td>1254</td>
<td></td>
</tr>
<tr>
<td>1984-85</td>
<td>13</td>
<td>448</td>
<td></td>
</tr>
<tr>
<td>1985-86</td>
<td>14</td>
<td>590</td>
<td></td>
</tr>
<tr>
<td>1986-87</td>
<td>16</td>
<td>527</td>
<td></td>
</tr>
<tr>
<td>1987-88</td>
<td>16</td>
<td>493</td>
<td></td>
</tr>
</tbody>
</table>

* Number of total nests from a different reference.
** Reference number in this position applies to all counts for this year.
*** Individual counts not available for all colonies for this year.
A = Colony active with a small number of nests. No count made.
? = Status unknown.
2 Ground counts.
4 Flight line counts of adults at nesting islands.
5 Aerial counts, W. B. Robertson, Jr., ENP, Homestead, Florida.
6 Ground counts, R. P. Allen field notes, NAS Research Department.
7 Ground counts. Rangers Log, ENP.
10 Ground counts, W. B. Robertson, Jr. Bird Observation Cards, ENP.
11 Ground counts, J. C. Ogden field notes, ENP.
12 Aerial survey, J. C. Ogden flight notes, ENP.
13 Number of nests estimated by ground counts of young. 2, J. C. Ogden field notes, ENP.
15 Aerial survey, W. B. Robertson flight notes, ENP.
17 Ground counts, ENP 1979 Annual Report.
18 Ground counts, George Powell field notes, NAS Research Dept.
19 Ground counts, Robin Bjork field notes, NAS Research Dept.
THE WILSON BULLETIN

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## Appendix IV

**Number of Roseate Spoonbill Nests in Northeast, Southeast, and West Florida Bay by Colony and Year**

<table>
<thead>
<tr>
<th>Year</th>
<th>Northeast</th>
<th>Southeast</th>
<th>West</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tern</td>
<td>South Tern</td>
<td>Projo</td>
</tr>
<tr>
<td>1935–36</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1936–37</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1937–38</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1938–39</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1939–40</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1950–51</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>1951–52</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>1952–53</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>1953–54</td>
<td>0</td>
<td>23(^a)</td>
<td>0</td>
</tr>
<tr>
<td>1954–55</td>
<td>0</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>1955–56</td>
<td>0</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td>1956–57</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>1958–59</td>
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<td>20</td>
<td>0</td>
</tr>
<tr>
<td>1959–60</td>
<td>0</td>
<td>24</td>
<td>0</td>
</tr>
<tr>
<td>1960–61</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>1961–62</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1962–63</td>
<td>50(^b)</td>
<td>0(^c)</td>
<td>0</td>
</tr>
<tr>
<td>1966–67</td>
<td>181(^e)</td>
<td>?</td>
<td>0</td>
</tr>
<tr>
<td>1968–69</td>
<td>175(^f)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1969–70</td>
<td>150(^h)</td>
<td>A(^j)</td>
<td>A(^j)</td>
</tr>
<tr>
<td>1975–76</td>
<td>495</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>1977–78</td>
<td>272</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>1978–79</td>
<td>591</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>1984–85</td>
<td>170</td>
<td>0</td>
<td>?</td>
</tr>
<tr>
<td>1985–86</td>
<td>184</td>
<td>0</td>
<td>?</td>
</tr>
<tr>
<td>1986–87</td>
<td>158</td>
<td>0</td>
<td>21</td>
</tr>
<tr>
<td>1987–88</td>
<td>110</td>
<td>0</td>
<td>21</td>
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For meaning of superscripts, see Appendix II.
SHORT COMMUNICATIONS

Low return rates of migratory Loggerhead Shrikes: winter mortality or low site fidelity?—From 1985 through 1988, only 14% of adult Loggerhead Shrikes (Lanius ludovicianus) banded during the 1984–1987 breeding seasons were resighted in North Dakota (10 returns out of 69 birds; CAH, unpubl. data), a figure which is much lower than return rates usually reported for site-faithful migratory birds (e.g., American Robin [Turdus migratorius] 46% and Brown Thrashers [Toxostoma rufum] 31%, CAH, unpubl. data; Gray Catbird [Dumetella carolinensis] 47%, Darley et al. 1977; Savannah Sparrow [Passerculus sandwichensis] 48%, Bedard and LaPointe 1984; Eastern Kingbird [Tyrannus tyrannus] 43%, Blancher and Robertson 1985; Bobolink [Dolichonyx oryzivorus] 34%, Gavin and Bollinger 1988). Because several authors have reported the Loggerhead Shrike to be site-faithful (Atkinson 1901, Bent 1950, Porter et al. 1975, Kridelbaugh 1983), the low return rates documented by CAH suggest a high winter mortality in the North Dakota population of shrikes. An alternative explanation is that shrikes exhibit low site fidelity. Indeed, our observations of nest reuse, mate desertion, and mate switching in two populations of shrikes suggest that high site fidelity should not be assumed. As part of a study on the relationship between reproductive success and breeding site fidelity in migratory passerines, CAH has observed a population of individually marked Loggerhead Shrikes since May 1984. The study area consists of a number of isolated shelterbelts and wooded creeks located in Sioux County, North Dakota. SAS studied winter territoriality of and territory use by non-migratory individuals from 1976 to 1981. The study site included several old fields in Alachua County near Gainesville, Florida. In the latter population male and female shrikes maintained separate and adjacent territories during the non-breeding season, but coalesced and defended a single breeding territory.

Most of the evidence for site fidelity in the Loggerhead Shrike comes from observations of the reuse of nests or nest sites by unmarked birds (Atkinson 1901, Miller 1931, Bent 1950, Porter et al. 1975). Observers assumed that if a nest was occupied in two consecutive years the original owners had returned. The tenuous nature of this assumption is illustrated by two kinds of nest reuse. First, shrikes may reuse nests of other shrikes. In North Dakota, for example, a banded female shrike with an unbanded mate was observed relining and later nesting in a nest that had been built and occupied by a different banded pair of shrikes the previous year. Second, shrikes have been observed re-using the nests of other species, including those of Black-billed Magpies (Pica pica) (Porter et al. 1975), Brown Thrashers (Bent 1950, CAH, pers obs.), Common Grackles (Quiscalus quiscula) (Patton 1884, CAH, pers. obs.), a Northern Mockingbird (Mimus polyglottos) and a Gray Catbird (Bent 1950). This lack of discrimination by shrikes in nest re-use, both within and among species, indicates that observations of shrikes nesting on old nests are not proof of site fidelity (e.g., Miller 1931).

We suggest that desertion and mate switching by female shrikes may be important contributors to low return rates at a particular site. Our observations suggest that female shrikes are not faithful to a territory within a breeding season and thus probably do not exhibit substantial site fidelity between breeding seasons. In North Dakota, one female was found nesting approximately 2 km from her nest site of the previous year. Low breeding site fidelity of females could account for the extreme bias toward males in return rates and, perhaps, the low overall return rate compared to other migratory passerines when data for both sexes are combined. For example, Kridelbaugh (1983) found that, although 47% (7/15) of males banded in central Missouri returned to the general area, no females (0/15) did. The overall return rate, 23% (7/30), is similar to that in North Dakota. CAH also found a male bias in
return rate, with 28% (8/29) of banded males but only 5% (2/38) of banded females returning to the study area. Although many studies report a male bias in site fidelity, this five-fold difference between the sexes is unusual (summarized in Greenwood 1980). In Florida both males and females tended to remain on the study area because birds held territories year-round.

Females may wander during mid-season to locate unpaired males. In both the North Dakota and the Florida populations, we observed females that deserted their first mate for a new mate during the breeding season. In North Dakota, a marked female shrike successfully fledged young in June and moved approximately 0.5 km to renest with a new male while her previous mate continued to tend the first brood. The female’s second set of young fledged in early August. At least two instances of mate switching occurred during the breeding season in Florida. In the first case, a banded female left her original mate after the eggs had hatched. She immediately laid eggs with an adjacent male that already had a completed nest available on his territory. The female’s first mate gradually had stopped singing and the neighboring male had begun to court the female before she deserted. The nestlings from the first nest died, presumably from starvation. In the second case, the male successfully raised two nestlings to fledging after the female disappeared. The female was later found feeding fledglings on the territory of a neighboring male.

Our observations suggest that there is a need to re-evaluate reported site fidelity in populations of the Loggerhead Shrike. This is especially important since the Loggerhead Shrike has experienced a marked decline throughout North America; it is declining rapidly in the midwest and no longer breeds in New England (Geissler and Noon 1981, Robbins et al. 1986). In evaluating causes of the decline, low return rates cannot be taken as evidence of high winter mortality. Realistic evaluation of trends in population size are of paramount importance if we are to understand and perhaps rectify this alarming decline.

Acknowledgments.—North Dakota observations were supported in part by a Herbert and Betty Carnes Research Award (AOU), a Paul A. Stewart Award (WOS), an E. Alexander Bergstrom Award (AFO), a Walter E. Benning Award (Cornell Laboratory of Ornithology), a Kathleen S. Anderson Award (MBO), grants from the National and Cornell chapters of Sigma Xi, the Andrew W. Mellon Student Research Fund, the Graduate School of Cornell University, the George D. Harris Foundation, and CAH’s National Science Foundation Graduate Fellowship and Doctoral Dissertation Improvement Grant. CAH thanks all of her field assistants, particularly Katherine Haas, for their invaluable help, and Eric Bollinger, Tom Cade, Mike Pol, and Russell Titus for comments on earlier drafts of this manuscript. SAS thanks the University of Florida Department of Zoology for financial support and A. M. Barton for comments on this manuscript. Special thanks go to J. H. Kaufmann for advice and encouragement and to K. Mueller and M. Kinnaird for help in the field. We both appreciate K. L. Bildstein’s and Jeffrey Walters’ thoughtful comments on the manuscript.

LITERATURE CITED


Female Hooded Warbler plumage does not become more male-like with age.—Dwight (1900:284–285) provided two hypotheses to explain the variable amount of black plumage in female Hooded Warblers (Wilsonia citrina): “The adult winter plumage . . . shows a variable amount of black about the head and throat. How much of the black is due to individual vigor and how much to successive postnuptial moults is a question not easily answerable. We know that some females in the breeding season are almost indistinguishable from males, and there are all sorts of intermediates from these mature birds down to those of the worn first winter dress, which are guiltless of black.”

Dwight’s description of the variable black coloration in adult female Hooded Warblers was apt, although we are not likely to accept his suggestion that female “vigor” is defined by comparison with the male plumage color. However, his suggestion that females might attain more melanism with each molt is often repeated. Chapman (1917:270) also suggests that the development of the “hood” in the female is dependent upon age.

Lynch et al. (1985) classified female plumages into 6 classes ranging from no black (class 0) to male-like in hood development (class 5). Class 5 females were rare, constituting about 1–6% of eighty museum skins examined, a figure reasonably representative of the proportion of this female plumage class in their field observations of wintering birds in Mexico. They suggested that this rarity of melanistic females would be predicted if females increase in melanism as they become older, and supports the hypothesis that female plumage melanism is age-related.

I tested the hypothesis that female Hooded Warblers become more melanistic with age.
by maintaining five females in captivity for from one to five years. Four of the captive females were killed accidentally in June of their second calendar year of life, and before molting. The surviving captive female underwent the second prebasic molt, when the adult plumage is attained. This individual was photographed after each prebasic molt for the next three years. In addition, four wild females in adult plumage were recaptured after one to two years and their degree of melanism sketched in the field. The field observations were made in northwestern Pennsylvania, which was also the origin of the captive birds.

These observations showed that the degree of melanism does not increase with age in female Hooded Warblers. The five hand-raised females, after completing the first prebasic molt, were either devoid of black feathers (4) or had four black feathers scattered inconspicuously in the superciliary region (1). This conforms to the description for females in their first winter (Lynch et al. 1985). However, the surviving hand-raised female attained a class 2 plumage score which was then retained for the life of the bird (Fig. 1).

The recaptured wild females also showed no change with age. One remained class 4 when captured for two subsequent years. One class 3 had a slight outline of black on her throat when first captured. In two subsequent years, she retained this black outline but became neither more nor less melanistic. Two females captured in class 2 plumage had not changed upon recapture in one more year of life.

I conclude that these observations provide no support for the often cited hypothesis that melanism increases with age after the first prebasic molt in Hooded Warbler females. Instead,
the adult plumage is likely retained unchanged for the life of the individual. The biological significance of this highly variable adult female plumage is unknown but may be unique among passerines. The possibility exists that highly melanistic females select more male-like habitat in the nonbreeding season (habitats described in Lynch et al. 1985). In this case, the melanism might function as a threat and be displayed in aggressive situations, as is the case with males (Rappole and Warner 1980). However, more recent studies of territorial female Hooded Warblers in Mexico indicate that males and females prefer different habitat in the nonbreeding season and do not compete with each other for territories. Moreover, females exhibiting all plumage classes were seen in the same habitat (Morton et al. 1987). Furthermore, we found no evidence that subadult female plumage or degree of melanism exhibited by individual adult females was related to winter territory habitat quality, although this possibility needs further testing. The existence of both a distinctive subadult female plumage, a rarity among passerine birds (Stutchbury and Robertson 1987), and a highly variable adult female plumage, suggests that more study of the Hooded Warbler is warranted throughout its annual cycle.

Acknowledgments.—This study was supported by Smithsonian Scholarly Studies Grant 1235S501. I thank R. Greenberg, J. F. Lynch, and K. Young, for comments and assistance in the field or in handraising young warblers, and to Mr. and Mrs. E. L. Morton for providing support in Pennsylvania. J. Anderton produced the figure from photographs taken by J. Cohen and P. Vosburgh of the captive female.

LITERATURE CITED


The impact of male parental care on female Eastern Kingbird reproductive success.—Male parental care generally is assumed to improve survival of nestlings and increase female reproductive success (fitness). Consequently, the need for male assistance is considered by some to be responsible for the evolution of monogamy when the investment of the male is
not shareable among mates (Wittenberger and Tilson 1980). However, Gowaty (1983) found
that reproductive success was not different between lone and paired female Eastern Bluebirds
(Sialia sialis) and argued that monogamy is not necessarily maintained only by the need
for male care. Bart and Tones (1989) cite several examples of male-removal studies that
indicate the presence of a male is of little value in many species, but they conclude that
apparent care by the male does tend to benefit the young.

In this study we attempted to determine the impact of male parental care on female
reproductive success in the monogamous Eastern Kingbird (Tyrannus tyrannus). Male East-
ern Kingbirds help to feed, guard, and defend their young throughout the breeding cycle.
Males also aid in the 3- to 4-week period of post-fledging care (Morehouse and Brewer
1968).

Methods.—This study was conducted at Eastern Kingbird nests on and around Lake
Opinicon, Ontario, from May to August 1986. The study site is described in detail by
Blancher and Robertson (1985). Five resident males were removed experimentally by shoot-
ing when the nestlings were one day old. Shooting (Canadian Wildlife Service Permit #EK290)
was necessary because we did not know of any way to keep these aerial insectivores alive
in captivity for the necessary time period. For this reason a very small sample size was used.
Seven nests that corresponded in nesting time and habitat to the experimental nests were
chosen at the time of the removals and were used as unmanipulated controls. We measured
feeding rates per nestling by watching nests for 60 min intervals every other day during the
nestling period. These observations were carried out at approximately the same time each
day. Nestlings were watched from a distance of approximately 30 m to avoid disturbing the
birds. Following each watch, nestlings were weighed with a Pesola spring balance, and each
nestling's 9th primary was measured to the nearest mm. We also quantified nest defense at
each nest four times during the nesting cycle (incubation days 1–6, 7–14; and nestling days
1–4, 5–8) by scoring the aggressiveness of the birds during a 5-min trial to a simulated
predator (plastic crow) placed approximately 1 m from the nest. Responses were scored on
a scale of 0 to 5 (0—no response; 1—silent observation; 2—vocalization and hovering; 3—
few single dives; 4—continuous diving; 5—striking the crow). Repeat testings on nests were
conducted to minimize the time between presentations in an effort to avoid
habituation. Males and females were distinguished by their behavior (for example, favorite
perch locations) and by noting which bird was at the nest. In nesting pairs, one of the birds
is almost always guarding the nest, resulting presumably in fewer losses to predators. Smith
(1966) noted this trade-off pattern, and found that the male was present 82% of the time
when the female left the nest and 91% of the time when she returned. Predation was assumed
if the entire brood disappeared at one time with no evidence of poor weather or dead
nestlings.

Results.—Following removal of resident males, potential replacement males were seen at
all five experimental nests. In two cases, the resident female was aggressive and the intruders
did not persist. In two other cases, the intruders likely were neighboring males which
occasionally were accompanied by a third bird, presumably a mate. In the fifth case, a
replacement male arrived on the day of the removal and persisted until the nestlings fledged.
This male defended the territory but was indifferent toward the nestlings (failure to feed
and/or harass). Broods at all five experimental nests were raised by the female alone, since
the only persistent male did not feed the nestling.

There was no significant difference between the clutch sizes of unassisted ($\bar{x}_1 = 3.4 \pm 0.49$
[SD]) and assisted groups ($\bar{x}_2 = 3.5 \pm 0.50$; Mann-Whitney U-test, $N_1 = 5$ $N_2 = 7$, $U =
14.5$, $P > 0.30$). The brood size at hatching also indicated no significant difference between
the unassisted ($\bar{x}_1 = 2.60 \pm 0.49$) and assisted groups ($\bar{x}_2 = 2.85 \pm 0.64$; Mann-Whitney
U-test, $N_1 = 5$ $N_2 = 7$, $U = 14$, $P > 0.30$) (Conover 1980).
A significant difference did exist between the survival of the nestlings in broods raised by unassisted females and those having biparental care. None of the five unassisted females managed to fledge her entire brood, however, in 57% (4/7) of the broods attended by two parents, all nestlings survived to fledge (G-test, $G_{adj} = 4.96$, $P < 0.03$).

The entire brood was lost to predators in 60% (3/5) of the nests attended by unassisted females, but only 29% (2/7) of the nests of assisted females were depredated (G-test, $G_{adj} = 1.05$, $P > 0.30$). Unassisted females also suffered greater partial brood loss than did assisted females. Of the seven nestlings that escaped predation in nests of unassisted females, four died (57.1%), apparently due to starvation (based on mass, size, and appearance of the nestlings). However, only 7.7% (1/13) of the nestlings that escaped predation in nests of assisted females died prior to fledging (G-test, $G_{adj} = 5.24$, $P < 0.02$). As a result of both predation and partial brood loss, only 23% (3/13) of the nestlings which hatched in unassisted females’ nests eventually fledged, whereas 60% (12/20) of the nestlings that hatched in the nests of assisted females survived to fledge successfully (G-test, $G_{adj} = 2.04$, $P > 0.10$).

Although there were differences in survivorship between nestlings in assisted and unassisted nests, there was no significant difference in either mean nestling weight or mean 9th primary length between the two groups (Table 1). The growth of the surviving nestlings was apparently kept at a normal level by unassisted females through partial brood loss. That growth was normal in surviving young in both groups is indicated by the same ages at fledging for nestlings in assisted and unassisted nests (17 days).

A repeated measures analysis of variance was used to determine whether feeding rate (deliveries/nestling/hour) was affected by the presence or absence of a male care-giver (treatment) and/or the age of the nestlings (stage). It was found that unassisted females fed at a higher rate ($\bar{x} = 1.25 \pm 0.37$) than did assisted females ($\bar{x} = 0.99 \pm 0.26$; $F_{1,57} = 5.49$, $P < 0.03$), indicating an attempt to compensate for the loss of a mate. Neither stage ($F_{2,55} = 1.09$, $P > 0.30$) nor the interaction treatment × stage ($F_{2,55} = 0.56$, $P > 0.55$) significantly affected feeding rate. The latter does not, however, correspond with Morehouse and Brewer (1968) and Murphy (1983) who found feeding rates to be affected by stage.

There was no significant difference between the feeding rates of the unassisted female and the combined feeding rates of the control males and females ($F_{1,57} = 0.06$, $P > 0.80$). Unassisted females thus achieved the same feeding rates per nestling per hour as the control pairs; however, this was possible only because of both partial brood loss and an apparent reduction of time spent brooding and nest guarding. It is also possible that they increased their rates by substituting quantity for quality of prey type, since the food quality of the females was not determined. Replications of the ANOVA tests using ranked data indicate that our results were valid and not artifacts of non-normal distributions (Conover 1980).

Prior to removing the males, nest defense aggression scores for unassisted and assisted females were similar (unassisted: $\bar{x}_1 = 1.33 \pm 0.94$; assisted: $\bar{x}_2 = 1.43 \pm 0.78$; Mann-Whitney U-test, $N_1 = 3$ $N_2 = 7$, $U = 8$, $P > 0.30$), and although not significant, the males tended to vocalize, hover near the nest, and dive and strike at the simulated predator more often and more aggressively ($\bar{x}_1 = 2.00 \pm 1.41$) than did the females ($\bar{x}_2 = 1.43 \pm 0.78$; Mann-Whitney U-test, $N_1 = 7$ $N_2 = 8$, $U = 17$, $P > 0.10$). Once their mates were removed, a change was noted in the unassisted females; they became significantly more likely to dive at and strike the crow ($\bar{x}_1 = 4.25 \pm 0.75$) than their paired female counterparts who seldom struck the model ($\bar{x}_2 = 2.67 \pm 1.67$; Mann-Whitney U-test, $N_1 = 3$ $N_2 = 7$, $U = 0$, $P < 0.01$). Unassisted females thus increased their aggressiveness toward the predator once they lost their mates. In general, the unassisted females seemed to take on a behavioral role midway between that of the control males and females. They chased away predators and guarded the nest more aggressively than the control females did, but they appeared unable to reach the level of defense achieved by the control pair combined.
Table 1
MEAN NESTLING WEIGHT AND MEAN 9TH PRIMARY LENGTH ON DAY 11 (LAST DAY OF MEASUREMENTS PRIOR TO FLEDGING) FOR UNASSISTED AND ASSISTED FEMALES

<table>
<thead>
<tr>
<th></th>
<th>Assisted females</th>
<th>Unassisted females</th>
<th>t*</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of nestlings</td>
<td>12</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean nestling mass (g)</td>
<td>34.46 ± 2.96</td>
<td>32.67 ± 0.85</td>
<td>1.04</td>
<td>&gt;0.10 ns^b</td>
</tr>
<tr>
<td>Mean 9th primary length (mm)</td>
<td>26.08 ± 2.25</td>
<td>23.33 ± 1.25</td>
<td>2.04</td>
<td>&gt;0.05 ns</td>
</tr>
</tbody>
</table>

^a t = Student’s t-test.
^b ns = not significant.

Discussion. — In kingbirds it appears that although some females can successfully fledge some young on their own, nesting success is reduced in the absence of male parental care. Although not essential, male help plays a very important role in raising young. Decreased survival rate of nestlings of unassisted females was caused both by increased predation and increased single nestling deaths. Increased predation is likely a result of decreased time spent on nest guarding and defense, since a parent was no longer almost constantly at the nest. Blancher and Robertson (1982) found that kingbirds are capable of successfully deterring predation by their aggressive behavior.

The increase in the number of single nestling deaths in nests of unassisted females appeared to occur due to starvation and/or increased exposure to adverse weather conditions. This increase in the death rate indicates that males play an important role in feeding nestlings and allowing the female to brood the young. This care is probably most important in years of poor weather. Beissinger (1986) found a decrease in nesting success during bad weather in Snail Kites (Rostrhamus sociabilis) and proposed that postfledging success declined in drought years concluding that during favorable weather one bird could successfully raise the brood. Bart and Torres (1989) also found that parental care by male House Wrens (Troglydotes aedon) benefited the nestlings only in unfavorable periods.

Environmental conditions may also affect parental responses such as the allocation of male reproductive effort. For example, increased polygyny could result if weather conditions are favorable (Beissinger 1986). This could be a partial explanation for the apparent attempts of the two neighboring males to acquire an additional mate, and their subsequent failure to do so. That is, the weather in the spring and summer of 1986 was wetter and cooler than normal: June 1986, average temperature = 15.6°C (normal = 16.7), total precipitation = 131.6 mm (normal = 64 mm); July 1986, average temperature = 19.6°C (normal = 20.1), total precipitation = 74.6 mm (normal = 53.2 mm) (Environment Canada Climate Service, pers. comm.).

Murphy (1983) found that unpredictable changes in temperature and precipitation dramatically affect the ability of adult Eastern Kingbirds to feed young. The main diet of flying insects decreases in cool and wet weather. He found that most nestlings that died of starvation did so during cold, rainy periods. It follows that the impact of weather could have important implications for the present study since the summer of 1986 was cooler and wetter than normal. If data collection had been during favorable feeding conditions, female reproductive success might have been greater, possibly indicating that male parental care is necessary only during unfavorable conditions.

Although some nestlings raised by unassisted females survived to fledge, whether or not they survived the 3- to 4-week period of post-fledging care is not known. It is possible that
they did not survive this period, since Morehouse and Brewer (1968) report that this is the time of maximum parental care and energy requirements of the young.

The unassisted females’ attempts to compensate for the loss of their mates resulted in their increasing the number of feeding trips over the breeding cycle, and increasing aggressiveness in nest defense. The experimental nest with the largest nestlings best demonstrates the need for male help. Here, the replacement male was indifferent to the nest, but did help the female defend the territory. The time required for nest defense by the female probably was reduced, allowing her to brood and feed the nestlings more successfully. These nestlings were slightly larger on Day 5 (chosen since there were still a total of 9 nestlings alive) than were those of experimental nests without a defending male (however, the difference was not statistically significant).

Our results are consistent with aspects of other studies of the significance of male parental care to female reproductive success. Hannon (1984) reported an increase in predation with the loss of male Willow Ptarmigan (Lagopus lagopus), indicating that male vigilance in other species also plays an important role in nest defense. Lyon et al. (1987) found widowed female Snow Buntings (Plectrophenax nivalis) increased their feeding rates in an attempt to make up for the loss of their mates. Despite this compensation by the females, they suffered reduced reproductive success compared with assisted females. Similarly, Leffelaar and Robertson (1986) found that female Tree Swallows (Tachycineta bicolor) could compensate for a mate’s absence for a short period of time, but lone females were less successful in rearing young than paired females.

In addition to the possible necessity of male parental care (Wittenberger and Tilson 1980), Freed (1987) proposed that males may be constrained to monogamy for various reasons. For Eastern Kingbirds these constraints could include a limited number of females, female aggression, short breeding season, and variable weather conditions. Whether the evolution of monogamy in this and other species has resulted from advantages or constraints will require further study.

Bart and Tornes (1989) review a number of male-removal studies and conclude that for species in which the male appears to be helping, survival of the young, and hence female reproductive success, is reduced in his absence. In Eastern Kingbirds, males appear to play an important role in nest defense and in provisioning the young. Our results indicate that this contribution by the male plays a significant role, at least in some years, in determining the reproductive success of the female.

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LITERATURE CITED


Nesting ecology of Mourning Doves in a cold desert ecosystem.—Mourning Doves (*Zenaida macroura*) are distributed widely across the shrub deserts and grasslands of the western United States (McClure 1950), even where there are few or no trees. Doves are adaptable nesters, and a number of studies have dealt with, or mentioned, ground nesting by Mourning Doves (Cowen 1952, Hon 1956, Downing 1959). Fichter (1959) studied Mourning Dove production in four Idaho orchards, and Dahlgren (1955) studied tree-nesting doves in the intermountain region of Utah. However, there have been no published studies relating specifically to ground-nesting Mourning Doves in intermountain shrub deserts. Herein, we provide estimates of Mourning Dove nesting success and identify the vegetative cover variables associated with nest-site selection in ground nesting Mourning Doves in such an ecosystem.

Study area and methods.—Nesting Mourning Doves were studied on the Idaho National Engineering Laboratory (INEL) from 1983 to 1985. The INEL is located 80 km west of Idaho Falls on the upper Snake River Plain in southeastern Idaho and is administered by the U.S. Department of Energy. It encompasses about 231,600 ha at the northern extent of the Great Basin desert and receives 18–20 cm of precipitation annually (Anderson et al. 1978). The major vegetation types of the INEL were reported by McBride et al. (1978). Dominant shrubs on the INEL include big sagebrush (*Artemisia tridentata*) and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*); common grasses include squirrel tail (*Sitanion hystrix*), Indian ricegrass (*Oryzopsis hymenoides*), needle-and-thread grass (*Stipa comata*), and wheatgrasses (*Agropyron spp.*). Common forbs on the INEL include prickly pear cactus...
(Opuntia polyacantha), Hood’s phlox (Phlox hoodii), longleaf phlox (P. longifolia), and milkvetches (Astragalus spp.).

Nests were found by locating radio-tagged (Howe and Flake 1988) doves on their nests, by chance flushes by ourselves or other personnel, and by systematically searching 4-ha plots. Plots were located at random within the major plant communities on the INEL (McBride et al. 1978), with 15 plots searched twice (mid-June and late July) in 1983 and once (late July) in 1984. Plots were searched by pulling a rope drag between two or three persons on foot. The rope drag was 7.5 m long with 1 m long weighted trailers fixed at 30-cm intervals. Even though Mourning Doves flushed readily from nests during rope dragging, extremely low densities of nests and the need to reduce manpower costs led to our dropping this technique in 1985.

Ages of nestlings were estimated from their appearance and size. Ages of eggs were determined by candling (Hanson and Kossack 1957, Muller et al. 1984). Apparent nesting success (Klett et al. 1986) overestimates nesting success but was calculated for comparison with earlier studies. Daily survival of nests was determined from the period the clutch/brood was exposed to risk and under our observation; these rates were used to estimate actual nesting success (Mayfield 1975, Miller and Johnson 1978). Nests were visited within one or two days after predicted hatch and on day 12 of fledging. We visited the nests at these infrequent intervals to reduce the risk of human-induced abandonment (Swank 1952) or other human-induced impacts on nesting success (Westmoreland and Best 1985). The ages of trapped or collected hatching year (HY) doves were estimated by primary molt progression (Swank 1955) to provide an estimate of the length of the nesting season and of peak nesting activity. On our study area, HY doves had not completed primary replacement through P7 prior to early September and could be separated from adult birds based on the characteristics of the remaining primaries (Haas and Amend 1979, Cannell 1984). HY Mourning Dove wings (N = 33) were obtained from the few hunters that conservation officers (Idaho Fish and Game Department) observed within 65 km of the INEL in early September. HY doves were live-trapped (N = 61) throughout the summer at the Test Reactor Area, Naval Research Facilities, and Auxiliary Reactors Area ponds on the INEL; 30 doves were also collected by shotgun at the Test Reactor Area and Argonne National Laboratory ponds in July and September for use in this study and for a separate food habits analysis.

Random sites were chosen within 50 m of each nest site for paired comparisons of all nest cover measurements. Horizontal nesting cover was measured with a point-frame (Floyd and Anderson 1987) in the 1 m² (microhabitat) centered on dove nests and at random sites. Percent cover was recorded by plant species and by cover type, i.e., shrub, grass, forb, and bare ground. The line-intercept method (Stoddart et al. 1975) was used to determine the major vegetation components and general cover composition within 5 m of each nest site and at random sites. Coverage (cm) was recorded for shrubs, grasses, forbs, and bare ground found along a 5-m transect in each cardinal direction; dominant plant species along the line-intercept also were recorded.

Visual obstruction of the nest site by vegetation was measured with a 30-cm wide vegetation profile board (Nudds 1977) divided into 0.5-m intervals. Obstruction of the board by vegetation (0%, 1–20%, 21–40%, 41–60%, 61–80%, and 81–100%) in the first meter above nest and random sites was estimated from 5, 10, 15, 20, and 25 m in the cardinal directions and one non-overlapping random direction. Visual obstruction above 1 m was negligible on the INEL. Analysis of variance was used to test for differences between nest sites and random sites for both point-frame and line-intercept data. Visual obstruction data were subjected to chi-square analysis to identify differences between nest and random sites.

Results.—Dove nests in the cold desert were dispersed widely and difficult to find. Density of nests during the two searches of 4-ha plots in 1983 and one search in 1984 averaged only
0.02 nest/ha. During three years of study 28 nests were found, but four of these apparently were abandoned due to our initial disturbance and were dropped from estimates of nesting success. Of 28 nests, three were located by systematic search of plots, 11 by radiotelemetry, and 14 by chance flushes. All nests were on the ground. Of the 24 nests, 18 (75%) fledged young; only one of 10 clutches found during laying or incubation was destroyed before hatching. Even with four abandoned nests included, 63% (apparent success) of the clutches produced fledged young. Yearly successful nest/total nests and fledglings/successful nest were: 1983 (5/6, 1.8), 1984 (7/10, 2.0), and 1985 (6/8, 1.7). In our estimates, we classified 12-day-old young as fledglings to avoid forced fledging of young on days 13 and 14 when they more readily abandoned the nest site. Actual survival (Mayfield 1975, Miller and Johnson 1978) from the beginning of incubation to fledging (26 days) for the 24 nests was 0.50 (daily rate = 0.974). Nine nests found during laying or incubation had a survival rate to hatching of 0.82 (daily rate = 0.986). Nests reaching the hatching stage and nests found during the nestling stage had a survival rate to fledging of 0.68 (N = 23, daily rate = 0.968). The difference in survival rates between incubation and nesting stages indicates the assumption of constant survival was not met in estimating overall survival from the beginning of incubation to fledging. When a nest was found destroyed, we assumed the loss occurred half way between the date found and the date last checked in calculating daily survival rates, as suggested by Mayfield (1975). All nests were active when initially found.

Data from collected wings (N = 63) and live-trapped juveniles (N = 61) indicated that peak hatching occurred the fourth week of June, the third week of July, and the first and second weeks of August (Fig. 1). Wings collected in late July or early August and live-trapped juveniles taken prior to August bias the August peak downward; nevertheless, the third peak in hatching is still clear. Other possible biases include those due to possible early departure of older HY doves and potential ingress of HY doves to the study area. Data from collected wings indicated that the nesting season on INEL began around mid-May and ended in early September.

Analysis of variance revealed differences in the percentage of bare ground (P = 0.02) and grass cover (P = 0.02) between nest and random site microhabitats (1 m²). Nest sites
Table 1

Average Vegetation Coverage (±SE), by Cover Type, at Mourning Dove Nest Sites and Paired Random Sites on the Idaho National Engineering Laboratory

<table>
<thead>
<tr>
<th>Microhabitata</th>
<th>N</th>
<th>Shrub</th>
<th>Bare</th>
<th>Grass</th>
<th>Forb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest</td>
<td>28</td>
<td>44.0 (3.32)</td>
<td>43.9 (2.82)c</td>
<td>10.0 (1.39)c</td>
<td>6.6 (1.38)</td>
</tr>
<tr>
<td>Random</td>
<td>26</td>
<td>37.8 (3.44)</td>
<td>53.9 (2.93)</td>
<td>5.4 (1.44)</td>
<td>5.0 (1.43)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>5-m areab</th>
<th>N</th>
<th>Shrub</th>
<th>Bare</th>
<th>Grass</th>
<th>Forb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest</td>
<td>28</td>
<td>30.5 (1.70)</td>
<td>57.4 (1.71)</td>
<td>7.6 (1.00)</td>
<td>4.6 (0.60)</td>
</tr>
<tr>
<td>Random</td>
<td>26</td>
<td>29.5 (1.70)</td>
<td>57.5 (1.71)</td>
<td>8.6 (1.00)</td>
<td>4.4 (0.60)</td>
</tr>
</tbody>
</table>

a Cover measured with a 9 × 9 point frame in the 1 m² centered on the nest or a random point.
b Cover measured with a 5-m line intercept tape. The number of cm of each cover type was combined across the four cardinal directions at each site and divided by the total number of cm measured.
c Nest site differs significantly from random site (P < 0.05).

d contained less bare ground and more grass than random sites. Shrub cover (P = 0.20) and forb cover (P = 0.43) were similar at random and nest sites (Table 1). Twenty-three of 28 ground nests were under big sagebrush; the remaining nests were under rubber rabbitbrush (Chrysothamnus nauseosus) and Douglas rabbitbrush. The average percentage of big sagebrush cover in the 1 m² around each nest was slightly higher (35% vs 26%) than that at random sites but the difference was not quite significant (P = 0.06). Within a 4 × 4 decimeter quadrat directly over nest sites and random sites, 100% and 81%, respectively, contained shrub cover, mostly living. Line-intercept data from the 5-m radius area immediately around the nest and random sites indicated no differences (ANOVA) in shrub (P = 0.67), bare ground (P = 0.96), grass (P = 0.45), or forb (P = 0.86) cover (Table 1).

The variation in visual obstruction of the vegetative profile board at the nest site was greatest when measured from 15 m, thus all obstruction measurements used in analysis were taken from that distance. Visual obstruction was not different between the nest sites and random sites at either the 0.0–0.5 m (P = 0.32) height or the 0.5–1.0 m (P = 0.51) height. Most of the samples at 0.0–0.5 m indicated 41–100% obstruction, but most of the 0.5–1.0 m samples indicated 0–20% obstruction.

Discussion.—The apparent nesting success rates for ground nesting Mourning Doves in this study were somewhat higher than those observed in other studies in the intermountain region. Fichter (1959) reported a nesting success of 66.5% and 1.21 fledglings produced per nest attempt for Mourning Doves nesting in orchards in southeastern Idaho. Dahlgren (1955) reported 58% nesting success and 1.8 Mourning Doves fledged per successful nest, averaged over a 2-year period, in orchards and canal bank vegetation in Utah. The success rates in our study are partly influenced by our recognition of observer-caused abandonment of four nests. Daily survival rates (Mayfield 1975, Miller and Johnson 1978) provide more realistic estimates of nesting success but are not directly comparable with most earlier studies.

Other studies of ground nesting Mourning Doves reported lower nesting success and slightly higher nesting densities than our study. Downing (1959), in northwestern Oklahoma, reported 29% nesting success and 0.06 nests/ha, and Hon (1956) reported 33% nesting success with 0.08 nests/ha for Mourning Doves on the coastal islands of North Carolina. Hon’s estimate included high abandonment, at least 50% of which was due to human interference. Reynolds and Trost (1981), when using a rope dragging procedure similar to
ours, found Mourning Dove nesting densities on the INEL identical to those reported in
our study. Fichter (1959) recorded peak nesting activity in the latter two-thirds of July in
southern Idaho, whereas Dahlgren (1955), in northern Utah, reported the greatest nesting
activity in mid-June and late July. Our observations from nests, live captures, and collected
doves confirmed peaks in nesting activity in June and July but also noted a substantial peak
from early to mid-August.

Downing (1959) stated that overhead cover did not appear to be essential to ground
nesting Mourning Doves in Oklahoma while Hon (1956) found that 93% of the ground
ests on his study site in North Carolina had at least partial overhead cover. All of the nests
found in our study were located under shrubs, primarily big sage. We strongly suspect that
shading and overhead cover, especially from big sage, were important to nesting doves on
the INEL even though the association with shrubs was not statistically significant. A larger
sample size of nests is needed to evaluate this relationship. Reynolds and Trost (1981) also
noted that Mourning Doves (N = 6) on the INEL nested under shrubs. We suggest that land
use practices that maintain substantial shrub cover intermixed with grasses should provide
excellent nesting cover for Mourning Doves in the cold desert.

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Program.

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Nest sites of the Micronesian Kingfisher on Guam.—The Guam subspecies of the Micronesian Kingfisher (Halcyon cinnamomina cinnamomina) is one of the casualties of the recent extinction of Guam’s avifauna. Predation by the introduced brown tree snake (Boiga irregularis) is thought to be the prime factor (Savidge 1986, 1987). The Micronesian Kingfisher was formerly widespread and common throughout the forested regions of Guam (Marshall 1949, Baker 1951) and was one of the last bird species, along with the Mariana Crow (Corvus kubaryi) and Guam Rail (Rallus owstoni), to decline to critical population levels (Savidge 1987).

The present study, conducted from March to July 1985, was part of a joint effort by the Guam Division of Aquatic and Wildlife Resources, Wildlife Conservation International, and the American Association of Zoological Parks and Aquariums. I censused the remaining kingfishers and studied nest sites in order to assess habitat requirements for conservation and captive breeding.


**Table 1**  
RELATIVE FREQUENCY AND RELATIVE DOMINANCE OF TREE SPECIES FOUND AT 16 MICRONESIAN KINGFISHER NEST SITES ON GUAM

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Relative frequency</th>
<th>Relative dominance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Premna obtusifolia</em></td>
<td>21.3 ± 13.8</td>
<td>18.0 ± 13.6</td>
</tr>
<tr>
<td><em>Pandanus fragrans</em></td>
<td>15.9 ± 12.2</td>
<td>11.6 ± 7.9</td>
</tr>
<tr>
<td><em>Cycas circinalis</em></td>
<td>15.7 ± 15.3</td>
<td>16.8 ± 16.3</td>
</tr>
<tr>
<td><em>Aglaia mariannensis</em></td>
<td>11.6 ± 10.2</td>
<td>6.0 ± 5.7</td>
</tr>
<tr>
<td><em>Neisosperma sp.</em></td>
<td>10.0 ± 6.2</td>
<td>11.8 ± 9.2</td>
</tr>
<tr>
<td><em>Tristriopsis acutangula</em></td>
<td>9.2 ± 14.5</td>
<td>16.0 ± 16.7</td>
</tr>
<tr>
<td><em>Guamia mariannae</em></td>
<td>5.7 ± 5.4</td>
<td>3.2 ± 3.6</td>
</tr>
<tr>
<td><em>Hibiscus tilaceus</em></td>
<td>3.6 ± 8.4</td>
<td>1.3 ± 2.1</td>
</tr>
</tbody>
</table>

*a Only tree species with 1.0% relative frequency or more are included in the table.  
b Mean ± SD per 0.04 ha plot.

*Study area and methods.*—Guam is the southernmost of the Marianas Island group in the western Pacific. The study area lay within Andersen Air Force Base on the elevated limestone plateau at the northern end of the island. The Conventional Weapons Storage Area and Northwest Field (hereafter referred to as CWSA and NWF) are two adjoining areas comprising approximately 1860 ha at the northwest corner of the Air Base. The area is covered with second-growth typhoon forest (Fosberg 1960, Stone 1970). The CWSA is characterized by a network of intersecting service roads and regularly spaced mowed areas for munitions storage which very effectively break the forest up into a series of islands. Human disturbance is frequent in the maintained areas but rare in the forest. There is extensive disruption of the forest floor by foraging feral pigs (*Sus scrofa*) which are common in the area. NWF was not heavily used by the Air Force at the time of the study. The forest there is broken into larger islands, being divided by unused runways, stands of *Casuarina equisetifolia*, and early succession areas. The kingfishers were censused by playback of tapes of territorial Guam Micronesian Kingfisher calls. An area-wide census was first conducted on perimeter roads and internal transect roads. More intensive efforts subsequently were made in areas in which kingfishers were heard or sighted. Due to the variability of the response and movement of the birds, censusing was repeated regularly throughout the entire area. Pairs were considered to be on a territory if observed engaging in excavation behavior or entering a nest cavity. The kingfisher is the only nest hole excavator on Guam, therefore all nest cavities were assumed to be Micronesian Kingfisher nest sites. Incomplete nest excavations (those which did not terminate in a nest chamber) were also assumed to be the work of kingfishers. No Guam bird species are recorded as making foraging excavations in dead trees, and in the course of this study, no kingfishers were observed foraging in dead trees. However, during bouts of excavation, pairs were observed to work on as many as five excavation sites on a given tree. Only at a later stage of excavation did the pairs focus on one hole. Macrohabitat variables were recorded for 16 nest sites, as outlined by James and Shugart for 0.1-acre circles (1970). These 0.04-ha circles were centered on the nest tree. Only live nest trees were included in the tree count. Canopy height was determined with a forester’s sextant. Four characteristics of nest cavities were measured: entrance width (one horizontal measurement across the circular entrance mouth), entrance depth (entrance mouth to nest chamber entrance), cavity depth (entrance mouth to back of nest chamber), and height from ground. In the case of multiple excavations, height from ground was measured.
for the highest and lowest excavations only. An assessment of density of the nest-cavity substratum was made by taking the mean of 10 manual penetrations with a 12.5-cm long ice pick into the nest tree in the vicinity of the existing excavations. To standardize as much as possible the same posture was used throughout, and the ice pick was pushed only as far as it would go in a single thrust. Sites for testing penetrability were chosen by randomly stabbing the substrata. This was also done with live trees for comparison with dead trees. Arboreal termitaria were not included in the statistical analysis of penetrability. Two of the active nest sites were snake-proofed by pruning back the surrounding canopy vegetation and installing a 1.2-m wide sheet-metal collar approximately 2 m from the ground.

Results.—A total of eight pairs and 10 solitary male Micronesian Kingfishers were found on the northern half of the CWSA. Only two pairs were on NWF. Solitary males were most variable in their site tenacity, sometimes being found in the vicinity of nest sites and sometimes in other areas. However, as none of the birds were marked, the extent of local migration is unknown. Three pairs were observed with eggs, but only one succeeded in rearing young (at one of the two snake-proofed nest sites). The nest-site vegetation species in the CWSA and NWF areas of AAFB are those typical of the typhoon forest found on the limestone plateau of northern Guam (Fosberg 1960, Stone 1970) (Tables 1 and 2). Despite the pattern of past deforestation, the vegetation species are mainly native. This history of past deforestation and the current maintenance of open areas (particularly in the CWSA) has rendered a major portion of the study area fragmented second growth vegetation. The nest-site macrohabitat characters were variable, but indicate that the Micronesian Kingfisher is a forest-nesting species with nest sites characterized by a high degree of canopy cover and vegetation density (Table 3). Nest excavations were always located in decaying standing wood, arboreal termitaria (the nests of Nasutitermes sp. termites), or arboreal fern root masses. No termitaria or decaying standing trees in the study area were ever encountered that lacked some evidence of kingfisher nesting activity. The mean penetrability of nest trees

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guamia mariannae</td>
<td>32.9 ± 16.5</td>
</tr>
<tr>
<td>Aglaia mariannensis</td>
<td>20.7 ± 13.7</td>
</tr>
<tr>
<td>Triphasia trifolia</td>
<td>10.3 ± 14.0</td>
</tr>
<tr>
<td>Neisosperma sp.</td>
<td>5.9 ± 6.7</td>
</tr>
<tr>
<td>Piper guahamense</td>
<td>4.0 ± 7.7</td>
</tr>
<tr>
<td>Cycas circinalis</td>
<td>3.6 ± 4.4</td>
</tr>
<tr>
<td>Maytenus thompsonii</td>
<td>3.4 ± 4.7</td>
</tr>
<tr>
<td>Mammeea odorata</td>
<td>3.3 ± 9.4</td>
</tr>
<tr>
<td>Morinda citrifolia</td>
<td>2.1 ± 2.7</td>
</tr>
<tr>
<td>Eugenia sp.</td>
<td>2.0 ± 6.0</td>
</tr>
<tr>
<td>Pandanus fragrans</td>
<td>1.9 ± 3.9</td>
</tr>
<tr>
<td>Melanolepsis multiglandulosa</td>
<td>1.6 ± 4.0</td>
</tr>
<tr>
<td>Premna obtusifolia</td>
<td>1.5 ± 2.6</td>
</tr>
</tbody>
</table>

* Only shrubs and small trees with a diameter breast height <7.5 cm, and with 1.0% relative frequency or more are included in the table.
* Mean ± SD per 0.04-ha plot.

**Table 2**

**Relative Frequency of Shrub Species Found at 16 Micronesian Kingfisher Nest Sites on Guam**
TABLE 3
MACROHABITAT VARIABLES FOR 16 MICRONESIAN KINGFISHER NEST SITES ON GUAM

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean ± SD²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trees (7.5–15.0 cm DBH¹)</td>
<td>19.6 ± 7.7</td>
</tr>
<tr>
<td>Trees (15.0–22.5 cm DBH)</td>
<td>9.3 ± 5.5</td>
</tr>
<tr>
<td>Trees (22.5–37.5 cm DBH)</td>
<td>2.0 ± 1.0</td>
</tr>
<tr>
<td>Trees (&gt;37.5 cm DBH)</td>
<td>1.0 ± 1.0</td>
</tr>
<tr>
<td>Total tree frequency</td>
<td>32.9 ± 10.9</td>
</tr>
<tr>
<td>Total basal area cm²</td>
<td>3378.8 ± 1378.3</td>
</tr>
<tr>
<td>Shrubs</td>
<td>195.0 ± 66.9</td>
</tr>
<tr>
<td>% Ground cover</td>
<td>43.0 ± 24.9</td>
</tr>
<tr>
<td>% Canopy cover</td>
<td>83.5 ± 14.1</td>
</tr>
<tr>
<td>Canopy height (m)</td>
<td>9.5 ± 2.5</td>
</tr>
</tbody>
</table>

¹ DBH = diameter breast height.
² On each 0.04-ha plot.

(\bar{x} = 7.4 ± 1.8 cm [SD], N = 5) was significantly greater than that of live trees (\bar{x} = 1.0 ± 0.41 cm, N = 4; df = 7, t = 6.84, P = 0.0002). In five termitaria tested, the ice pick always entered the full 12.5 cm. Nest cavity dimensions did not differ significantly between tree (N = 13) and termitaria (N = 6) nests for the dimensions of entrance width (t = 0.10, df = 17, P = 0.92) or entrance depth (t = −0.12, df = 17, P = 0.90). The difference was slightly significant for cavity depth (t = −2.18, df = 17, P = 0.04). Nest trees always had multiple excavations, the majority of which (80.1% of all examined) were incomplete. Termitaria had far fewer excavations than trees (Table 4). Nest trees fell well into the largest tree size class (see Table 3), with a mean diameter breast height of 42.7 ± 12.7 cm. During the present study, tree cavity nests were found in Tristriopsis acutangula, Pisonia grandis, and Artocarpus sp.

Discussion.—The decline of the Micronesian Kingfisher follows a general pattern of extinction seen in other Pacific island birds (Greenway 1967). The Guam extinction differed from others in that an introduced reptile, the brown tree snake, was the final agent of extinction. The kingfisher is a cavity nester and this behavior is known to confer some protection from nest predators. However, it is also known to incur a cost in that the availability of suitable nest sites may limit the number of suitable breeding territories (von Haartman 1957, Collias and Collias 1984). Due to the protection it offers the eggs and young, cavity nesting may in part account for the Micronesian Kingfisher’s outlasting open-nest native bird species of similar size and smaller. The remaining population was found in disturbed habitat and, while apparently tolerant of human interference, the kingfisher has specific nest-site requirements. Known nest tree species are Pisonia grandis, coconut palms (Cocos nucifera), banyan trees (Ficus sp.), and breadfruit trees (Artocarpus sp.) (Baker 1951, Jenkins 1983, R. Beck, Jr. and G. Wiles pers. comm.). In addition, Tristriopsis acutangula was found being used as a nest tree during the present study. The repeated use of nest sites, as evidenced by multiple excavations, indicates their importance. The kingfishers require a soft substratum for nest cavity excavation. It is unlikely that suitable trees remain standing for long due to their advanced state of decay. Nest-site trees are softer than live trees and termitaria are softer still.

One of the last populations of the kingfisher was found just north of the study area below the limestone plateau in the vicinity of Ritidian Point (R. Beck, Jr. pers. comm.). This area
TABLE 4
MICROHABITAT VARIABLES FOR MICRONESIAN KINGFISHER NEST SITES ON GUAM

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number excavations per site</td>
<td></td>
</tr>
<tr>
<td>Trees (N = 6)</td>
<td>19.3 ± 17.7</td>
</tr>
<tr>
<td>Termitaria (N = 6)</td>
<td>2.7 ± 1.9</td>
</tr>
<tr>
<td>Nest excavation status (N = 166)</td>
<td></td>
</tr>
<tr>
<td>Complete</td>
<td>12.7%</td>
</tr>
<tr>
<td>Not complete</td>
<td>80.1%</td>
</tr>
<tr>
<td>Undetermined</td>
<td>7.2%</td>
</tr>
<tr>
<td>Height of excavations</td>
<td></td>
</tr>
<tr>
<td>Trees (N = 6)</td>
<td>4.9 ± 1.5 m</td>
</tr>
<tr>
<td>Termitaria and arboreal fern root masses</td>
<td></td>
</tr>
<tr>
<td>(N = 5)</td>
<td>5.2 ± 2.1 m</td>
</tr>
<tr>
<td>Nest cavity dimensions</td>
<td></td>
</tr>
<tr>
<td>Trees (N = 13)</td>
<td></td>
</tr>
<tr>
<td>Entrance width</td>
<td>5.29 ± 0.58 cm</td>
</tr>
<tr>
<td>Entrance depth</td>
<td>7.21 ± 1.46 cm</td>
</tr>
<tr>
<td>Cavity depth</td>
<td>17.07 ± 3.14 cm</td>
</tr>
<tr>
<td>Termitaria (N = 6)</td>
<td></td>
</tr>
<tr>
<td>Entrance width</td>
<td>5.26 ± 0.46 cm</td>
</tr>
<tr>
<td>Entrance depth</td>
<td>7.29 ± 0.47 cm</td>
</tr>
<tr>
<td>Cavity depth</td>
<td>20.21 ± 1.68 cm</td>
</tr>
</tbody>
</table>

is largely undisturbed native forest. The Ritidian Point population was extinct at the time the present study was begun and the finding of a more southerly population in the CWSA and NWF was contrary to the northward pattern of extinction noted by previous researchers (Ralph and Sakai 1979, Jenkins 1983, Savidge 1984). The area around Ritidian Point differs from the study area in both the degree of habitat modification and human use. The forest there is contiguous and relatively untouched. A large number of former kingfisher nest sites were observed there in *Pisonia grandis*. I saw no brown tree snakes at the one successful nest site at the CWSA, and attempts to trap snakes there failed. However, at the edge of the plateau which defined the north edge of the study area less than 1 km away, nine snakes were captured by hand in 90 min by walking the forest edge and spotlighting them after dark. Thus, the persistence of the kingfisher at the CWSA and NWF may have indirectly been enhanced by forest fragmentation limiting local migration of the arboreal brown tree snake coupled with the abundance of feral pigs which are known to eat snakes.

The Micronesian Kingfisher of Guam will soon be extant only in captivity. The captive population is breeding and it is hoped to reintroduce them to Guam at a time when the snake population may be controlled. The brown tree snake is not likely to be eradicated completely from the island, however its numbers may be controlled. The situation in the CWSA may be a model for future management of the species. The best hope may lie in creating snake-controlled refugia using traps and drift fences. The kingfishers' dependence on suitable nest sites may be exploited by the supplying of artificial nest sites, such as by relocating termitaria and selectively killing suitable trees in snake-controlled areas. Extensive habitat still lies on military reservations as well as on private land. Secure nest sites might be created using criteria established in the present study.

Acknowledgments.—I thank C. Sheppard of the New York Zoological Society for the
opportunity to perform this research; R. Beck, Jr. for his invaluable guidance while on Guam; the entire staff of the Guam Division of Aquatic and Wildlife Resources, especially G. Wiles for his help in plant identification and H. Muna and C. Kerns for assistance in the field. Field work on Andersen Air Force Base was facilitated by B. Sachse, V. Tobey, and the Air Force. Funding was provided by Wildlife Conservation International and the Friends of the National Zoo. I would additionally like to thank R. Beck, Jr., M. Hodge, J. Savidge, G. Uetz, and G. Wiles for helpful comments on an earlier draft of the manuscript.

LITERATURE CITED


Release of gaping in hummingbirds (Trochilidae).—Gaping is an instinctive behavior of many altricial birds in which the nestling displays a widely opened bill and, in most cases, produces loud begging calls to stimulate feeding by the parents (Stresemann 1927-1934). Gaping may be elicited by non-specific or specific stimuli (Skutch 1976, Bischof and Lassak 1985). At one time, gaping was considered to be restricted to passerines, but it has also been documented in certain non-passerines, e.g., woodpeckers (Picidae), cuckoos (Cuculidae), and mousebirds (Coliidae) (Stresemann 1927-1934).
Within the non-passerine order Apodiformes, Lack (1956) describes gaping in swifts (Apodidae), and Wagner (1945) and Schuchmann (1983) studied gaping in hummingbirds (Trochilidae). Here, I describe ontogenetic variation in gape-release stimuli in hummingbirds and discuss its ecological significance for nesting behavior. The results discussed are based on field and laboratory studies of 14 trochilid species (Table 1) over an observation period of 8–23 days, during which the behavioral interactions between adults and chicks were recorded. I also studied reproductive biology of four of these hummingbird species in the laboratory, using hand-reared young. In all cases, experiments described below were conducted on chicks which had recently been fed, thereby increasing the threshold of any gape-release response to its maximum.

Generally, hummingbirds build open, cup-shaped nests, often placed in an exposed location on the terminal branches of trees and shrubs. The female builds the nest alone, and in all species studied thoroughly to date, rears the young without the help of her mate. From studies on North, Central, and South American species, it appears that they can achieve, at most, two successful broods per year.

For all hummingbird species studied here, three well-differentiated stages of development were identified:

Stage I.—From day 1 to about day 5 after hatching, the nestling is unfeathered except for two dorsal rows of neossoptiles about 5 mm long (Collins 1978), and its eyes are still closed. During this stage the chicks, generally two in hummingbirds, are inactive in the nest.

For all 14 species studied, when the female arrived with food, she landed on the edge of the nest and touched the nestlings behind the eye-bulges with her beak. In response to this stimulus, the young birds always gaped and were fed by the female. Indeed, gaping could be induced 4–6 times successively in nestlings of this age by touching the eye-bulges (e.g., with a match-stick). Because feeding did not follow gaping in these experiments, a latent period of about one minute had to pass until a similar reaction could again be triggered in the offspring. No begging calls were heard at this stage.

Stage II.—Day 6 to day 9 was the period of major feather development on wings, tail and back. The dorsal neossoptiles were not shed but remained attached to the contour feathers. Begging calls were still not heard at this stage.

Stage III.—This period of the nestling development covered day 10 until fledging, i.e., days 17–19. By this time, chicks were almost completely feathered and often sat on the edge of the nest with their backs turned away from the nest cup, but still failed to give begging calls.

During stages II and III, the female gradually approached the nest and began to hover over the feathered young with an increased wing-beat frequency that was acoustically perceptible. When the dorsal neossoptiles attached to the chicks' contour feathers were visibly agitated by the resulting air movement, chicks invariably began to gape. In fact, gaping was easily triggered in the chicks at this stage of development by blowing on their dorsal neossoptiles (e.g., with a straw). No touching of the eye-bulges was observed during these stages. Thus, it appeared that the gape-releasing stimulus had changed. When gaping, and also during feeding, the chicks raised themselves only slightly and remained in a rather stooped position in the nest.

With increasing age (from about day 15 onwards), the chicks often sat at the edge of the nest during the day, mostly with their backs turned away from it. At feeding time, the female hovered just above the chicks, causing movements of their dorsal neossoptiles. Only after this stimulus would the nestlings gape and then be fed by the female. In all species observed, begging calls were still not heard at this developmental stage.

When the dorsal neossoptiles for seven chicks of four species (marked with asterisks in Table 1) were plucked out with forceps from laboratory-reared hummingbirds on day 10 after hatching, gaping reactions were not elicited by the female's hovering closely over their
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Place of study</th>
<th>Habitats</th>
<th>Nest architecture</th>
<th>No. of nests</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Glaucis hirsuta</em></td>
<td>ASA Wright Nature Centre, Trinidad</td>
<td>tropical rain forest</td>
<td>open, hanging</td>
<td>17</td>
</tr>
<tr>
<td><em>Phaethornis ruber</em></td>
<td>Voltzberg Mts., Surinam</td>
<td>tropical rain forest</td>
<td>open, hanging</td>
<td>1</td>
</tr>
<tr>
<td><em>Colibri coruscans</em></td>
<td>Quito, Ecuador; laboratory</td>
<td>cultivated area</td>
<td>open, on branch</td>
<td>2</td>
</tr>
<tr>
<td><em>Chlorestes notatus</em></td>
<td>Arima Valley, Trinidad</td>
<td>garden</td>
<td>open, on branch</td>
<td>2</td>
</tr>
<tr>
<td><em>Thalurania furcata</em></td>
<td>NW Cali, Colombia; laboratory</td>
<td>subtropical wet forest</td>
<td>open, on branch</td>
<td>1</td>
</tr>
<tr>
<td><em>Coeligena coeligena</em></td>
<td>NW Cali, Colombia</td>
<td>cloud forest</td>
<td>open, on branch</td>
<td>1</td>
</tr>
<tr>
<td><em>Eriocnemis luciani</em></td>
<td>E Quito, Ecuador</td>
<td>subpáramo</td>
<td>open, on branch</td>
<td>1</td>
</tr>
<tr>
<td><em>Hoplophasia aureliae</em></td>
<td>NW Cali, Colombia</td>
<td>cloud forest</td>
<td>open, hanging</td>
<td>2</td>
</tr>
<tr>
<td><em>Metallura tyrianthina</em></td>
<td>Pan de Azucar, Colombia</td>
<td>subpáramo</td>
<td>semi-domed</td>
<td>2</td>
</tr>
<tr>
<td><em>Aglaioecus celestis</em></td>
<td>Nariño, Colombia; laboratory</td>
<td>cloud forest</td>
<td>completely domed</td>
<td>3</td>
</tr>
<tr>
<td><em>Trochilus polytmus</em></td>
<td>Greenhills, Jamaica; laboratory</td>
<td>elfin forest</td>
<td>open, on branch</td>
<td>8</td>
</tr>
<tr>
<td><em>Philodice evelynae</em></td>
<td>Andros, Bahamas</td>
<td>pine forest</td>
<td>open, on branch</td>
<td>7</td>
</tr>
<tr>
<td><em>Calyphte anna</em></td>
<td>San Bernadino Mts., California</td>
<td>pine forest</td>
<td>open, on branch</td>
<td>5</td>
</tr>
<tr>
<td><em>Archilochus alexandri</em></td>
<td>Averill Park, L.A., California</td>
<td>park</td>
<td>open, on branch</td>
<td>6</td>
</tr>
</tbody>
</table>

* Dorsal neosoptiles removed to study gaping reactions.
backs. However, when a hovering female landed on a chick’s back, it gaped immediately and was fed. Two days after neossoptiles were removed, gaping reactions could once again be observed with the approach of the female. The absence of tactile stimulation suggests that optical signals may now have become adequate stimuli.

Begging calls were given by the hummingbird chicks only after fledging. They gave loud begging calls, irrespective of the presence of the female, but called more vigorously when she was within view.

Details of chick-feeding behavior are known for many passerines which produce altricial young. As comparative ethological studies show, the release of gaping stimuli in passerines is relatively non-specific. For example, gaping can be stimulated in young finches through nest vibration caused by the parents’ landing on the edge of the nest (Tinbergen 1951). Furthermore, by the time that chicks can perceive and react to supplementary visual stimuli, gaping in passerines continues to be relatively non-specific (Tinbergen op. cit.).

Although the begging behavior of chicks of many passerine species may easily alert the attention of a potential nest predator, this danger can be reduced through the choice of a concealed nesting site, protective nest construction (e.g., enclosed domed nests), and by camouflaging the nest with plant material from the immediate vicinity. The mortality rate of young passerines by predators is further compensated for by a relatively high reproduction rate of several broods per year (reviewed by Cody 1971).

Comparatively little is known about the chick-feeding behavior of those non-passerines whose young hatch as blind altricial birds. From observations of Lack (1956), European Swifts (Apus apus) gape in reaction to relatively non-specific tactile stimuli by the parents. In contrast, in hummingbirds, the closest modern relatives of swifts, non-specific tactile and acoustic stimuli appear to be rare.

Because hummingbirds forage while hovering, they can no longer climb with their feet which serve only for perching. Consequently, they build exposed but camouflaged nests easily accessible in flight. The exposed nest site and low reproductive output probably also favored the development of this very specific gape-response behavior. Loud begging calls of the offspring as well as uncontrolled begging and gaping movements through non-specific causes, e.g., vibration of nest by wind, would be types of behavior that could potentially betray the nest site to predators such as tree lizards, snakes, and birds. Thus, I suggest that the highly specific stimuli described herein which elicit gaping by unfledged hummingbird chicks are adaptations for reducing predation on exposed nest sites. Consistent with this hypothesis is the fact that chicks of those hummingbirds, e.g., sylphs (Aglaio cercus spp.) and metaltails (Metallura spp.) which build enclosed domed nests, give begging calls very shortly after hatching, presumably in response to tactile stimuli from the female as she enters the nest.

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LITERATURE CITED


Decline of the Long-eared Owl in New Jersey.—Long-term observations of the Long-eared Owl (Asio otus) in New Jersey suggest that numbers are decreasing at traditional winter roosts (Kane pers. obs.). Nesting activity is rare within the state and also may be decreasing. In this paper, we review the previous wintering records of Long-eared Owls in New Jersey and analyze Christmas Bird Count (CBC) data from 1956 to 1986, published annually in American Birds.

Methods.—We have monitored Long-eared Owls for 10 or more years in New Jersey, New York, Connecticut, and Pennsylvania. Most of our field work has involved checking of known roost sites (Smith 1981, Bosakowski 1984), as well as frequent reconnaissance trips of new areas. During the breeding season, intensive ground searches for raptor nests have been made primarily in northern New Jersey, southeastern New York, western Connecticut (e.g., Bosakowski 1982; Speiser and Bosakowski 1984, 1987, 1988; Bosakowski et al. 1989), and northeastern Pennsylvania, but no active nests of the Long-eared Owl have been discovered during these surveys. In addition to field observations of winter roosts, we summarized all winter Long-eared Owl sightings reported in “Records of New Jersey Birds” since 1966. We also summarized all CBC data for New Jersey from 1956–86. Only CBC stations that recorded at least one Long-eared Owl in their history were included in this analysis. Due to the increasing number of counts and observers since 1956, the data were normalized relative to a measure of field effort. Raynor (1975) found that party-hours had the highest correlation with numbers of birds observed. Since wintering Long-eared Owls are faithful to their day roosts (Smith 1981, Bosakowski 1984), some observers make special trips in advance to find these roosts for the CBC day, thus somewhat biasing the data. This effect reduces the value of normalizing factors such as party-hours and therefore we have presented the data using several different indices of abundance or effort.

Results.—We have observed a decrease in Long-eared Owls at many traditional winter roosts. Of 58 known winter roost sites during 1967–1988, six have been eliminated, and three have been thinned or affected by land development. With 49 roost sites remaining, most of the owls should also remain, but many roosts have had noticeable decreases or abandonment during the past decade. Unfortunately, long-term coverage at these roosts was too inconsistent to lend numerical support to our inquiry, although Smith (1981) has documented a decline at a traditional winter roost in central Pennsylvania that was checked annually for nearly 20 years. Prompted by these preliminary observations, we decided to search the regional literature and CBC records for evidence of a decline.
Fig. 1. Annual total number of Long-eared Owls found on all New Jersey Christmas Bird Counts (dotted line) and number of Long-eared Owls found per 1000 party-hours (solid line). Regression line (dashed line) for party-hours data shows a significant negative slope for the 31-year period (see graph for line formula and statistics). Regression line for total owls is \( Y = -0.629X + 31.9 \), \( P = 0.005 \) and had a lower correlation coefficient \( (r = 0.50) \).

The number of Long-eared Owls reported each winter in "Records of New Jersey Birds" was tallied from 1966-85 (Table 1). On first inspection, the yearly totals appear to be somewhat stable, if not irregular, but one must consider that the number of observers has increased steadily and that rare species are often considered more desirable to report. Furthermore, Smith and McKay (1984) report that interest in ' owling ' has increased in the past several decades, leading to increased efforts to locate and count this and other owl species. To reduce these biases and effects, we next examined New Jersey CBC data corrected for the number of party-hours which showed a highly significant negative trend in winter populations of Long-eared Owls (Fig. 1). Even without adjustment for search intensity (party-hours afield), the total number of owls still showed a significant negative trend although with a smaller slope. The graph also reveals irruptive years which may reflect the well known 3–4 year cycles of vole populations. Thus, the normal wintering population of Long-eared Owls in New Jersey may be greatly augmented by owls retreating from cyclic vole shortages to the north. We frequently observe owls arriving at roosts in late January which also may explain some of the irregularities in the cycles observed in the CBC data (collected mainly in mid- to late December).

Theoretically, the number of parties afield should correlate with the number of roost sites found, but this relation is complicated by the fact that observers often locate roost sites prior to the count day, so owls are sometimes found regardless of the number of parties or party-hours spent. Complimentary methods of analysis are to record the percentage of CBC
Table 1

<table>
<thead>
<tr>
<th></th>
<th>Region 1 NW</th>
<th>Region 2 NE</th>
<th>Region 3 Central</th>
<th>Region 4 SW</th>
<th>Region 5 SE</th>
<th>Annual totals</th>
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<td>10</td>
<td>0</td>
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</tr>
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<td>4</td>
<td>6</td>
<td>5</td>
<td>0</td>
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<td>8</td>
<td>10</td>
<td>0</td>
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<tr>
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<td>3</td>
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<tr>
<td>1981-82</td>
<td>2</td>
<td>19</td>
<td>5</td>
<td>0</td>
<td>0</td>
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<tr>
<td>1982-83</td>
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<td>2</td>
<td>4</td>
<td>2</td>
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<tr>
<td>1983-84</td>
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<td>4</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>1984-85</td>
<td>20</td>
<td>8</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>33</td>
</tr>
</tbody>
</table>

* If exact numbers were not given, the following interpretation was assigned: 1 owl = "the species," "noted," "present," "reported." 2 = "owls." "small numbers," "others were at . . .," "a few," "several."

* Formerly a section of New Jersey Audubon.

stations that reported Long-eared Owls or to record the average number of owls per CBC station (Fig. 2). The first method is weak with regard to numerical abundance, but provides an indication of Long-eared Owl distribution in New Jersey each winter. Both the "percentage stations with owls" and "average number of owls per station" methods show peak years, but the decline in numbers is not apparent with the percentage of CBC stations method. This result indicates that the decline in Long-eared Owl numbers has not resulted in a diminution in distribution but rather from an overall reduction across all CBC stations.

Discussion. — Bent (1938) noted that the Long-eared Owl could hardly be classed as a bird of deep forests. This fact is borne out in the current literature in which most of the Long-eared Owl breeding studies have come from largely non-forested, open terrain (e.g., Craig and Trost 1979, Village 1981, Marks 1986). Likewise, nearly all studies of winter roosts have reported a close proximity of the roost grove to open habitats (see Bosakowski 1984).

Throughout much of New Jersey, open habitats have steadily dwindled in area this century due to changes in land use which include: (1) a shift in farming to the midwest allowing many fallow fields to undergo natural forest succession, (2) urbanization of fields for housing, industry, and high-impact recreation, and (3) decreased needs for wood as an energy source due to gas and oil efficiency. As a result of these major economic shifts, much of the former open lands of New Jersey are now urbanized or heavily wooded, thereby reducing Long-eared Owl nesting habitat. Currently, the only known regular breeding area in the state is southwestern Hunterdon County, one of the largest agricultural counties in New Jersey.
Fig. 2. Average annual number of Long-eared Owls found per Christmas Bird Count (CBC) station in New Jersey (solid line) and percentage of CBC stations reporting owls each winter (dotted line). Regression line (dashed line) for average numbers shows a significant negative slope for the 31-year period (see graph for line formula and statistics). Regression line for percentage of CBCs was not statistically significant.

Given the present amount of farmland, grassland, and marsh in the state, the number of owls is still comparatively small, suggesting that other factors may also limit Long-eared Owl numbers in New Jersey. In Michigan farm country (only 11% wooded), the Craigheads (1956) also found the Long-eared Owl to be a relatively scarce component of the total raptor population. Similarly, Smith and Murphy (1973) found only one Long-eared Owl nest in their intensive four-year study of a desert-scrub raptor community in Utah. We suggest that competition with other raptors could be limiting Long-eared Owl numbers in the remaining open lands of New Jersey, especially in light of widespread habitat alterations. In particular, Great Horned Owls (*Bubo virginianus*) will compete for small rodents and nest sites and appear to be increasing throughout New Jersey (Bosakowski and Kane pers. obs.). Great Horned Owls will also prey upon the Long-eared Owl (Bosakowski et al. 1989, F. and N. Lilly pers. comm.).

Throughout most of its range the Long-eared Owl feeds primarily on voles (*Microtus*) (Marti 1976). Declining vole habitat (grasslands, cropland) and predation pressure from other increasing sympatric raptor populations namely, Great Horned Owl, Common Barn-Owl (*Tyto alba*), and Red-tailed Hawk (*Buteo jamaicensis*) could account for the lack of suitable food resources in most open lands of New Jersey. In addition, changing agricultural practices and increased use of chemical rodenticides may be eliminating the niche of vole specialists such as the Long-eared Owl. The paucity of nests reported and our own surveys suggest that the Long-eared Owl should be considered a rare and local nesting species in
New Jersey. Thus, there is no evidence to suggest that the Long-eared Owl has been largely overlooked in recent times as was formerly postulated by Bent (1938) and Bull (1964, 1974).

**LITERATURE CITED**


The evolution of reversed sexual dimorphism in owls: corrections and further analyses.—My paper on reversed sexual dimorphism (RSD) in owls (Mueller 1986) contains three errors in transcription and one serious computational error. In Table 1, the dimorphism ratio for wing loading for the Great Horned Owl (Bubo virginianus) is 0.836, not 0.845. In Table 2, the dimorphism ratio for the cube root of weight for the European Eagle-Owl (Bubo bubo) is 0.906 not 0.960, and the ratio for dimorphism in wing loading for the Great Gray Owl (Strix nebulosa) is 0.808, not 0.888. In computing the Spearman Rank correlation coefficient between female dominance and RSD in weight, I inadvertently used a sample of weights taken from Glutz and Bauer (1980), which I had used in a preliminary version of the manuscript. The weights used in all other calculations were taken from Mikkola (1983), which I chose because it provided much more data on diet and slightly more data on weights and wing measurements. The correlation between the weights from Mikkola and female dominance is only $r_s = 0.486$, far from statistically significant and far from the $r_s = 0.943$, $P = 0.01$ obtained using the weights from Glutz and Bauer. I discovered this computational error in comparing my paper with that of Lundberg (1986).

The considerable differences between the samples of Lundberg, Mikkola, and Glutz and Bauer led me to extract yet another sample from Cramp (1985). This sample was selected with the following guidelines: (1) that an adequate sample be obtained, (2) where possible, weights from the breeding season were avoided because of the great changes that occur in the weights of females at this time, and (3) where possible, weights and wing measurements were from the same locality or region because RSD in wing and weight appear to vary geographically. The sample I extracted from Glutz and Bauer (1980) followed guidelines (1) and (3) but used weights from the entire year. Lundberg (1986) attempted to calculate an average weight for the entire year and generally used the largest sample or samples available for both weight and wing. Mikkola (1983) simply lists the sources from which he compiled his sample. The four samples of RSD in wing and weight are given in Table 1. Rankings for female dominance as given in Mueller (1986) are correlated with RSD in weight in two of the four samples: Glutz and Bauer (as indicated above), Cramp ($r_s = 0.943$, $P = 0.01$) and nearly so for Lundberg ($r_s = 0.771$, the critical value for $P = 0.05$ is 0.829). Female dominance is correlated with RSD in wing for the samples from Lundberg, Glutz and Bauer, and Cramp, and nearly so for the sample from Mikkola ($r_s = 0.829, 0.886, 0.829$, and 0.714, respectively).

Cramp (1985) provides further information on female dominance in intra-pair interactions, allowing the ranking of two additional species. Description of the essentials of behaviors suggesting female dominance as extracted from Glutz and Bauer (1980) and Cramp (1985) are summarized below, with the species listed in descending order of estimated relative female dominance. All of these owls have been well studied in the field and in captivity except where noted. Scientific names are given in Table 1.

1) Eurasian Pygmy-Owl. — Males and females appear to be shy of contact with each other, even during the breeding season. Pairbonding includes alternation of fear and aggression to the mate. Pursuits and attacks occur and females chase males for 20–30 m. If the male loiters in the vicinity of the nest without food when the young are hungry, the female will drive him away. In small cages, females will kill males.

2) Boreal Owl. — Captives have not been observed. Territorial males drive off all intruders including females that fail to give the appropriate vocalization. A male will break-off courtship if a female ceases vocalizing or switches to aggressive vocalizations. Pair formation may take days when behavioral interactions are not balanced and the male is strongly
### Table 1
**Reversed Sexual Dimorphism (Male/Female) in Wing and the Cube Root of Weight<sup>a</sup> of European Owls**

<table>
<thead>
<tr>
<th>Species</th>
<th>Mikkola</th>
<th>Lundberg</th>
<th>Glutz</th>
<th>Cramp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Barn-Owl (Tyto alba)</td>
<td>0.997</td>
<td>1.000</td>
<td>1.002</td>
<td>0.997</td>
</tr>
<tr>
<td>Eurasian Scops-Owl (Otus scops)</td>
<td>0.977</td>
<td>0.978</td>
<td>0.972</td>
<td>0.994</td>
</tr>
<tr>
<td>Northern Eagle-Owl (Bubo bubo)</td>
<td>0.932</td>
<td>0.943</td>
<td>0.945</td>
<td>0.921</td>
</tr>
<tr>
<td>Snowy Owl (Nyctea scandiaca)</td>
<td>0.926</td>
<td>0.931</td>
<td>0.926</td>
<td>0.913</td>
</tr>
<tr>
<td>Northern Hawk-Owl (Surnia ulula)</td>
<td>0.992</td>
<td>0.985</td>
<td>0.993</td>
<td>0.983</td>
</tr>
<tr>
<td>Eurasian Pygmy-Owl (Glaucidium passerinum)</td>
<td>0.942</td>
<td>0.919</td>
<td>0.924</td>
<td>0.926</td>
</tr>
<tr>
<td>Little Owl (Athene noctua)</td>
<td>0.988</td>
<td>0.973</td>
<td>0.968</td>
<td>0.982</td>
</tr>
<tr>
<td>Eurasian Tawny Owl (Strix aluco)</td>
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<td>0.953</td>
<td>0.965</td>
<td>0.960</td>
</tr>
<tr>
<td>Ural Owl (S. uralensis)</td>
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<td>0.979</td>
<td>0.978</td>
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<td>Great Gray Owl (S. nebulosa)</td>
<td>0.931</td>
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<td>—</td>
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<tr>
<td>Long-eared Owl (Asio otus)</td>
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<td>0.983</td>
<td>0.985</td>
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<td>Short-eared Owl (A. flammeus)</td>
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<td>0.989</td>
<td>0.995</td>
<td>0.988</td>
</tr>
<tr>
<td>Boreal Owl (Aegolius funereus)</td>
<td>0.933</td>
<td>0.961</td>
<td>0.947</td>
<td>0.977</td>
</tr>
</tbody>
</table>

<sup>a</sup> In parentheses.

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intimidated by the female. When food deliveries are insufficient, the female will leave the nest cavity and chase the male for minutes at a time.

(3) **Northern Eagle-Owl.**—No intersexual aggression has been recorded in the wild. Seldom show aggressive tendencies in captivity if kept at high densities. If only one female and one male are placed in an aviary, the female will kill the male if pair formation does not occur.

(4) **Ural Owl.**—No observations of intrapair aggression in the field, but considerable aggression seen in captivity (Scherzinger 1980). Although each sex will threaten and attack the other, most frequently females are the aggressor, particularly in intrapair interactions. High intensity aggressive behavior includes an owl flying rapidly at and over another and grazing it with outstretched talons. Birds displace partners from a roosting perch by bumping them or pulling them by the beak. A female will show a threat display to her mate if he is slow to deliver food or will even tug strongly on his beak.
(5) Northern Hawk-Owl. — All observations of pair formation and other interpair interactions are from captives in aviaries. Females react to courting males with aggressive vocalizations and with high intensity threat displays. In one case a female attacked her suitor and rammed him with her breast.

(6) Little Owl. — Little information from field studies and not much more from captives. In small cages, a female strikes strangers of both sexes and will even strike her own mate at the end of the period of the dependency of the young.

(7) Eurasian Scops-Owl. — Essentially no information from the field. Females will strike strangers of both sexes; males will not attack strange females. A male entering the nest cavity is repelled by vocalizations of his mate.

(8) Common Barn-Owl. — Although usually very sociable in captivity a female will chase a courting male if she is not in a mood for pairing.

These rankings for female dominance are significantly correlated with both RSD in weight and wing in all four samples: Lundberg, wing $r_s = 0.826$, weight $r_s = 0.762$; Mikkola, wing $r_s = 0.810$, weight $r_s = 0.667$; Cramp, wing $r_s = 0.833$, weight $r_s = 0.857$; Glutz and Bauer, wing $r_s = 0.786$, weight $r_s = 0.857$ ($P = 0.05$ at $r_s = 0.643$, $P = 0.01$ at $r_s = 0.833$). An evaluation of the limited amount of information available relevant to female dominance in owls by another investigator might yield rankings that differ from mine. I found indications of intersexual dominance from field studies for only two species and for seven species from studies of captives. Species (1), (3), (4), and (8) have been well studied in both field and captivity; in three species intrapair aggression was noted only in captivity, in species (1) females were more aggressive in captivity than in the field. Pair formation and intrapair interactions are certainly much easier to observe in captives, but it appears that confinement escalates levels of aggression. It also appears likely that the size of the cage and presence or absence of con-or even heterospecifics in the same, adjacent or nearby aviaries may influence the levels of aggression. This is obvious for the European Eagle-Owl and at least some of Scherzinger's (1980) observations of Ural Owls could be interpreted as aggression redirected to the mate because of the presence of mated pairs of conspecifics in nearby aviaries. In my rankings I gave priority to field observations. A more conservative approach would be to consider only the information from captive studies thus deleting species (2). Further conservative steps would be to assign tied ranks to species (1) and (3) because females of both species will kill potential mates, consider species (4), (5), and (6) as ties because all three females actually strike suitors or mates, and assign tied ranks to (7) and (8) because females both threaten suitors or mates but do not make aggressive physical contact. This approach eliminates the correlation between female dominance and RSD in weight: Lundberg, $r_s = 0.567$; Mikkola, $r_s = 0.472$; Cramp, $r_s = 0.661$; Glutz and Bauer, $r_s = 0.661$ ($P = 0.05$ at $r_s = 0.714$; $P = 0.01$ at $r_s = 0.893$). However, the correlation remains between female dominance and RSD in wing: Lundberg, $r_s = 0.810$; Mikkola, $r_s = 0.756$; Cramp, $r_s = 0.945$; Glutz and Bauer, $r_s = 0.756$. This quite conservative method of examining the information available yields a strong suggestion that there is a relationship between RSD and female dominance. However, we need considerably more, and better, data on behaviors associated with the formation and maintenance of pair bonds before we can really evaluate the possibility that RSD evolved to facilitate pairing in owls.

Jehl and Murray (1986) have proposed that reversed sexual dimorphism (RSD) evolved as a result of selection for small size in males for agility in aerial displays, and they predicted that aerial displays would be found in owls. This hypothesis was not considered in my 1986 paper. The 13 species of European owls have been sufficiently well-studied to permit a comparison of the degree of RSD in a species with the agility of aerial displays.

I present below condensed accounts of behaviors that appear to be aerial displays taken from each of the 13 species, with the species ranked in order of the complexity, variety and frequency of aerial displays (Glutz and Bauer 1980, Cramp 1985).
1) *Short-eared Owl.*—Overall, this owl is primarily crepuscular, but during territory establishment it is inactive only for about 3–4 h during mid-day and for a longer period at night. It clearly has the most varied, elaborate and acrobatic flight displays of any species of European owl. Individual display flights may last for more than an hour, with the bird climbing quite rapidly to heights as great as 350 m with rhythmic wing-beats, with the wings appearing to pause momentarily at the peak of the upstroke and then bouncing back rapidly from the horizontal at the end of the downstroke. At the end of the circular climb, further climbing is interspersed with multiple wing-clapping in which the bird claps its wings together beneath the body usually 3–10, and sometimes as many as 20, times between wing-beats, producing sounds audible at some distance and losing altitude rapidly with each such display. The display flight culminates in a nearly vertical dive with wings held in a deep V and the bird rolling from side to side. Territorial encounters between males include aerial pursuit, rearing up in flight, attempting to get above the rival and grappling with each other, occasionally resulting in both males spiraling downward. The most spectacular and ritualized territorial display is the underwing-display in which a male flies with slow, deep wing-beats, bringing the wings high over the back to expose the undersides to rivals.

2) *Long-eared Owl.*—This owl is crepuscular and nocturnal. The male regularly performs display flight, zig-zagging between trees, sometimes rising above them, flying with deep, slow wing-beats interspersed with glides and wing-claps. Maximum rate of wing-clapping is once per three wing-beats. Females also wing-clap occasionally, and the dominant of the two females paired with a bigamous male wing-clapped more often than the male.

3) *Snowy Owl.*—This species primarily is diurnal and crepuscular. Displays are frequent; when the female is present (even as much as 1 km away) the male flies with wings held in a very deep V at the top of the stroke, causing it to drop ca 0.5 m; the height is regained with the subsequent downstroke. This undulating flight may cover as much as 1.5 km, and at the end the male rises 1.5 to 3 m and drops to the ground vertically with wings held in a V, sometimes flapping, sometimes not.

4) *Common Barn-Owl.*—This species is nocturnal. The male often flies steadily over the territory, repeatedly changing direction and calling frequently. Males have been observed to ascend to a height of 50 m and descend in a spiral with exaggerated wing-clapping. In courtship, a male pursues a female in a twisting and turning flight with occasional wing-clapping, but the sound produced is variable in volume and the display does not appear to be as ritualized as in either species of *Asio.* In “moth flight,” the male hovers over the female for up to 5 sec, with occasional wing-clapping. The male flies with rapid wing-beats repeatedly in and out of the prospective nest site in the presence of a female.

5) *Great Gray Owl.*—It is primarily crepuscular but is also active in daylight and at night. In courtship display, the male, usually carrying food in his beak, approaches the female in slow undulating flight, alternately flapping and then gliding with wings held in a V, although not as high as in the Short-eared Owl. Males will also pursue females in flight and there is one observation of a pair spiraling upwards in a circle of 6–10 m diameter, touching each other’s wings and later performing circular undulating flight, audibly beating wings against branches.

6) *Eurasian Pygmy-Owl.*—This owl is crepuscular and diurnal. A highly aggressive species both in territorial defense and in early courtship, and most observations are of chases and attacks. When highly aroused by a rival, an individual may leave its perch in a flight that appears stiff and clumsy, moving to another perch or spinning upward in the air in tight circles.

7) *Northern Hawk-Owl.*—This species is diurnal and crepuscular. The male performs territorial display-flights among trees, vocalizing frequently. Wing-clapping has been observed.
(8) **Northern Eagle-Owl.**—This owl is primarily crepuscular and nocturnal. Individuals of both sexes will chase others of their sex, but no contact has been recorded. The only apparent aerial display is driving flight in which the male follows the female in apparently normal flight behavior. Wing-clapping has been recorded once.

(9) **Boreal Owl.**—This species is nocturnal. Territorial defense appears to be almost entirely vocal. Males will approach playbacks and, exceptionally, swoop low over the observer. In one such case, the male bill-snapped and wing-clapped. Extensive observations of courtship have revealed no aerial courtship displays.

(10) **Tawny Owl.**—This species is crepuscular and nocturnal. Possible flight displays have been recorded only rarely. In one instance, a male left its roost 30 min after sunset and flew silently in broad spirals to a height of 200 to 250 m. In four other cases, a male descended to the female on stiff quivering wings. Reports of wing-clapping given in older handbooks have not been confirmed by modern observations.

(11) **Little Owl.**—This owl is active both nocturnally and diurnally. The only described behavior that might be an aerial display is that the male occasionally hovers over a perched female.

(12.5) **Eurasian Scops-Owl.**—This owl is nocturnal. No aerial displays have been noted, but the dominant pair will perform diving attacks on other individuals attempting courtship in an aviary.

(12.5) **Ural Owl.**—This owl is crepuscular and nocturnal. No aerial displays have been noted. Other courtship and territorial behaviors are similar to those of the Tawny Owl, and it is likely that aerial displays are absent or rare.

Spearman rank correlations between the ranks for aerial displays and RSD are: weight, Mikkola, \( r_s = -0.022 \); Lundberg, \( r_s = -0.143 \); Glutz and Bauer, \( r_s = -0.019 \); Cramp \( r_s = -0.146 \); wing, Mikkola, \( r_s = -0.078 \); Lundberg, \( r_s = -0.311 \); Glutz and Bauer, \( r_s = -0.396 \); Cramp, \( r_s = -0.017 \). None of these approach statistical significance and all are negative. One might argue with some of my rankings of aerial displays, but no remotely reasonable reordering of ranks will begin to provide a significant positive correlation between RSD and the complexity, variety, and frequency of aerial displays in the species of European owls. This strongly suggests that the hypothesis of Jehl and Murray (1986) is not a viable explanation for the evolution of RSD in owls.

I have noted the inadequacies in the available data on pairbond formation and maintenance. There are also deficiencies in the data on weights and wing measurements. Some samples merely give means and not the sample size; few present standard deviations. Some samples are very small, e.g., the total number of individuals in all four samples of weights of the European Scops-Owl is six males and seven females; three of the samples are identical, consisting of average annual weights of four captives of each sex. A few of the samples of wing measurements are also of fewer than 10 individuals. The weights for some species (e.g., the Boreal Owl) appear to be entirely from the breeding season, for others the weights appear to be from all times of year. In some cases, weights are from one locality and wing measurements from another. There are more samples of weights and wing measurements available for the Little Owl than for any other species in Table 1. The range of the means of individual samples of RSD in wing for the Little Owl is 45% to 54% of that shown between the 13 species within the four compiled samples in Table 1. RSD in wing tends to increase with increasing geographic latitude in the Little Owl (\( r_s = 0.725 \), \( N = 6 \), \( P > 0.05 \)). The range of the means of RSD in the cube root of weight for individual samples of the Little Owl is 77%–116% of that shown between the 13 species within the four compiled samples in Table 1. RSD in weight tends to decrease with increasing geographic latitude (\( r_s = 1.000 \), \( N = 4 \), \( P = 0.05 \)). The range of the monthly means for a sample from a restricted geographic area (Westphalia) (Glutz and Bauer 1980) is 50% to 63% of the range between
the 13 species within the 4 compiled samples in Table 1. At the beginning of the breeding season, the weight of male Little Owls decreases 5.8% between March and April ($P < 0.07$), and that of females increases 11.4% ($P < 0.001$), producing a change in RSD from 0.977 to 0.924. The considerable differences in RSD between geographic regions, plus the seasonal differences in weights, can easily result in biased estimates of RSD.

Weights are subject to greater bias than wing measurements because they can vary with the season as well as tending to show greater geographical variation. Many of the samples in Table 1 are compilations from several sources; these sources often are used in more than one sample. All of the four samples in Table 1 for some species may be biased. We need more data on all aspects of the biology of owls before we can attempt to resolve the question of the evolution of RSD.

Acknowledgments.—I thank N. S. Mueller for independent rankings of flight displays and C. Marti, M. Green, and N. S. Mueller for comments on previous drafts of the manuscript.

LITERATURE CITED


Incidental “egg dumping” by the House Wren in a Yellow Warbler nest.—Incidental deposition of eggs in the nests of other species has been recorded occasionally in several species of birds (e.g., Bailey 1887; Wiens 1965, 1971; Holcomb 1967; Gustafson 1975; Carter 1987). Here I describe an instance of “egg dumping” by the House Wren (Troglodytes aedon) in a nest of the Yellow Warbler (Dendroica petechia). In addition, I introduced House Wren eggs into active Yellow Warbler nests to reveal the extent to which these eggs are tolerated and the likelihood that wrens will hatch and be reared by warblers.

On 31 May 1982, while studying the nesting biology of the Yellow Warbler in the dune-ridge forest, Delta Marsh, Manitoba (study area described in MacKenzie 1982), I discovered a lined, empty warbler nest about 1.5 m high in a sand-bar willow (Salix interior). Single Yellow Warbler eggs were laid in the nest each day from 1 through 3 June; three eggs were present on 4 June, but on 5 and 6 June the nest was empty. Single Yellow Warbler eggs
were then laid daily in this nest by the same color-banded female from 7 through 11 June. A House Wren egg was added to the 5-egg clutch on 14 or 15 June, and all six eggs were incubated until the nest failed on 20 June. The wren did not remove or damage any of the warbler eggs when it laid in the nest.

Several explanations exist for finding the egg of one species in another species’ nest: (1) Brood parasitism. I could not find any records in the literature of interspecific brood parasitism in the House Wren, although evidence for intraspecific brood parasitism has been reported recently (Picman and Belles-Isles 1988). (2) Nest usurpation. I have 17 records, between 1974 and 1987, of House Wrens using non-cavity nests of other species in the ridge forest (two of the Northern Oriole [Icterus galbula] and 15 of the Barn Swallow [Hirundo rustica]). However, the oriole nests were used after the young orioles had departed earlier in the season, and the swallow nests had been built in previous years. (3) Egg dumping. Wiens (1971) presented three hypotheses to explain the incidental laying of eggs in other species’ nests, a phenomenon he termed “egg-dumping.” Hypothesis I stated that egg dumping was possibly a consequence of nest destruction during or immediately prior to egg laying; II, accidental placement of eggs (see also Hamilton and Orians 1965); or III, the inappropriate synchronization of nest building and egg laying. Wiens’ (1971) first and third hypotheses predict egg dumping in this context to be adaptive responses to situations that would otherwise preclude any successful reproduction. If at least some young are raised by the “host,” then it will always be advantageous for a female to lay eggs in another nest if its own is incomplete or has been destroyed. At the same time it should be disadvantageous to the “host” to accept the dumped egg. Wiens’ second hypothesis suggests that the bird made a mistake and “intended” to do something else.

I find accidental placement of the House Wren egg in the Yellow Warbler nest to be the most plausible of the alternatives, in view of the overlapping periods of egg laying in the two species, laying of the wren egg after the warbler clutch was complete, the juxtaposition of the nests of the two species in the ridge forest, and the rarity of the event. The present observation of egg dumping by the House Wren is the only one obtained on the study area from 1974 through 1987 during monitoring of 599 active nests of 10 nonpasserine species, 1885 Yellow Warbler nests (0.05%), and 1248 nests of 25 other passerine species.

As part of a broader study of the egg recognition capabilities of Yellow Warblers, I confirmed experimentally in 1987 and 1988 that Yellow Warblers generally accepted House Wren eggs added to their clutches but that they apparently cannot hatch them. Yellow Warbler and House Wren eggs are nonmimetic but about the same size ($\bar{x} = 1.52$ g, $N = 36$ YW eggs; $\bar{x} = 1.49$ g, $N = 30$ HW eggs). I introduced single wren eggs into 28 warbler nests at the following stages: unlined ($N = 3$), lined but empty ($N = 6$), egg laying ($N = 14$), and incubation ($N = 5$), i.e., clutches of 4 or 5 eggs completed. The 13 wren eggs introduced into warbler nests prior to egg laying and during early egg laying, i.e., 1- or 2-egg stages, were viable; all of the eggs were number 2-4 in the wrens’ laying cycles. All three wren eggs introduced into unlined nests were buried, apparently because the warblers simply continued building their nests (Emlen 1941, Hobson and Sealy 1987). Thus, wren eggs added to unlined nests were buried more often than when added to nests that were lined or contained eggs ($\chi^2 = 15.63$, df = 1, $P < 0.0001$). Of the remaining 25 introduced wren eggs, 20 were accepted: one wren egg was rejected through burial, and four nests failed before responses could be recorded, i.e., before six days had elapsed. None of the 13 viable wren eggs hatched; three disappeared during hatchling, eight contained dead embryos in advanced stages of development, and two eggs were added with undeveloped embryos. The warbler’s incubation period is shorter than the wren’s: 11–12 days in the Yellow Warbler ($\bar{x} = 11.2$ days, $N = 22$ clutches, Goossen 1978), 12–15 days in the House Wren ($\bar{x} = 14.0$ days, $N = 33$ clutches, Kendeigh 1952).
The known tendency of House Wrens to destroy eggs of their own and other species (Belles-Isles and Picman 1986) seems to be inconsistent with the present observation of egg dumping. However, Belles-Isles and Picman (1986) reported that female House Wrens ceased pecking eggs when they started laying.

Acknowledgments.—These observations were made during studies of riparian forest birds funded by the Natural Sciences and Engineering Research Council of Canada (grant A9556). The Portage Country Club permitted me to make some of these observations on their property. G. C. Biermann provided the weights of the Yellow Warbler eggs. B. A. Granthum, D. W. Kinnear, and W. A. Manchur provided excellent field assistance. I thank J. V. Briskie, K. A. Hobson, J. Picman, and the reviewers, S. I. Rothstein and J. R. Walters, for constructive criticism of the manuscript. This paper is contribution number 171 of the Univ. Manitoba Field Station (Delta Marsh).

LITERATURE CITED


Bald Eagles killing American Coots and stealing coot carcasses from Greater Black-backed Gulls.—Bald Eagles (*Haliaeetus leucocephalus*) feed on a variety of prey, and have been reported killing American Coots (*Fulica americana*, Grubb and Kennedy 1982) and stealing prey from many species (see Fischer 1985 for a review). Erskine (1968) observed Bald Eagles stealing fish from Greater Black-backed Gulls (*Larus marinus*), however, they have not been reported stealing American Coots. From a study of Greater Black-backed Gull predation on American Coots (Unpubl. data) and related observations on Bald Eagles foraging, we document immature Bald Eagles killing American Coots and stealing coot carcasses from Greater Black-backed Gulls.

**Study area and methods.**—The study was conducted at Lake Mattamuskeet, a 16,200-ha lake in east-central North Carolina’s Mattamuskeet National Wildlife Refuge. During 22 October–18 December 1983, we watched, dawn-to-dusk, from two 5-m towers, located on points extending 600 m from shore, and from a vehicle parked on shore. Any eagle activity was recorded until it departed, usually toward a night roost south of the lake. We recorded date, time, eagle age and behavior, gull age and behavior, presence or absence of gull mobbing, and number of gulls mobbing for each eagle-gull interaction. A gull landing within 20 m of a carcass or a live coot, which subsequently attracted an eagle, was considered a cue. Mobbing was defined as one or several gulls approaching, following, or attacking an eagle. Eagles with white heads were aged as adult and those with dark heads as immature. Gulls were aged as adult (≥4 years), 3-year-olds, or 1- and 2-year-olds (pooled since few were seen), according to Robbins et al. (1966). A “strike” was defined as a gull hitting a coot. A gull successfully singing out and pursuing a coot but failing to strike was a “pursuit.” An eagle flying low over a carcass or live coot with talons lowered was an eagle “attempt.”

**Results.**—During 435 h of observation, Bald Eagles killed four coots and took eight of 33 kills from Greater Black-backed Gulls. Eagle piracy success on gulls with fresh kills was 100% (N = 8), and overall piracy success was 97% (N = 35). Coots comprised >82% of items taken by eagles (Table 1). The proportion of observations of eagles obtaining food with a gull cue versus those taking food without a gull cue is greater than 75% (Binomial test, $P = 0.0003$). Eagles obtained 94% of food items with a gull cue. There was no difference between the proportion of observations where gulls mobbed immature eagles at coot carcasses versus observations where no mobbing occurred (Binomial test, $P = 0.876$) (Table 1). Gulls of all ages mobbed eagles. Eagles were mobbed by a maximum of five gulls ($\bar{x} = 2.8 \pm 1.13$ [SD], N = 28) and obtained food in 23 of 28 observations. Mobbing occurred twice during gull pursuits and three times as an eagle flew low over a gull on the water. Once, five gulls successfully prevented an eagle from stealing food. All observed Bald Eagle foraging was by immatures. Five “piracy attempts” between immature Bald Eagles (Fischer 1985) were recorded, of which two were successful.

All four eagle kills either began as a gull strike or a gull pursuit. Eagles killed three coots by flying low, lowering their talons, and grasping them on the fly-by. Once an eagle landed where a coot dove in 50 cm of water and remained half submerged for 1 min; it then flew to a perch with the coot. Eagles attempted unsuccessfully to capture coots singled out by gulls during two of 31 strikes by gulls. Eagles stopped four of 41 gull pursuits; twice making their own unsuccessful attempts, and twice just flew over the coot and gull with no attempt on the coot. Eagle predation success on coots was 50% (N = 8 attempts).

**Discussion.**—Dependence on one prey species is not unusual for wintering Bald Eagles. Coots were the major food of immature eagles at Lake Mattamuskeet. Bald Eagles relied on dead waterfowl in Missouri (Griffin et al. 1982) and on American Coots in Arizona and New Mexico (Grubb and Kennedy 1982).
Eagles should have little difficulty locating and learning the foraging habits of highly visible Greater Black-backed Gulls. Jorde and Lingle (1988) also suggest such eagle learning behavior. Perched eagles often waited for a gull to land or begin circling before flying to that area. Eagles found most of their food by using a gull cue. Along the Mississippi River, eagles used American Crows (Corvus brachyrhynchos) as a cue by waiting until crows freed a fish from the ice, then robbed the crows (Fischer 1985).

Eagles were not always successful. Attempts failed because coots dove at the last moment. After a maximum of four passes over a diving coot an eagle would return to its perch. We observed eagles grasp prey on the water and dive after prey in a way similar to that described by Grubb and Kennedy (1982). Baker (in Batchelder 1880) observed an eagle dive after a diving coot and remain submerged for a few seconds before surfacing and slowly taking off with the coot. Mobbing did not reduce the success of eagle piracy on gulls. Gulls mobbed eagles which: stole and killed coots; disturbed gulls engaged in pursuits with a coot and flew over gulls on the water without food. Mobbing by gulls tended to increase as: the number of gulls present increased; gull age increased; and the amount of food left on the carcass increased, but we lack data to provide conclusive evidence. We never observed gulls chasing an eagle away from a prey item, contrary to Lien (1975). Any gull staying at a carcass while an eagle approached was at risk. Herring Gulls (L. argentatus) have been attacked by Bald Eagles (Yeager 1950, Poor 1936), and Greater Black-backed Gulls have been found in food remains of eagles (Todd et al. 1982). In this study, Greater Black-backed Gulls always lifted off the water before an eagle arrived at a carcass.

All eagles we observed feeding were immatures, perhaps because many immature eagles may seek wintering areas not used by adults (Griffin 1981). Also, immature eagles winter farther south than adults (Sprint and Ligas 1966). In Maine, survival of immature Bald Eagles increases when food is provided at feeding stations (McCullough 1986). At Lake Mattamuskeet, immature eagles may have higher survival rates because coots killed by gulls provide an easy food source and because adult eagles are not present in competitive numbers. Two explanations could account for the frequency of piracy by Bald Eagles on Greater Black-backed Gulls at Lake Mattamuskeet. First, if as prey size increases, handling time increases, then opportunities for piracy increase (Grubb 1971, Fischer 1985). Gull feeding time on a coot averages 35.2 min (Sobkowiak 1986), increasing the chance of piracy. Secondly, with increases in gull population (Drury 1973), the probability of an encounter with eagles, and consequently eagle piracy, has increased.
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LITERATURE CITED


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Relative contribution of the sexes to chick feeding in Roseate and Common terns.—The relative parental contribution of the sexes during the entire chick-rearing period has received very little attention in marine terns. To our knowledge, no published reports exist for Roseate Terns (Sterna dougallii) and only one study of the role of sexes throughout the entire chick-rearing period has been completed on Common Terns (S. hirundo; Wiggins and Morris 1987). Here we provide some data on this topic.

Methods.—The study area was Cedar Beach, a barrier beach on the south shore of Long Island, New York (Lat. 40°N, Long. 73°W). We trapped, measured, and color marked incubating adult Common Terns in 1984–1987. We trapped and color marked Roseate Terns in 1984 and 1985, but not in 1986 or 1987 because we wanted to reduce disturbance to breeding pairs after the species was proposed for Endangered listing (52 FR 42064). Deliveries of prey to nests of 13 pairs of Roseate Terns and 24 pairs of Common Terns were observed from blinds. We recorded data between 05:00 and 09:00 h EST 3–5 days per week through the chick-rearing period. Longer-billed members of each pair were assumed to be males (see Coulter 1986). Observations of begging corroborated this assumption in four Roseate Tern pairs; we assumed that only females begged from mates (I. Nisbet pers. comm.). Chicks were fenced (as in Safina et al. 1988) to keep them at the nest site. Prey fish length was estimated relative to adult tern bill length (e.g., 1.5 bill-lengths). Data were analyzed using SAS (Ray 1982).

For analysis of prey species composition and prey length, we used data from all pairs in which mates could be differentiated at least part of the time. For these analyses we used 748 nest-h for 13 pairs of Roseate Terns and 1682 nest-h for 24 pairs of Common Terns, 1984–1987.

Analysis of intersexual differences in the number of fish contributed to growing chicks requires that the sexual identity of mates be known for all prey deliveries observed. In 1984, dyes used on both species faded before the end of the chick-rearing period; these individuals were deleted from this analysis. In 1986 and 1987, we did not color mark Roseate Terns. Attempts to identify individual Roseate Tern pair members by other characters (e.g., old bands) were only partially successful during rapid prey exchanges, making the data for most pairs unsuitable for analysis of number of prey delivered. We also deleted from this analysis any pairs which did not raise at least one chick to flying age, because we wished to exclude any parents whose delivery rate may have been abnormal. Consequently, for our analysis of intersexual differences in the number of fish delivered, we were able to use only the 1985 data for Roseate Terns (5 pairs, 305 nest-h) and 1985–1987 data for Common Terns (20 pairs, 1580 nest-h).

Results.—During our 1985 observations, Roseate Tern males delivered 65% (N = 181) of the prey to chicks while females delivered 36% (N = 101; goodness of fit $\chi^2 = 22.7$, df = 1, $P < 0.001$).

During our observations of 1933 Common Tern prey deliveries, males made 45% of 264 prey deliveries in 1985, 51% of 924 prey deliveries in 1986, and 56% of 745 prey deliveries in 1987. Overall, male Common Terns accounted for 51% of prey deliveries observed ($\chi^2 = 2.60$, df = 2, ns).

In both species, males brought longer fish than did females (Kruskal-Wallis $\chi^2 = 8.44$, df = 1, $P < 0.01$ for Roseate Terns, $\chi^2 = 5.74$, df = 1, $P < 0.02$ for Common Terns). For analyses of fish length, we used unconverted bill-length units, not converted mm length estimates; thus our measure of the intersex differences in fish size is conservative, because a male with a fish of 1.5 bill lengths has, in reality, a longer fish than a female with a fish of 1.5 bill lengths. Roseate Tern males (mean culmen = 39.2 ± .04 mm [SE]) brought fish

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averaging 1.6 bill lengths (ca 63 mm), while females' (mean culmen = 37.3 ± .04 mm) fish averaged 1.5 bill lengths (ca 56 mm). Common Tern males (mean culmen = 36.8 ± .03 mm) brought fish averaging 1.6 bill lengths (ca 59 mm), while females' (mean culmen = 34.7 ± .04 mm) fish averaged 1.5 bill lengths (ca 52 mm).

Roseate Tern males brought longer sandeels (Ammodytes sp.), the principle prey, to their chicks than did females, but there was no intersexual difference in the length of sandeels brought by Common Terns (Kruskal-Wallis $\chi^2 = 5.5$, df = 1, $P < 0.02$ for Roseate Terns, $\chi^2 = 1.4$, df = 1, ns for Common Terns). For other fish species, both Roseate and Common tern males brought longer fish to their chicks than did females (Kruskal-Wallis $\chi^2 = 9.43$, df = 1, $P < 0.002$ for Roseate Terns, $\chi^2 = 5.91$, df = 1, $P < 0.01$ for Common Terns).

For combined years, species composition of prey brought to chicks did not differ between adult male and female Roseate Terns (Contingency Table $\chi^2 = 2.46$, df = 1.5, $P < 0.8$; Fig.
In 1985, however, males brought 70 bluefish to nests while females brought only 19 bluefish (goodness of fit $\chi^2 = 29.22$, df = 1, $P < 0.0001$).

The species composition of prey delivered by Common Tern adults for combined years differed between sexes ($\chi^2 = 61.56$, df = 1.5, $P < 0.0001$; Fig. 1). For Common Terns, of the major prey species we individually analyzed, males delivered a significantly higher proportion of sandeels (compared to total prey they delivered; Contingency Table $\chi^2 = 16.86$, df = 1, $P < 0.0001$), and juvenile bluefish (Contingency Table $\chi^2 = 16.86$, df = 1, $P < 0.0001$), while females delivered a higher proportion of pipefish (Contingency Table $\chi^2 = 53.33$, df = 1, $P < 0.0001$). There were no significant inter-sex differences in the proportion of total prey composed of herring, anchovies, or butterfish.

Discussion.—In contrast with our results for a marine system, Wiggins and Morris (1987) found that, throughout the chick-rearing period at a freshwater colony, male Common Terns consistently delivered prey at a rate three times higher than that of females. They cite other studies (e.g., Nisbet 1973) which reported that male Common Tern parents fed chicks more than did females in the period immediately after hatching, when females still do much brooding. Like Wiggins and Morris, we studied provisioning throughout the chick period. The differences in results between our study and that of Wiggins and Morris may relate to basic differences between freshwater and marine systems. We suspect that prey distribution is less predictable and is much patchier in marine systems. Marine and freshwater systems differ fundamentally because tides, interactions with pelagic predatory fish, and large-scale schooling and migration greatly influence prey availability in salt water (Safina and Burger 1988).

Pierotti (1981) found that in Western Gulls (Larus occidentalis) some aspects of the relative contributions of the sexes to parental care were affected by environmental conditions. This, and the contrast between our results and those of Wiggins and Morris, suggest that generalizations about parental care in a species ought not be inferred from a single study if conditions which might affect such important factors as food availability vary fundamentally with differing habitat types within the species' range.

Prey species composition did not differ between sexes for Roseate Terns, but it did for Common Terns. Greater proportions of sandeels and bluefish delivered by male Common Terns suggest a diet more similar to that of Roseate Terns, which concentrate their foraging in the nearby ocean inlet (Safina, Unpubl. data). This raises the possibility that male and female Common Terns forage in different areas.

Interspecific and intersexual differences in mean prey size, if reflective of differences in the range of prey captured and not simply of differences in selecting which prey to deliver to chicks, suggest subtle differences in feeding ecology. However, we cannot rule out the possibility that birds may differentially select which prey to deliver out of the range of prey captured. Such differential selectivity could relate to bill size, wing loading, and/or distance to the colony.

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LITERATURE CITED


Prolonged parental care and foraging of Greater Snow Goose juveniles.—The importance of prolonged parental care in geese and swans (see Kear 1970) in the foraging behavior of juveniles recently has received close attention from researchers. Scott (1984) has shown that Mute Swan (Cygnus olor) juveniles still with their parents spend more time feeding in their daily activity budget than do juveniles which have left theirs. Similarly, Gregoire (1985) found that in foraging flocks of Lesser Snow Geese (Chen caerulescens caerulescens), lone juveniles fed less and moved more than family juveniles. In foraging flocks of Barnacle Geese (Branta leucopsis), family juveniles feed for longer, uninterrupted periods than do juveniles that have been separated from their parents (Black and Owen, in press a). Furthermore, within these flocks, families are more likely to feed in the leading edge of flocks, where the biomass is higher, than do lone juveniles (Black and Owen, in press b). In all instances, these results were related to the lone juveniles’ low status in the dominance hierarchy. The purpose of this study was to compare the foraging activities of lone juveniles and those of juveniles belonging to families in Greater Snow Geese (C. c. atlantica).

We conducted field observations in the springs of 1985 and 1986 along the south shore of the St. Lawrence river estuary between Montmagny and St-Jean-Port-Joli, Québec. Some 40,000 Greater Snow Geese stage along this stretch of shoreline from late March until about 20 May, when they depart for their high-arctic breeding grounds (Gauthier et al. 1984a, 1984b). Most ten-month-old juveniles are still with their parents at that time of the year. Although the birds have recently turned to feeding in cultivated lands to some extent (Bédard et al. 1986, Gauthier et al. 1988), they still obtain well over half of their energy intake from the tidal marshes (Bédard and Gauthier, in press) where they dig up rhizomes of three-square bulrush (Scirpus americanus) (Giroux and Bédard 1988). We studied only geese feeding in marshes. In early April, the ice has just started to disappear, leaving a marsh surface almost totally devoid of aerial vegetation.

We watched (Y. T. and one assistant) the foraging geese from dawn to dusk, from permanent blinds and vehicles located near the edge of the marshes, using 15-45× spotting scopes.
Our daily schedule was dictated by the semi-diurnal tidal pattern, the marsh being inaccessible to geese at high tide. We scanned through the flock and chose in succession a lone juvenile and then families of size ranging from three (two adults and one juvenile) to ten (two adults and eight juveniles). For families of size four and over, we randomly selected only one juvenile for observation. As determining exact family size required some time (up to 25 min), selection of a family for observation was at first based upon a rough estimate of its size: final diagnosis of status was based on cohesion shown during movements.

We recorded the behavioral state of each focal juvenile on a mechanical counter every 6 sec, using an electronic metronome, during 10-min periods (instantaneous sampling; Altmann 1974). We classified behavioral states as follows: (1) Digging. Includes all activities directly oriented toward the consumption of rhizomes at a given digging site: removing mud with the bill, softening the mud with the feet, and pulling, washing, and swallowing rhizomes. This also includes drinking, a rare event. (2) Searching. Refers to displacements made with the head lowered and the bill pointed toward the ground, typical of a goose looking for potential digging sites, and occasionally probing the mud with the bill. Toward the end of the season, this also includes occasional grazing of the new shoots piercing the mud surface. (3) Walking. Refers to displacements made with the head raised. (4) Alert. Refers to situations where a goose is not moving, head raised. (5) Others. Refers to all other behaviors not described above, including agonistic encounters and comfort movements.

We wanted to compare the foraging activities of the birds rather than their total time budgets. Therefore, a small number of focal sequences were discarded when they contained 5% or more of the time devoted to the following behaviors: comfort movements, sleeping, or swimming. This screened out birds with a low feeding drive. We also recorded the number of attacks to which the focal juvenile was subjected. In the case of family juveniles, we pooled aggressions in which the focal juvenile was a victim and those in which it was involved as a secondary participant (aggression originally directed toward another member of its family). The flocks observed were very large (over 1000 individuals), and as we used several observation locations along the 20-km shoreline, we considered the data to be totally independent. We carried out statistical analysis using the SAS package (SAS Institute Inc. 1985a, 1985b).

Digging accounted for most of the recorded behaviors in all categories of juveniles (Table 1). However, juveniles of all categories did not spend the same amount of time digging (Kruskal-Wallis test, $P < 0.0001$; Table 1). A Noether (1976) multiple comparisons test (with $\alpha$ fixed at 0.05) revealed that the only prevailing difference was between lone juveniles and family juveniles taken as a unit. When compared to family juveniles as a whole, lone juveniles spent more time searching (Wilcoxon two-sample test, $P < 0.0001$; Table 1) and

<table>
<thead>
<tr>
<th>Status</th>
<th>N</th>
<th>Digging</th>
<th>Searching</th>
<th>Walking</th>
<th>Alert</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lone juveniles</td>
<td>104</td>
<td>70.5 ± 1.8</td>
<td>23.6 ± 1.5</td>
<td>3.6 ± 0.6</td>
<td>1.9 ± 0.8</td>
</tr>
<tr>
<td>Juveniles from families of 3</td>
<td>90</td>
<td>78.0 ± 1.9</td>
<td>17.2 ± 1.6</td>
<td>3.3 ± 0.6</td>
<td>0.9 ± 0.2</td>
</tr>
<tr>
<td>Juveniles from families of 4</td>
<td>99</td>
<td>81.3 ± 1.7</td>
<td>14.5 ± 1.3</td>
<td>2.7 ± 0.6</td>
<td>1.2 ± 0.3</td>
</tr>
<tr>
<td>Juveniles from families of 5</td>
<td>83</td>
<td>80.2 ± 2.0</td>
<td>15.9 ± 1.9</td>
<td>2.2 ± 0.4</td>
<td>1.5 ± 0.3</td>
</tr>
<tr>
<td>Juveniles from families of 6+</td>
<td>110</td>
<td>79.1 ± 2.0</td>
<td>15.1 ± 1.5</td>
<td>3.5 ± 0.8</td>
<td>1.5 ± 0.3</td>
</tr>
</tbody>
</table>
walking (Wilcoxon two-sample test, \( P < 0.01; \) Table 1). However, both groups spent the same amount of time alert (Wilcoxon two-sample test, \( P > 0.10; \) Table 1). Also, lone juveniles were about 20 times as frequently attacked as were family juveniles (Wilcoxon two-sample test, \( P < 0.0001; \) Table 2). Lone juveniles were most often attacked when digging (80%: 177 of 221 cases) as were family juveniles (85%: 35 of 41 cases). Attacks usually resulted in the departure of the victim both for lone juveniles (98%: 225 of 229 cases) and family juveniles (79%: 33 of 42 cases). If the victim was digging and the aggressor victorious, the latter generally used the digging site it had stolen (84%: 147 of 175 cases).

Therefore, we conclude that when foraging, lone juveniles spend less time digging because they are more often attacked than are family juveniles. Furthermore, the fact that family juveniles can solicit and obtain their parents’ digging sites (Turcotte and Bédard, in press), thereby reducing their searching time, may increase the gap between the two groups. To conclude that energy budgets of lone juveniles are directly affected, we would have to show that they do not make up for their deficit in digging time by devoting a larger fraction of their time budget to feeding. Finally, we also conclude that our data provide no evidence that belonging to a larger family results in more time being available to a Greater Snow Goose juvenile for foraging.

Acknowledgments.—We are grateful to N. Hamel, G. Rochette, G. Picard, and many others for help in the field. G. Gauthier, J. Huot, and G. LaPointe made useful comments on an early draft of this manuscript. This study was supported by an operating grant from the Natural Sciences and Engineering Research Council (NSERC) of Canada to J.B. Y.T. acknowledges receipt of a NSERC scholarship.

LITERATURE CITED


Posthatch brood amalgamation by Mallards.—Eadie et al. (Can. J. Zool. 66:1701-1721, 1988) reviewed the occurrence of brood amalgamation by North American anatids and the hypotheses advanced to account for it. Posthatch brood amalgamation (e.g., creching, gang-brooding, or kidnapping) has been reported more frequently among species of geese (Anserini) and sea ducks (Mergini) than among puddle ducks (Anatini). It has never been reported for Mallards (Anas platyrhynchos; Eadie et al. 1988). Here we report two observations of short-term creche formation by Mallards on wetlands in southern Gotland, Sweden (57°00’N, 18°10’E).

Between 07:45 and 08:15 h on 23 May 1988, while observing waterfowl with a spotting scope on a wetland 1.3 ha in size and 30 cm deep, JDB observed two distinct Mallard broods, each 14-18 days of age (Class IC; Gollop and Marshall, 1954, p. 27 in: Bellrose, Ducks, Geese and Swans of North America, Stackpole Books, 1976). Each brood was attended by a single hen and was feeding in a different part of the wetland. One had 14 ducklings, the other eight. At 08:15 h, the broods were within 10 m of each other. Very soon thereafter, a large brood formed that was attended by a single hen; no other hens were visible. At this time, a Hooded Crow (Corvus corone cornix) swooped to within 20 cm of the brood. Hooded Crows are predators of ducklings (P. Lundberg pers. comm.; K. Sjöberg
pers. obs.). The hen responded by flapping her wings, vocalizing loudly and stretching upwards to meet the crow. The ducklings were clustered together tightly, and when two of them left the brood, the hen quickly herded them back into it. The crow departed, and two min later the brood disappeared into vegetation. By 08:30 h, three distinct broods, each attended by a hen, reappeared close to the site of the crow attack. One brood had 14 ducklings, another eight, and the last, four. (Evidently, the brood of four had been present earlier but was not visible.) Although the wetland was observed continuously from 06:00 h to 10:00 h, no other ducklings were seen. We conclude that the large brood observed comprised a temporary association of the smaller ones.

About 13:00 h on 10 June, 1988, KS and another observer approached a wetland (1.1 ha and 50 cm deep) while conducting brood surveys. There were two distinct Mallard broods, of 12 and 13 ducklings, in different parts of the wetland. Each was 14–18 days of age (Class IC, Gollop and Marshall 1954) and each was with a single hen. One brood was sitting on a rock and the other was swimming about 20 m from it. At the approach of the person, whose job it was to flush any other broods concealed by vegetation, both broods swam toward a narrow constriction in the wetland which led to a heavily vegetated, adjacent water body. They disappeared into vegetation and a brood of 25 was observed following a single hen shortly after. A second hen without ducklings remained behind and made no attempts to retrieve any ducklings from the other hen. No other hens or broods were observed except an older brood at the opposite end of the wetland. We conclude, therefore, that the brood of 25 was a composite of the broods of 12 and 13.

These events shared two important features. First, distinct broods apparently joined together in response to a threat. In one case, the amalgamated brood disbandied soon after the threat, and at least two broods were the same size as before the appearance of the threat. Second, one or more hens appeared to abandon their ducklings to the care of single hen. In one case, the abandoning hens could not be seen while the threat was present; in the other case, the abandoning hen was well away from the amalgamated brood.

In the second case, it might be argued that brood amalgamation resulted as a consequence of the simultaneous approach of the two broods to the single, constricted passage out of the wetland, i.e., that the amalgamation was “accidental” and imposed by physical habitat constraints. This hypothesis, however, does not adequately account for the behavior of the abandoning hen.

Posthatch brood amalgamation may result for a variety of reasons (Eadie et al. 1988), including accidental mixing of ducklings from different broods during predator attacks (Munro and Bedard, J. Anim. Ecol. 46:799–810, 1977), though ducklings in large groups nevertheless survive better than those in small groups (Munro and Bedard 1977; Kehoe Am. J. Zool. 67:406–411, 1989). In the first of the cases we report, however (although marked ducklings are required to know for sure), the constancy of brood sizes before and after the crow attack suggests that these Mallards reestablished family groups. If so, the predator attack did not result in accidental mixing. Regardless, both of our observations of short-term creche formation are consistent with the idea that one selective advantage of creche formation may result from a “safety in numbers” effect (Eadie et al. 1988). Perhaps individuals of some species of waterfowl, like White-winged Scoters (Melanitta fusca) (Kehoe 1989) or Common Eiders (Somateria mollissima; Munro and Bedard 1977) form creches permanently for this reason, while others, like Mallards, do so opportunistically.

Acknowledgments.—We thank J. P. Ball, K. Danell, and J. McA. Eadie for comments. Financial support was provided by the Swedish Natural Science Research Council (NFR), a NFR Visiting Scientist Fellowship, the National Environmental Protection Board, the Swedish Sportsmen’s Association, the Swedish Univ. Agricultural Sciences, and the Natural Sciences and Engineering Research Council of Canada (Grant A7757).—John D. Boos,
**Effects of radio transmitters on the foraging behavior of Barn Swallows.**—In studies using radiotelemetry, it is important to determine the effects of transmitters on the animal’s behavior. Studies on small bats and large birds (>75 g) have shown that the effects of transmitter packages vary greatly depending on species, weight of the package, and means of attachment (Boag 1972, Ramakka 1972, Sayre et al. 1981, Caccamise and Heddin 1985, Gessaman and Nagy 1988, Obrecht et al. 1988). Aldridge and Brigham (1988) showed that a 1:1 relationship should theoretically exist between percent transmitter load and percent decrease in maneuverability of small bats. Bats carrying increasingly heavier loads demonstrated significantly lower maneuverability as predicted. The purpose of the present study was to determine if radio transmitters have a measurable effect on the foraging behavior of Barn Swallows (Hirundo rustica). Transmitter loads weighing 5% of body mass might negatively affect maneuverability making insect capture more difficult (Aldridge and Brigham 1988). If prey capture efficiency is reduced, I predict that the number of foraging bouts and the duration of individual bouts, and the proportion of total time spent foraging by tagged birds should increase.

I monitored five female Barn Swallows (mean mass 18.2 g) nesting on a building on the east shore of Vaseaux Lake, 10 km south of Okanagan Falls, British Columbia. I attached transmitters, resembling in shape those which produce minimum drag (Obrecht et al. 1988), to four individuals mid-dorsally using Skinbond (Pfizer Hospital Products, Largo, FL) cement after clipping a small area of feathers to expose the skin. The transmitters remained attached for 1–4 days, and in two instances, I reattached transmitters to individuals. The transmitter package weighed 0.8–1.0 g representing loads of 4.1–5.6% of a bird’s body mass.

The birds were observed from 10 June to 23 June 1987 during the egg laying or incubation stage of nesting. I assumed that females incubating or laying eggs would leave the nest only for the purpose of foraging. Data were collected during all daylight hours with the majority of observations made in the afternoon. During all observation periods, at least one untagged and one tagged individual were monitored. On several occasions I monitored the behavior of the same bird visually and by radio tracking. The visual observations confirmed my ability to determine by radiotelemetry when birds departed and returned to their nests.

In 121 bird hours of observation I recorded the duration of 264 foraging trips. Tagged birds spent a significantly greater time away from the nest during each foraging bout than did untagged individuals (\(\bar{x} = 11.6 \pm 0.9 \) [SE] and 7.9 \( \pm 0.8 \) min, respectively; \( F = 8.5, P < 0.001 \)). However, tagged birds were not absent for a significantly greater proportion of the total observation period (\( \bar{x} = 35.3 \pm 4.4 \) and 36.6 \( \pm 5.5 \) percent, respectively; \( F = 0.1, P > 0.10 \)). This apparent paradox is due to the tendency for tagged individuals to make fewer bouts per hour than untagged individuals (\( \bar{x} = 1.7 \pm 0.2 \) and 2.4 \( \pm 0.2 \) bouts per hour, respectively; \( F = 3.35, 0.05 < P < 0.10 \)). If the load imposed by radio transmitters influences foraging, only bout duration increased in the manner I predicted. A decrease in the number of bouts by tagged birds resulted in virtually identical total foraging time. This suggests that if the 5% “rule” of transmitter loads for small volant animals is used, there.
may be minimal behavioral effects on foraging. I do not mean to suggest, however, that if the 5% "rule" is observed, caution need not be exercised. Where possible, animals to which transmitters are attached should be observed to confirm "normal" behavior.

Acknowledgments.—I thank P. Hart for field assistance and Mr. and Mrs. F. Dorsey for access to the birds. I am grateful to P. Faure, A. Brigham, C. Koehler, M. Saunders, R. Barclay, K. Cash, and G. Chilton for critically reading the manuscript. The study was funded by Natural Sciences and Engineering Research Council grants to M. B. Fenton and by NSERC and Ontario graduate scholarships and fellowships to the author.

LITERATURE CITED


Attempted polygyny by a Merlin.—The Merlin (Falco columbarius) typically is a monogamous raptor (Palmer, Handbook of North America birds, Vol. 5, Yale Univ. Press, New Haven, Connecticut, 1988). Here I report a polygynous nesting attempt by a male Merlin observed 18 April–27 May 1988, in Saskatoon, Saskatchewan. This color-marked male occupied two different nesting sites (A and B), about 450 m apart, each with a different female. I made sporadic observations totalling about 20 h (10 h at each nest). I saw the male make six prey transfers at nest A and four at nest B. I also observed him copulate twice with female A and once with female B, and I observed him going into both nests, presumably to incubate. During the same period, I made 14 trips to nest A and 15 trips to nest B to collect food remains presumably brought to the nests by the male. The male appeared to have deserted nest B in the fourth week of May. The female remained near the nest until early June, after which she also deserted. Four young were raised successfully at nest A (the hatching date of the oldest young was approximately 1 June).

Polygyny is rarely reported in raptors but is suspected in many of them (Newton, Population Ecology of Raptors, Buteo Books, Vermillion, South Dakota, 1979). Although polyg-
A possible foraging relationship between Black-billed Magpies and American Kestrels.—While studying the behavior of American Kestrels (*Falco sparverius*) in Washoe County, Nevada, I observed a possible foraging relationship between Black-billed Magpies (*Pica pica*) and kestrels. On 20 occasions, June 1987–January 1988, I observed lone magpies flying from distances of up to 100 m away and perching within 2 m of solitary kestrels. During 15 of these observations, magpies remained at their perch and seemed to observe perched, non-feeding kestrels. During the remaining observations, however, magpies perched for 30–90 sec., then slowly approached feeding kestrels along the kestrels’ perch to approximately 30–40 cm before kestrels flew carrying their prey. On two occasions, magpies followed kestrels to subsequent perches and repeated the behavior.

It is possible that magpies which perch near hunting or feeding kestrels utilize food leftover by kestrels. This idea is supported by one observation of a magpie eating food left by a female kestrel. It is well documented that magpies occasionally cooperate to harass larger, less agile raptors and steal their prey (Ryser, *Birds Of The Great Basin*, Univ. Nevada Press, 1985).

In addition, some researchers have suggested that magpies watch hunting coyotes in anticipation of a kill (Ryser 1985). Similar hunting relationships have been reported between certain raptorial species (Bourne, *Ibis* 102:136, 1960; Merchant, *Raptor Research* 16:26–27, 1982). However, this may be the first observation of a corvid systematically seeking a hunting or feeding raptor with the intent of securing food. This strategy may be energetically more efficient than chasing smaller more agile kestrels for the entire prey.

We observed a Loggerhead Kingbird (Tyrannus caudifasciatus) capture five small (1-cm carapace) crabs, Sesarma sp., at 1450 hours on 24 January 1988, on the beach at Casuarina, Great Abaco, Bahamas. The bird was first observed in the branches of a dead Australian pine, Casuarina sp., at the beach edge. After we observed the bird for 3–4 min at a distance of 5 m, it flew directly to the ground and captured a crab almost at our feet. The bird returned to its perch, struck the crab against the branch three times and swallowed it within 5 sec. In 6 min the kingbird captured four more crabs, struck them 0–2 times each and swallowed them shortly after returning to the tree.

Lefebre and Spahn (1987) and Wunderle (1981) suggest that island flycatchers and kingbirds may broaden their diet opportunistically by using typical foraging behavior to capture novel prey. The behavior recorded here is similar to that observed by Lefebre and Spahn, in which a kingbird captured small fish.

Acknowledgments.—This observation was supported in part by grant number 667188 from the PSC-CUNY Research Award Program of the City University of New York. We wish to thank two anonymous reviewers for helpful comments and J. Pratt for renting his house to AEB. The Bahamas Government, through its Ministry of Agriculture and Fisheries gave AEB permission to conduct scientific research on Abaco.—ALBERT E. BURCHSTED, Dept. Biology B-204, College of Staten Island, 715 Ocean Terrace, Staten Island, NY 10301; AND GRACE CHAMBERS, 23 Beechill Park Ave, Belfast BT8 4PR, Northern Ireland, UK. Received 13 Sept. 1988, accepted 29 Jan. 1989.


Common Moorhen parasitizes a Boat-tailed Grackle nest.—On 18 April 1988 in a cattail (Typha angustifolia) marsh at Magnolia Gardens, Charleston County, South Carolina, Post found a Boat-tailed Grackle (Quiscalus major) nest that contained one grackle egg and one Common Moorhen (Gallinula chloropus) egg. He removed the moorhen egg to confirm its identity and to obtain measurements. The moorhen egg was not returned until 20 April, at which time the nest contained three grackle eggs. The first grackle young hatched on 30 April, and the second on 3 May. The third hatched, but died when it was less than one-day-old. Two nest checks made before the grackles hatched showed that the moorhen egg remained in the bottom of the nest under the grackle eggs. On 13 May, Seals checked the nest and saw a downy young moorhen sitting on the rim of the nest. As she approached, the bird jumped down onto some prostrate cattails below the nest. It then jumped into the water, and swam away. There were no moorhen eggshells in the grackle nest. At this time the two grackle young were well grown (10 and 13 days old). If we assume that the moorhen hatched on 13 May, then the interval between hatching and the day it was returned to the nest is 22 days, which is within the known incubation period of the Common Moorhen (19–22 days; Ripley, Rails of the World, David R. Godine, Boston, 1977).

In addition to accepting this extremely large egg (weight: 26.8 g, vs Boat-tailed Grackle egg weight of 7.7 g; Bancroft, Auk 102:43–48, 1985), it appears that the female grackle incubated and turned it even after her own young had hatched and were well-grown. Boat-tailed Grackles in this population do not brood their young for extended periods after they are seven days old, therefore it is surprising that the moorhen egg received enough heat to hatch. Common Moorhens have been reported using old nests of other species (Ripley, op. cit.), and in some populations intraspecific brood parasitism has been reported (Petrie, in Ecological Aspects of Social Evolution, D. I. Rubenstein and R. W. Wragh, eds., Princeton Univ. Press, Princeton, 1986). In this study area they sometimes build their nests on
old grackle nests. This occurrence may be viewed either as an attempted nest take-over or a case of egg dumping. As the nest was not altered in any way, the latter is more likely. The moorhen may have lost her own nest before clutch completion and then used the just-completed grackle nest. The little evidence available (Post, Wilson Bull. 99:724, 1987) indicates that Boat-tailed Grackles will lay eggs in nests containing foreign eggs. This appears to be the first report of inter-specific brood parasitism by the Common Moorhen, as well as the first of a rail parasitizing a passerine nest.—W. Post and C. Seals, The Charleston Museum, 360 Meeting Street, Charleston, South Carolina 29403. Received 21 June 1988, accepted 15 Jan. 1989.
ORNITHOLOGICAL LITERATURE

HANDBOOK OF NORTH AMERICAN BIRDS. By Ralph S. Palmer (ed.), illus. by R. M. Mengel. Yale University Press, New Haven and London. Sponsored by the Smithsonian Institution. 1988. Vol. 4 Diurnal Raptors (Part 1): 433 pp., numerous maps and drawings without legends, one color plate. ISBN 0-300-04059-8. $40.00. Vol. 5 Diurnal Raptors (Part 2): 465 pp., numerous maps and drawings without legends, one color plate. ISBN 0-300-04060-1. $40.00. (ISBN 0-300-04062-8 (v. 4 & 5 set. $80.00).—At last, the fourth and fifth volumes of the “Handbook of North American Birds” are out in print! It has been several years since the editor, Ralph Palmer, first corresponded with this reviewer requesting information on species to be included in this addition to his continuing series. After reading the volumes, the long delay since the last two volumes were published in 1976 is understandable. Palmer has written most of the text himself while enduring the problems associated with a switch in sponsorship from the American Ornithologists’ Union to the Smithsonian Institution. Without a doubt, the set represents the result of years of hard work and personal sacrifice.

The editor basically follows the same format used in previous volumes. There are species accounts for 42 species of raptors. Volume 4 covers vultures through the genus Asturina, and volume 5 includes the remainder of the family Accipitridae (Broad-winged Hawk [Buteo platypterus] through Golden Eagle [Aquila chrysaetos]) through the family Falconidae. The accounts range from two pages or less for hypothetical and controversial North American types such as the King Vulture (Sarcoramphus papa), Roadside Hawk (B. magnirostris), and Northern Hobby (Falco subbuteo) to more than 50 pages for widely occurring species such as the Bald Eagle (Haliaeetus leucopephalus), Northern Harrier (Circus cyaneus), Golden Eagle, and Peregrine Falcon (F. peregrinus). Over 2500 references are cited with the average number per species ranging from approximately 100 each for the American Swallow-tailed Kite (Elanoides foricitatus), Cooper’s Hawk (Accipiter cooperii), Northern Goshawk (A. gentilis), Red-tailed Hawk (B. jamaicensus), Rough-legged Hawk (B. lagopus), and Merlin (F. columbarius) to more than 200 for the Bald Eagle, Northern Harrier, Golden Eagle, American Kestrel (F. sparverius), and Peregrine Falcon. A total of 24 authors, most of whom are well known raptor experts such as S. R. Beissinger, K. L. Bildstein, D. M. Bird, J. M. Gerrard, C. J. Henny, J. A. Jackson, W. J. Mader, B. A. Milsap, D. P. Mindell, J. A. Mosher, J. C. Ogden, J. W. Parker, W. B. Robertson, Jr., J. H. Schnell, M. V. Stalmaster, and C. M. White either wrote or co-authored portions. Names of contributors occur at the ends of their respective sections.

Each account is divided into topics such as description, subspecies, field identification, voice, habitat, distribution, migration, banding status, reproduction, survival, habits, and food. Because of the symbolic nature of raptors in various societies, rather lengthy discussions have also been included in these volumes on human-related subjects. They range from uses of species such as California Condors (Gymnogyps californianus) and Golden Eagles in ceremonies of native Americans to the use of Peregrine Falcons in the sport of falconry. There is one color frontispiece in each volume, while the remainder of the illustrations consisting of black-and-white maps showing breeding and wintering distributions and numerous, uncaptioned line drawings by R. M. Mengel.

Many of the criticisms expressed about earlier volumes continue to apply to volumes 4 and 5. The initial goal of the project which was begun in 1950 was to produce a series in telegraphic style similar to that of the “British Handbook” (Auk 68:384–385, 1951). The many abbreviations used in this style of writing at first make comprehension of the text awkward. This is definitely not leisure reading. The editor frequently lapses from telegraphic style in making anecdotal comments on species in a fashion similar to that used in Bent’s
“Life Histories.” These discussions are more amusing than factual and have previously been published. Since the original concept was to use a concise, space-saving style, it would have been preferable for it to have been used throughout the text. Lengthy discussions of “The numismatic eagle,” “The Washington Eagle,” “A famous eagle,” and “The culinary eagle” (Vol. 4, pp. 230-232), for example, rehash previously published information that could have simply been referenced, saving two printed pages in the species account on the Bald Eagle.

I felt there were two more serious problems with the set. The first concerns the editor’s decision not to adopt common and scientific nomenclature used in the sixth edition of the A.O.U. Check-List (1983). He arranges the species accordingly, but when naming representatives of North American “hawks,” he differs drastically. For example, Harris’ Hawk (Parabuteo unicinctus) is referred to as the Bay-winged Hawk and Roadside and Red-shouldered hawks (B. lineatus) are placed in the genus Asturina while the scientific name for the Gray Hawk is completely changed from Buteo nitidus to Asturina plagiata. A less serious but troubling flaw concerns the editor’s treatment of subspecies classifications. Controversial subspecies of the Osprey (Pandion haliaetus), Red-shouldered Hawk, Rough-legged Hawk, and American Kestrel are treated as valid, but in presenting the Red-tailed Hawk, “Harlan’s” (B. j. harlani) and “Krider’s” (B. j. krideri) subspecies are considered to be merely color morphs without taxonomic status. I felt this presentation is based mainly on the editor’s opinion and could be misconstrued as scientific fact by uninformed or otherwise naïve laypersons for whom even the editor admits these volumes are intended. In view of current controversy over subspecies classifications in birds in general and classification of the Buteo group specifically, I would have preferred a more standard taxonomic arrangement, or at least a presentation of the various views to enable readers to come to their own conclusions concerning the taxonomic status of such a variable group of raptors as Buteo hawks.

My second criticism concerns the distribution maps in individual species accounts. I noted several errors and missing information. For example, there is a shading error on the distribution map for the Black-shouldered Kite (Vol. 4, p. 137). The lack of recent breeding records for Swainson’s Hawk (Buteo swainsoni) in Alaska and Northwest Territories make it questionable if the species actually breeds as far north as shown (Vol. 5, p. 55), the map showing Ferruginous Hawks (B. regalis) as breeding residents of central and northern Idaho is wrong since there have never been any nests recorded in this part of the state (Vol. 5, p. 139) and the map of the historical breeding range of the Peregrine Falcon fails to show the species as a breeding resident of the province of Saskatchewan in historical times (Vol. 5, p. 340).

Despite these criticisms, the set is overall a sound collection of current information on North American raptors. These volumes will undoubtedly find their way into the libraries of raptor specialists, but they should also be seriously considered for inclusion in the reference collections of all professional ornithologists. I intend to adopt them as required texts in my North American Birds of Prey class. Both volumes should be included in the holdings of college and university libraries striving to maintain authoritative collections of works on this group of birds.—Marc J. Bechard.

The Value of Birds. By A. W. Diamond and F. L. Filion (eds.). International Council for Bird Preservation, Technical Publication No. 6, Cambridge, England. 1987:viii + 267 pp., text figs. and tables. £18.50 (paper).—Based on studies presented in 1986 at the 19th World Conference of the ICBP in Kingston, Ontario, this soft-cover volume contains two groups of papers, the first resulting from a symposium on birds as socioeconomic resources, and the second, a workshop on birds as bioindicators of environmental conditions. Most
of the papers are recently completed case studies, but a few are proposals for future work. The title of this publication results from the conviction that, although the "cash value" of wildlife is often an effective argument for conservation, especially when dealing with government officials, it should never be allowed to become subservient to ethical values. Thus this volume is filled with studies of economic ornithology, yet the total worth of birds is not forgotten.

The section on socioeconomics not only contains several general discussions and dollars-and-cents evaluations of avian economic impact in both industrial and "emerging" nations but also has some interesting specific case studies such as one by H. A. Isack on the impact of birds on the culture and economics of the Boran people of Kenya. I found the report by I. J. Skira on muttonbirding in Tasmania particularly enlightening: The annual commercial take of ca 400,000 Puffinus tenuirostris chicks for meat, feathers, and oil by aboriginal Tasmanians is still an important cultural tradition. It is also a cottage industry for people who have little other source of income (it produced a profit of $81,500 in 1985) and has generally been conducted on a sustained-yield basis for centuries. In contrast, the modern noncommercial take for meat (and presumably also for "sport") involves an additional 300,000 chicks and has led to "problems of over-harvesting, physical damage to habitat, alleged cruelty to birds, and general anti-social behaviour of muttonbirders caused partly by alcohol, particularly on opening day" (p. 63). Shades of the first day of deer season in Pennsylvania!

The section on socioeconomic factors concludes with a brief but solid overview of the subject by A. W. Diamond. This chapter could be highly useful for anyone preparing a lecture on modern economic ornithology.

The second part of the book, on birds as bioindicators of environmental conditions, contains papers on a spectrum of contamination of aquatic and marine environments and dry-land habitats and on various groups of birds and their eggs as indicators. Of particular current interest are papers on acid rain in North America and Europe.

The only drawback I found to what is otherwise a valuable resource book lies not in its content but its presentation. Presumably in an economy move (the volume is currently priced at $37.50 by a major American dealer; the back cover notes that it is available from the Smithsonian Institution Press at an undisclosed price in U.S. dollars), the book is printed in small type with inadequate spacing between words and leading between lines. The resultant pages are an effort to read—not impossible, but a real nuisance. Several people to whom I showed my copy agreed. Would that the publishers had foregone the unnecessary luxury of beginning each paper on a right-hand page, leaving 14 blank pages scattered through the book, and instead spread that wasted space among the words and lines of text. The figures are mostly (all?) computer-generated, adequate if often unattractive. Aside from the ICBP logo, the only representation of a bird in the entire book is on the cover—a pedestrian line drawing of a Maleo (Macrocephalon maleo), which is an endemic Sulawesi megapode being driven to extinction despite its economic potential for tourism and trade. The only color in the publication is purple on the cover.

This volume has packed type and good information; it is well worth the effort to read but it is unappealing and overpriced. If birds have esthetic and ethical values, shouldn't books on birds have the same qualities?—MARY H. CLENCH.

THE BALD EAGLE: HAUNTS AND HABITS OF A WILDERNESS MONARCH. By Jon M. Gerrard and Gary R. Bortolotti. Smithsonian Institution Press, Washington, D.C. 1988: 177 pp., 54 figs. in text, 11 appendices (figs. and tables), 10 pp. notes on chapters. $24.95 (cloth), $12.95 (paper).—Gerrard and Bortolotti have produced a delightful, informative and well-written
book; not in a "hard" scientific writing style. It follows closely on the heels of another book on the Bald Eagle (Haliaeetus leucocephalus) by M. Stalmaster (see review, Wilson Bull., 100:330–331, 1988) published in 1987, and thus, in some ways, invites comparison. Briefly, both books have about the same number of chapters covering roughly the same generic types of material but the emphasis differs somewhat. For example, while Stalmaster had a nice discussion on energetics not in Gerrard and Bortolotti, he lacked some of the interesting flight data given by Gerrard and Bortolotti. While the Stalmaster book is more a review of literature sources, Gerrard and Bortolotti draw heavily on their field experiences and on data gathered at a study area at Besnard Lake, Saskatchewan, Canada.

Gerrard and Bortolotti have 12 chapters more or less chronicling the life history of Bald Eagles through the annual cycle from arrival on the breeding grounds, pairbonding, and reproduction back to the non-breeding “wintering” quarters. The book also contains chapters on historical aspects of man’s interaction with Bald Eagles, systematics, and morphology. There is a pleasant departure from the standard chapter title; such as “Talons Awaiting” (meaning diet and hunting techniques), “Whither the Wind Blows” (meaning migration), etc. Each chapter is introduced by one or the other author with a personal evocation of a field experience, usually on their study area, that serves as a starting point for the material that follows. About half of the appendices are of data gathered at Besnard Lake. The book is relatively error free, but one sentence on page 40 says the eagles avoid nesting in sections of habitat where cabins occur and “...so restrict their breeding to the more remote locations...where there has been substantial development.” Shouldn’t it have read “...where there has not been...”? It was nice to see the authors use the term historical correctly. Most raptor types have a penchant for talking about the long term use of nesting sites as historic (being famous or an important event) rather than historical (having a character of history or of long standing). It was also nice to see the authors not engage in the old standby discussion of reversed sexual size dimorphism as many do without any empirical data of the right kind.

An interesting bit of data gathered at their study site was that immatures (with larger wings than adults and thus lighter wing loaded) had an average flapping rate of 167/min while adults were 188 flaps/min. The suggestion that eggs getting buried in the nest and not hatching served the equivalent function of the “Cain/Abel” battle of other Aquila eagle species (p. 83) was of interest. Perhaps more data could be gathered on this circumstance of egg burial and the idea further elaborated.

The book would have been easier to use if the many notes appeared as foot notes at the bottom of the page where that note was referenced rather than as a series of notes by chapter at the back. I did not like their use of “in the seventies and eighties” when referring to years. In the first place they were not consistent in the use of numerical or written years, and why not use 1970s—or did they mean 1870s? Some times I had to go back and reread to make sure I was in the right century. The authors used the word chick for a semi-altricial nesting when they were small and then called them young or nestlings later. Why not just call them eaglets—but at least avoid the word chick? At what point did they change from being a chick to a nestling?

Overall, I liked the book. It is a good review of Bald Eagle biology. It was written such that both the layman and professional will enjoy and benefit from it. The price for the paper back is very attractive.—CLAYTON M. WHITE.

ERIC HOSKING’S BIRDS OF PREY OF THE WORLD. By Eric and David Hosking, text by Jim Flegg. Stephen Greene Press. Lexington, Massachusetts. 1988:176 pp., 158 color and 34 black-and-white photographs. $19.95.—This most recent addition to the already crowded field of photo albums for raptorphiles suffers from a problem typical of works of the genre.
Although a few of the photographs in this 9 × 11 in. "coffee-table book" are quite stunning, readers wanting to know more about the birds depicted will find little satisfaction in the text. And, despite both a title and a passage in the introduction that suggest the inclusion of both diurnal and nocturnal birds of prey, coverage of owls is limited to less than 1% of the text and a single photograph of a Common Barn-Owl (Tyto alba).

More than half of the brief text consists of a lengthy chapter entitled "Family Portraits" that concentrates coverage on well-known diurnal raptors, such as Golden (Aquila chrysaetos) and Bald eagles (Haliaeetus leucocephalus), and Peregrine Falcons (Falco peregrinus). The remainder of the text is made up of three rather sketchy introductory chapters on vultures, hawks, eagles, caracaras, falcons, and the Secretary Bird (Sagittarius serpentarius), together with chapters on their conservation, distribution, and use in falconry. There are no references in the text. My major complaint with the work is not that what is said is necessarily wrong—although there do appear to be a fair number of at least questionable passages—but that what is said is often far from complete and, therefore, frequently misleading. For example, a statement in the chapter on conservation that "Falconers found themselves as a lone militant group opposing" the devastation of birds of prey earlier in this century is almost certain to infuriate a number of hard-working non-falconer conservationists. There are also a number of minor problems. The book was originally published in Great Britain, and although the subject matter appears to address a world-wide audience (there is, for example, a 6-page section on Australian raptors) novice North American readers are likely to be confused by the introduction and then inconsistent use of the term "buzzard" in the text and figure legends (i.e., "Red-tailed Buzzard" but "Red-shouldered Hawk").

In sum, while the book may be of limited value for its photographs, I cannot recommend it for its text. Readers wishing to purchase a colorful introductory work on diurnal birds of prey would do better trying to locate a copy of Leslie Brown's "Birds of Prey: Their Biology and Ecology" (A & W Publishers, New York, 1977).—KEITH L. BILDSTEIN.

**Birding in the San Juan Islands.** By Mark G. Lewis and Fred A. Sharpe. The Mountaineers Books, Seattle, Washington. 1987:220 pp., 75 black-and-white sketches. $9.95 paper.—This is not your ordinary "Birds of . . ." book. It contains a wealth of information for those birders who want to know more than just how to identify or where to find birds. The main body of this attractive book is divided into the following sections: Introduction, Going Birding, Species Accounts, Appendices, Bibliography, and Index.

The Introduction extolls the virtues of the diversity of birds and habitats in the San Juan Islands and tells the reader how best to utilize the information in the book. The authors are obviously concerned about the potential future negative impact of humans on the San Juans because they tell us that "Perhaps the most important goal of this book is to make readers aware of the effects human activities have upon the birdlife of the San Juan Islands and to emphasize the fragility of the environment found here." There is a nice description of the San Juan Island environment. These 350 rocks and islands lie in the rainshadow of the Olympic Mountains. The highest point in the archipelago is the 2409 foot high Mt. Constitution but most are well-below 1000 feet. Both the terrestrial and marine habitats are diverse. This allows the birder ample opportunity to see a cross-section of mainland birds as well as many resident and migrant marine birds. Perhaps the most unusual terrestrial habitats are the dry sites occupied by open woodlands of Oregon white oak (Quercus garryana) and Rocky Mountain juniper (Juniperus scopolorum) which are uncommon in western Washington. Most of the islands are covered by coniferous forest dominated by Douglas fir (Pseudotsuga menziesii), western red cedar (Thuja plicata), and western hemlock (Tsuga heterophylla). There is also a long discussion of the history of humans in the San Juans. With European colonization came dramatic changes in vegetation, much of it coming from
the introduction of the European rabbit (*Oryctolagus cuniculus*) by the British in the mid-nineteenth century. This has been a mixed blessing. On the one hand, its periodic large numbers have devastated parts of San Juan Island but have also attracted large numbers of raptors, particularly the Bald Eagle (*Haliaeetus leucocephalus*), Golden Eagle (*Aquila chrysaetos*)—rare in other parts of western Washington, Red-tailed Hawk (*Buteo jamaicensis*), Cooper’s Hawk (*Accipiter cooperi*), and Great Horned Owl (*Bubo virginianus*). The best area to see these birds is at American Camp on the south side of San Juan Island. This spot is also the only place in the contiguous United States where you can observe the Eurasian Skylark (*Alauda arvensis*) which made its way across Haro Strait from Vancouver Island where it was introduced in 1903. The authors briefly discuss other threats to birds such as construction of homes and roads, commercial fishing, oil pollution, toxic chemical pollution, aquaculture, and recreational boating.

The Going Birding chapter discusses the general principles of birdwatching and introduces the reader to major habitat types which include four marine/freshwater types, two open terrestrial types, five forest/shrub types, a town and garden type, and the aerial type. A site guide section directs the reader to specific locations where particular bird species can be found. My own particular favorite sites are the San Juan ferry route from Anacortes on the mainland to Friday Harbor on San Juan Island. There are usually stops at Lopez, Shaw, and Orcas Islands. If you walk on as a passenger, this is a great inexpensive way to see marine birds and Bald Eagles, particularly in the fall, winter, and early spring when there are large numbers of Bald Eagles, waterfowl, and seabirds in the area. My other favorite is the grasslands on the south side of San Juan Island where raptors are common, and you can see many marine birds from Cattle Point at the southeast tip of the island.

The bulk of the book is dedicated to Species Accounts. The authors follow the names established by the A.O.U. Checklist of North American Birds (1983 and supplements). Besides the basic information on occurrence and helpful hints on identification, most accounts have interesting tid-bits of natural history information that make the reading enjoyable and informative. For example, for the Rhinoceros Auklet (*Cerorinca monocerata*—a species with which I am very familiar) we learn that “Busying themselves during the daylight hours with capturing sand lance and herring, Rhinoceros Auklets fill their beaks with a half-dozen fish apiece before heading home. Both ‘Rhinos’ and puffins possess especially stiff tongues which they use to pin fish against their upper mandibles.” This chapter is liberally supplied with attractive illustrations of birds by Fred Sharpe, many seen engaged in some type of characteristic behavior or in typical habitat.

The appendices contain three major parts. There is a checklist with typical data on status and abundances as well as a calendar that shows when a species is most likely to be observed. A second part, which reflects the authors’ interest in bird conservation, lists the authors’ addresses as well as those of state and federal agencies responsible for bird and mammal protection in the San Juan area. The third part is a list of 127 references cited under the species accounts. Even then, I expect that the authors did not include several references. There is also a Bibliography which lists another 60 general references. There are some inconsistencies in the citation format used here.

This book is relatively free of typographical errors and is nicely illustrated. It is small enough (5.5 × 8.5 in.) to fit into a small day pack and is filled with more information than most bird books of its type and size. If you visit Washington State to see birds, you should buy this book and enjoy the San Juan Islands.

It is fitting that this book was dedicated to the memory of Frank Richardson, a gentle, sensitive man who, after many years as a faculty member at the University of Washington, spent his retirement years in the San Juan Islands. Frank would have been proud of this book.—DAVID A. MANUWAL.
BIRD FINDING IN NEW ENGLAND. By Richard K. Walton, illus. by Barry Van Dusen. David R. Godine, Publisher, Inc., Boston, Massachusetts. 1988:xx + 328 pp., 8 black-and-white drawings, 31 maps. $14.95.—This attractive, “flexibound” field guide size book introduces birders to a sampling of the best birding habitats in New England. The reader is introduced to the area with a six-page description of “New England’s Landscape” in which Walton points out that a particular species of bird is usually bound by fairly strict habitat parameters. He then describes the major physiographic characteristics of New England, including the major mountain ranges, the effects of glaciation on topography and soils, and the characteristics of the continental shelf, coastal, and forest communities. This brief description provides a pleasant and suitable introduction for those birders unfamiliar with New England.

The remainder of the text is divided into three parts. Part One presents detailed descriptions of particular birding sites, each with site map, for the New England states: six in Maine, five in Connecticut, Massachusetts, and New Hampshire, and four each for Rhode Island and Vermont. The verbal directions to the sites are clear and concise, and they utilize common sense landmarks such as McDonald’s restaurants. The site maps are easy to read and follow. In a visit to one site, I had no trouble whatsoever in locating all the recommended stops. In the text, the places which are considered likely to be the most productive are indicated in bold face type, and each site is prefaced by the season or seasons when it can provide the best birding. The text is lively and chatty, with tidbits of history and gossip, as well as notes on the flora and mammals, which perk interest in a site. For example, in the Plum Island description, Walton included a few lines about the famous ornithologists who have studied birds there, and for Newburyport, a paragraph on the well known 1975 sighting of a Ross’ Gull (Rhodostethia rosea). In the description of Concord and the Sudbury Valley, Massachusetts, we are treated to a few anecdotes about Henry David Thoreau. Some of these historical interludes may put off some hard-core birders, but I think that these brief digressions, along with the eight full-page drawings by Van Dusen, add a touch of elegance to a book on bird finding. Overall, the text is well written in a clear, simple, readable style. On the more practical side, the text includes addresses and telephone numbers for such things as motels, ferry and charter boats, and state and federal park headquarters. In addition, there are numerous practical tips such as the necessity for long-sleeved shirts at Plum Island in August when the greenhead flies are active. At the end of the section for each state is a supplemental list of a half dozen or so additional birding localities, together with brief annotations describing what might be found and when.

Part Two, entitled “Seabirds & Hawks,” contains a 10-page chapter on hawk watching localities and a 20-page chapter on pelagic birding in New England by guest author Wayne R. Petersen. The hawk chapter includes a chart showing the migration seasons for more than a dozen raptors, a discussion by season, and a list of 24 hawk watching sites and how to get to them. The pelagic birding chapter includes an “Oceanographic Primer” which discusses factors responsible for the production and concentration of food resources utilized by pelagic birds off the New England coast. This introduction is followed by a section “Pelagic Birding Through the Seasons.” The coverage is thorough and should be very helpful to anyone not experienced in pelagic birding in this area. The chapter concludes with a long list of names, addresses, and telephone numbers for whale watching and pelagic birding tours and two pages of helpful hints for surviving a first pelagic birding adventure. This is a very useful and important chapter.

Part Three, “New England Specialties: Species Accounts” is an annotated list of 66 species. The species accounts include where and when to find the birds. However, since many of the localities mentioned are not listed in the index or in the site descriptions, you had better have your road maps handy. One can quibble with the inclusion of some species (e.g., Black Duck [Anas rubripes]) or the exclusion of others (e.g., American Woodcock [Philohela
The appendices are full of valuable information, including lists of pertinent state organizations such as Audubon societies, New England bird alerts, floral and faunal references, regional and state journals, all with addresses and telephone numbers where appropriate.

The bibliography lists more than 70 titles including many “where to find birds” articles in local journals. It is not exhaustive, however, and fails to include three of the references given at the end of Petersen’s pelagic birds chapter.

The few quibbles that I have with the book are minor. I found no errors in the text, but there is a noticeable clash between the writing styles in Walton’s text and Petersen’s pelagic chapter, which a firmer editorial hand could have smoothed over. Although the maps are clear and well referenced in the text I would have preferred to see more of the distances described to the nearest tenth of a mile, and a map showing the major New England highways would have been helpful. The local bird journal listed for Massachusetts is Bird Observer, not Bird Observer of Eastern Massachusetts (the name was changed several years ago). The only problem with the book is its enormous scope. To limit, for example, Massachusetts to five birding sites means that a significant number of “good spots” went undescribed. If, however, you consider the book a sampling among the better birding localities in New England, the book should prove very useful to visitors from other areas, and, perhaps prompt some New England birders to probe new sites in their own region. Anyone planning to seriously bird New England should own a copy of this book.—William E. Davis, Jr.

The Birds of North Central Texas. By Warren M. Pulich, illus. by Anne Marie Pulich. Foreword by Keith A. Arnold. Contribution No. 9 by the W. L. Moody, Jr., Natural History Series, Texas A&M University Press, College Station, Texas. 1988:439pp., 134 figs., including 112 maps, 22 black-and-white drawings, and one color frontispiece. $45.00 (cloth), $16.95 (paper).—Although the publication of H. C. Oberholser’s two-volume “The Bird Life of Texas” (1974, Univ. Texas Press, Austin) provided a long-awaited and valuable synopsis of the state’s avian natural history, the distribution and status of many species were inadequately described or completely omitted. Consequently, several authors have recently produced books which, for smaller regions of the state, provide detailed and up-to-date information on avian occurrence, migratory patterns, peak numbers, breeding status, and change in population status. This is such a book.

This book focuses on 32 counties covering approximately 25,000 square miles in a zone surrounding the Dallas-Ft. Worth metropolitan complex. Not only is this one of the more densely populated regions in Texas (and home to thousands of birders), but the region also includes some of the state’s most agriculturally abused lands, historically speaking. Despite extensive urban and agricultural tracts, much open terrain persists and 62 percent of the 555 species recognized in Texas regularly occur there. North central Texas also serves as an important migratory corridor and offers winter habitat to many species, such as longspurs, which rarely reach other parts of the state.

The introduction furnishes a short but well-stated justification for the book. However, most of the chapter is devoted to descriptions of climate, topography, vegetative associations, and other environmental conditions found in the four vegetational complexes that occur in the area of coverage. The chapter closes with a brief overview of some of the better public-access areas in which to observe birds. Although this section provides no details such as route maps, the visitor who is unfamiliar with birding locales in north central Texas will nevertheless find this information worthwhile.

The second chapter describes how the data that went into the species accounts were
obtained and evaluated. In the process of describing how he traced the existence of some of the older records, Pulich supplies a thumbnail account of the ornithological history of the area. This leads to a brief discussion of the methods used to judge the validity of sight records and includes a testimonial for the collection of specimens. The terms that are used to describe abundance, frequency, and seasonal occurrence are defined near the end of this chapter.

The bulk of the book (395 pp.) is devoted to the species accounts of 385 species now known to occur within the area. Each species account includes a brief statement of abundance and occurrence for the region. Following this, the author provides extreme arrival and departure dates of species for which many data are available. Where necessary, erroneous or improbable sight records are discussed, as are unusual occurrences, changes in status, and other facts of reported interest. Species accounts close with a discussion of specimen records and identification of the specimens to subspecies. Distribution maps complete the accounts for most species.

The final chapter adds accounts of 33 species which are either extinct, extirpated from the study area but not the state, hypothetically present but unsubstantiated by valid specimen or sight records, or introduced by the state wildlife agency as game birds. Some might find this the most interesting chapter. I was unaware, for example, that Ivory-billed Woodpeckers (*Campephilus principalis*) were collected in the Trinity River bottoms near Dallas as late as 1910. This section of the book will undoubtedly direct the attention of ornithologists to the documentation of species for which better records are needed. The checklist of species in the counties, a cross-tabulated index of county occurrence which follows the last chapter, is a handy means of determining if a species has been properly documented in a given county.

The 22 pen-and-ink sketches and the color frontispiece are by Anne Marie Pulich, the author's wife. Most of the sketches are excellent and add to the volume. Unfortunately, a few of the drawings suffered loss of detail when they were reduced by the printer, but none was too poorly reproduced to be rendered recognizable.

This well-written volume is nicely produced and is virtually free of typographical errors. Although it is not to be confused with a field identification guide, it is an excellent source of reference for both the birding and the scientific community. Furthermore, the detail that is present in this book should be useful in future assessments of the effects of urbanization in an area undergoing tremendous ecological change.—**BRIAN R. CHAPMAN.**

**THE BIRD BIOGRAPHIES OF W. H. HUDSON.** By William H. Hudson, with a foreword by Jonathan Maslow. Capra Press, Santa Barbara, California. 1988:208 pp., with illustrations. Paper $9.95.—W. H. Hudson lived on the pampas of Argentina during the last half of the 19th century, when a sea of tall grasses extended for hundreds of miles and when the Rio Plata had many lagoons and marshes. Hudson lived intimately with the natural world and was an ardent field ornithologist. His major written contribution was "Birds of La Plata" (2 vols., 1920), and it is selections from this work that form the current small edition.

The book includes 49 "bird biographies." As an enthusiastic naturalist, Hudson describes the most interesting behaviors of each of the 49 bird species. He lived many years in the Argentine countryside, and he was one of the first to observe closely and write about these birds. True, the accounts are sometimes anecdotal and anthropomorphic, but remember that his field notes were written before 1875. Keen ornithological skills were reflected in his many interesting discoveries; here I'll briefly mention a few from the text. He found, for example, that the migrant White-banded Mockingbird (*Mimus triurus*) returns with songs
learned a thousand miles away, that various species compete with Ovenbirds (*Furnarius rufus*) for use of their earthen nests, and that Bay-winged Cowbirds (*Molothrus badius*) raise their own young. Frequently the interactions of the pampas gauchos and the birds are described (e.g., how hunting gauchos fed Carancho Hawks [*Polyborus plancus*] that then flushed quail), and for a variety of birds he describes their behavior in captivity. Sadly, even in his time, a host of pampas species were already declining; the Common Rhea (*Rhea americana*) “... is now becoming rare, and those who wish to have a hand in its extermination must go to a distance of three or four hundred miles from the Argentine capital before they can get a sight of it.” Hudson was a conservationist who believed we should set our goals toward a return to more natural conditions. The scientific merit of his writings are shown by his corrections of earlier authors, by many discoveries, and by some predictions that have been verified recently. Throughout the accounts it is evident that Hudson had literary skills (he also wrote the popular book, “Green Mansions”).

In addition to the text are a foreword that succinctly reviews the naturalist’s life and an afterword that “revises” the 1920 species nomenclature of the book. Alas, some errors of revision are evident (e.g., *Bolborhynchus monachus* of Hudson is clearly *Myiopsitta monachus* today, but the afterword lists it as *B. aymara*).

The book will be appreciated by a variety of bird students, particularly those interested in Argentine birds and behavior. (Hudson does include field experiences from elsewhere in South America.) Overall, it is an inexpensive and enjoyable introduction to the birds of the pampas from an era gone by.—Charles F. Leck.

**Biodiversity and Conservation in the Caribbean: Profiles of Selected Islands.** By Timothy H. Johnson. International Council for Bird Preservation. Monograph No. 1, Cambridge, United Kingdom. 1988: 144 pp., 3 Appendices.—During the 17th and 18th centuries, a mammalian species invasion (*Homo sapiens* explorers, conquerors, and entrepreneurs from the European continent) and subsequent *Homo sapiens* introductions (slaves from the African continent) altered for all time the biodiversity of the New World via the Caribbean. The “human introductions” have become the beneficiaries of a largely depleted, indeed threatened, biodiversity for which these disparate, agricultural peoples must now take responsibility in an increasingly interdependent and technological world.

Johnson has “fleshed-out” species lists for 11 Caribbean islands produced from the ICBP’s Island Database established in 1985 to document extant single-island endemic bird species. Mammals, reptiles, amphibians, fish, invertebrates, and plants are also described from the best available sources. Known or presumed extinctions since 1600 are also noted.

Biodiversity and Conservation in the Caribbean (BCC) is a collection of such lists forming profiles with concise subsections on geopolitics, important ecosystems, conservation infrastructure, conservation action, and reference information for 11 islands from the Greater (Jamaica and Puerto Rico) and Lesser Antilles (Dominica, Grenada, Guadeloupe, Martinique, Monserrat, St. Lucia, St. Vincent), a continental island, Cozumel, off Mexico and a true outlier, San Andres, in the southwestern Caribbean Sea.

Rather rigid criteria were employed to determine which islands would be profiled. Islands having an area less than 20,000 km² and at least one extant single-island endemic bird were chosen. In a region of islands where political units sometimes encompass other large islands or cays with single- and two-island endemics, a large number of West Indian species deserving management recommendations have been excluded. The presumption here is that small islands forming larger political units may be excluded as are islands larger than 20,000 km²,
because they have a large core of endemic diversity. Agreed, a primary caveat in the introduction excludes group-island endemics. Yet from a biogeographic point of view, potential users of this planning and management tool may be left with the impression that there are far fewer West Indian endemics to be concerned with, which is certainly not the case with the ICBP, and that small islands close to large ones (Cuba and Hispaniola) may not be as crucial because biodiversity is less of a priority or is more stable on such real estate.

A case in point is Isle of Pines, which has an area of 2560 km², is 49 km from its nearest neighbor, and has 11 two-island endemic bird species. Another case is Islas Saona and Beata, Dominican Republic, and Gonave Island, Haiti, which harbor several endemic species whose last chance for survival may be these off-shore refugia critical for endemic species losing habitat by the minute on Hispaniola. Other examples include the Bahamas archipelago where Andros Island has four species of endemic birds found on only two or three islands but were not included in this treatment.

Apart from this philosophical difference, some technical shortcomings include lack of appendices for listing two-island endemics, for example, which may be discussed in a future monograph, the lack of an index of all species mentioned in the text, which would have been useful, and the absence of island or regional maps illustrating the biogeographical relationship of these 11 islands. There are inconsistencies of single-island species totals for Jamaica and Puerto Rico in the profiles and Appendix 2. And the repeated notion that Peregrine Falcon (Falco peregrinus), a migrant in the Lesser Antilles, be included in the West Indian native fauna is puzzling. If Peregrine, why not Bachman’s Warbler (Vermivora bachmanii), Kirtland’s Warbler (Dendroica kirtlandii), Piping Plover (Charadrius melodus), and Roseate Tern (Sterna dougallii), also listed as endangered in North America and recorded in the Caribbean region?

Continental islands off South America were excluded from this collection of profiles, a convention perhaps acknowledging Bond’s Birds of the West Indies biogeographical description of the region. BCC in contrast includes Cozumel, a continental island off Mexico, which has far less diversity and governmental commitment than Grand Cayman, for example, excluded on the basis that the Grand Cayman Thrush (Turdus bairdii) has not been seen since 1938. Grand Cayman also has the Yucatan Vireo (Vireo magister) which exists at Cozumel, although not mentioned in its profile as a species with very limited Caribbean distribution. Other West Indian endemics, although not single-island species, are the Bahama Yellowthroat (Geothlypis rostrata) (Abaco, Grand Bahama, New Providence, and a few others), Olive-capped Warbler (Dendroica pityophila) (Grand Bahama, Abaco and limited areas of Cuba), Vitelline Warbler (D. vitellina) (Grand Cayman, Swan Island), and Green-tailed Ground Warbler (Microligia palustris) (Beata Island, Dominican Republic).

Notwithstanding minor short-comings from my perspective, this monograph is an important first step in providing concise lists of endemic flora and fauna and conservation recommendations for some of the unique small islands of the Caribbean region. The ICBP suggests that successive publications, though not in book form or comparable depth as this quarto-sized monograph, will include island-group endemics and that another publication covering Atlantic islands will be forthcoming. Perhaps the Bahamas will be represented there.

No other volume presents a species balance-sheet of the post plantation era in the West Indies. Essential descriptions of single-island endemic biodiversity, physical and political geography, government and non-government accomplishments in conservation, and specific recommendations for managing remnant biodiversity are now available in Johnson’s ICBP Monograph No. 1. I am a little disappointed that more species were not dealt with and that no summary was attempted to put into perspective the state of biodiversity and conservation in the Caribbean based on these profiles. And I suppose that editorializing to focus attention
on the conservation responsibility of former and current parent-nations and world conglomerates, that have reaped enormous power and wealth from these tiny nations over the last three centuries, was not attempted in order to remain scientific and objective. That, I suppose, will be left to the users, or bio-auditors, of this essential first step.

This monograph is a must for every student of Caribbean biota for several reasons. It supports continuing efforts of the ICBP, the world’s longest established conservation organization whose primary aim is the protection of wild birds and their habitats. Success of this volume implies data-base profiles for other West Indian islands, large and small, which harbor endemic subspecies and relicts. This volume establishes international recognition and impetus for conservation work in these 11 islands or countries under very difficult economic conditions. It illustrates how much more committed support developing nations require to “turn the corner” on habitat and species loss during the next half-century. Tim Johnson and ICBP are to be congratulated for producing this Caribbean collection first from its Island DataBase and for that we are grateful.—ROBERT L. NORTON.

LOVEBIRDS, COCKATIELS, BUDGERIGARS: BEHAVIOR AND EVOLUTION. By J. Lee Kavanau. Science Software Systems, Inc., Los Angeles, California. 1987:1001 pp., 3 figs., 4 tables. $69.00.—The topics of this book are by no means limited to Peach-faced Lovebirds (Agapornis roseicollis), Cockatiels (Nymphicus hollandicus), and Budgerigars (Melopsittacus undulatus), nor are they limited to just parrots. Instead, this book includes comprehensive discussions on the behavior, morphology, physiology, ecology, biogeography, and evolution of all birds. This is reflected in an impressive reference list (1408 citations) that encompasses almost all aspects of avian biology. The author “aspires to provide extensive factual bases that will facilitate the progress, not only of other students of avian evolution, but also of workers interested in other aspects of avian biology.” The author also strives to illustrate the validity and importance of laboratory studies in avian biology and the potential importance of aviculturists to studies of avian behavior. The author himself shares data from over five years of laboratory studies on lovebirds, cockatiels, and Budgerigars, including 17 clutches of eggs by cockatiels alone. Through the use of these studies, the author presents fascinating ideas on the evolution of bird reproductive behavior from their reptilian ancestors to modern day birds.

Chapter 1, “The Birds and the Continents,” begins with a thorough description of the paleobotany and paleoclimatology of Australia and the evolution of its present day avifauna. The author then gives an in-depth description of the morphology and general behavior of Budgerigars and cockatiels. This treatment continues with a similar description of Africa and the lovebirds. Included within this chapter is a very informative section on vocal mimicry in birds. Chapter 2, “Housing and Care,” includes avicultural information on the housing of lovebirds, Budgerigars, and cockatiels, and their health and veterinary needs. Chapter 3, “Challenging the Lovebird Pair Bond,” uses aviary observations to investigate the nature of the pairbond and courtship behavior in lovebirds. This chapter also includes an extremely detailed discussion of the avian brain. Chapter 4, “Reproductive Cycles, Relict Egg-Care, and Avian Evolution,” presents the central theorem of Kavanau’s book, that cockatiels in their egg-care behavior retain many behavioral features that trace back to ancient times in the reptilian-avian evolutionary lineage. The author recognizes five stages in the line of evolution from late or post-Triassic stem-reptilian ancestors to a modern day bird, the cockatiel. These stages include pre-aves (early post-reptilian ancestors), primitive pro-aves, advanced pro-aves, ancestral birds, and modern birds. This discussion includes
how such factors as endothermy, terrestriality, arboreality, foraging behavior, and habitat have influenced parental egg-care from the Mesozoic to the present day. The basis for much of Kavanau’s ideas on the evolution of incubation behavior and the use of cockatiels to illustrate “relict” behavior is his belief that behavior shows a high degree of evolutionary conservativeness. This chapter should provide much fuel for thought and some debate among students of avian evolution. Chapter 5, “Atypical Pair Bond Formation in Lovebirds,” Chapter 6, “Care of Eggs and Young, and Behavior of Young,” and Chapter 7, “Behavior and Social Interactions,” provide detailed accounts of various aspects of lovebird, cockatiel, and Budgerigar breeding behavior based on numerous laboratory observations and experiments.

The scope of this book is impressive. The amount of information conveyed by the author is almost overwhelming. Nonetheless, the material is presented in an organized fashion and the text is well written. My only complaint about the book is its price ($69) and the paperback binding, which began to fall apart almost immediately. Extended use of this book would soon result in numerous loose pages.

Nevertheless, this book is a must for anyone seriously interested in avian evolution and should be in every major library. It may also be of use to aviculturists who are interested in a more scientific approach to aviculture. Finally, the book’s detailed descriptions of captive bird breeding and experimentation provide numerous ideas for undergraduate and graduate research on captive birds.—Stewart T. Skeate.

AUDUBON WILDLIFE REPORT 1988/1989. By William J. Chandler (ed.). Academic Press, New York. 1988: xviii + 817 pp., many black-and-white photos, maps and graphs. $49.95 (cloth), $24.95 (paper).—This is the fourth volume in a series of summaries that emphasize the wildlife management activities of various agencies of the Federal Government. The 1987 volume was reviewed earlier (Wilson Bull. 100:707–708, 1988) and the current volume follows the format outlined in that review.


Part Four discusses 15 species (seven mammals, five birds, one reptile, and two crabs) that are either endangered or are of some concern. The Bird species are Common Barn-Owl (Tyto alba) by Carl D. Marti, Greater Flamingo (Phoenicopterus ruber) by Alexander Sprunt IV, Eskimo Curlew (Numenius borealis) by J. Bernard Gollup, Bachman’s Warbler (Vermivora bachmanii) by Paul B. Hamel, and Sanderling (Calidris alba) by J. P. Myers. These accounts include an outline of some of the natural history of the species, an Historical Perspective, and sections on Current Trends, Management, Prognosis, and Recommendations. As in the earlier volume, the selection of forms ranges from one that may be extinct (the warbler) to several that are abundant but may have specific problems facing them in the future.

A series of Appendices provides a set of directories for the various agencies as well as other useful information, including a listing of the Federal Endangered and Threatened Species.—George A. Hall.
The North American Loon Fund (NALF) announces the availability of two grant programs for support of new or current research, management, or education projects that may yield useful information for Common Loon conservation in North America. The first of these programs, the Robert J. Lurtsema Research Award, consists of a $1,000 stipend available annually for a suitable research project focused on a member of the Family Gaviidae. Preference will be given to students and independent researchers with limited availability of other funding.

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**INFORMATION FOR AUTHORS**

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THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.
PHYLOGENETIC PATTERNS IN THE GENUS HELIODOXA (AVES: TROCHILIDAE): AN ALLOZYMIC PERSPECTIVE

JOHN A. GERWIN1,2,3 AND ROBERT M. ZINK1

ABSTRACT.—Patterns of genetic variation at 42 presumptive genetic loci were analyzed in Heliodoxa (seven species), Polyplancta aurescens, Urosticte benjamini, and Schistes geoffroyi. Thirty-three loci were variable, either within or among taxa. Heterozygosity values for two representative taxa, H. leadbeateri (H = 0.017) and H. xanthogonys (H = 0.015) were low compared to other birds. Conversely, genetic distance values were high when compared to other birds. D(avg) for species in the genus Heliodoxa was 0.240.

Phenetic and phylogenetic analyses of the genetic data resolve several clusters within Heliodoxa: (1) the phenotypically similar H. jacula and H. leadbeateri are genetically similar (D = 0.025) and form a sister-group to H. rubinoides, (2) the phenotypically similar H. branickii and H. gularis were sister taxa but were genetically distinct (D = 0.090), (3) H. xanthogonys was the most genetically distinct member of Heliodoxa, and (4) H. schreibersii was most closely related to P. aurescens. Our data suggest that Heliodoxa is paraphyletic, and we recommend that P. aurescens be moved to Heliodoxa. Urosticte benjamini and S. geoffroyi were genetically distinct from all other taxa. If our phylogeny is correct, throat color (pink, blue or both) evolved twice (in parallel) within Heliodoxa. Received 28 Feb. 1988, accepted 15 Feb. 1989.

The Trochilidae (hummingbirds), with approximately 325 species, is one of the most diverse bird families. Although much research has focused on ecological and behavioral aspects of hummingbird biology, there have been few modern attempts to infer phylogenetic relationships at any taxonomic level (Zusi and Bentz 1982; Zusi 1985; Schuchmann 1987; C. G. Sibley, unpubl. data). The current taxonomic arrangement of trochilid genera (Morony et al. 1975) differs little from that used by Peters (1945).

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Reasons for this arrangement of taxa are unclear because few explicit character analyses have been performed; presumably, taxa have been grouped by overall morphological resemblance. In addition, 60 of 110 (55%) trochilid genera (ca 110) are monotypic, which likely indicates confusion concerning their systematic relationships (Platnick 1976, 1977). These monotypic genera often exhibit distinctive but unique plumage and morphological features, and thus few synapomorphies exist that reveal phylogenetic affinities of these genera. Understanding the phylogenetic relationships within the family must precede evolutionary interpretations of behavioral and ecological attributes (Felsenstein 1985a), and construction of informative classifications (Wiley 1981).

Biochemical systematic methods offer powerful ways to infer phylogenetic relationships, and especially are useful in groups in which morphological analysis is compromised by either plesiomorphy, extreme divergence, or convergence. We constructed a phylogeny using starch-gel electrophoresis of proteins for one group of hummingbirds, namely, the genus Heliodoxa (brilliants). Polyplanccta aurescens (Gould’s Jewelfront), a species in a monotypic genus, was included to test its purported close relationship to Heliodoxa (Zimmer 1951). Males of these taxa are illustrated in the frontispiece. No modern systematic studies of Heliodoxa exist and the intrageneric classification of Heliodoxa is likely based on overall (phenetic) morphological resemblance, which may not reflect phylogenetic relationships (Wiley 1981). Although molecular systematic studies are appearing with increasing frequency in ornithology (e.g., Lanyon and Zink 1987), no biochemical systematic studies of trochilids have as yet been published. We compare our estimate of phylogenetic relationships with traditional classifications, which in effect represents a comparison of generic and morphological evolution. Genetic distance values and heterozygosity estimates (for two taxa) are reported, and compared to temperate passerines. A classification following phylogenetic principles is presented.

Distribution and previous taxonomy. — Members of the genus Heliodoxa are found primarily in South America, although H. jacula occurs mostly in Central America (Meyer de Schauensee 1966). The genus Heliodoxa (Meyer de Schauensee 1966, Morony et al. 1975) includes eight species: leadbeateri (Violet-fronted Brilliant), jacula (Green-crowned Brilliant), xanthogonys (Velvet-browed Brilliant), rubinoides (Fawn-breasted Brilliant), schreibersii (Black-throated Brilliant), branickii (Rufous-webbed Brilliant), gularis (Pink-throated Brilliant), and imperatrix (Empress Brilliant). Previous workers (in Peters [1945] and Zimmer [1951]) have treated these taxa as members of six different genera (“Heliodoxa” leadbeateri, jacula, and xanthogonys; “Phaiolaima” rubinoides; “Ionolaima” schrei-
bersii; "Agapeta" gularis; "Lampraster" branickii; "Eugenia" imperatrix). As an example of taxonomic uncertainty, note that Zimmer (1951) suggested that H. branickii and H. gularis were conspecific, rather than members of separate genera (Peters 1945). Zimmer (1951) merged the eight species listed above into Heliodoxa because he believed that morphological characters previously used to delimit genera were only sufficient to delimit species, and he proposed the linear sequence (classification) given above. The brilliants possess a forward extension of feathering covering the nasal operculum, a potential synapomorphy for Heliodoxa. However, Zimmer (1951) concluded that "Polyplancta and Clytolaema possibly belong in the same assemblage." Polyplancta and Clytolaema have traditionally been placed adjacent to Heliodoxa.

METHODS

Starch-gel electrophoresis was used to analyze proteins occurring in extracts of liver, muscle, and heart tissue from 30 specimens representing 10 taxa within the Trochilidae and one from the Apodidae (Appendix I). We lacked tissue of one member of Heliodoxa (imperatrix). In addition to Polyplancta aurescens, Urosticte benjamina was included because it is a putative near-relative of Heliodoxa (Peters 1945, Zimmer 1951, Meyer de Schauensee 1966). Schistes geoffroyi was included because it is considered a distant relative of Heliodoxa (Zusi 1985) and served as an additional outgroup. We lacked samples of Clytolaema. Nomenclature follows Meyer de Schauensee (1966). Specimens were collected during several expeditions to various regions of the New World tropics (Appendix I). Samples of tissue were preserved in liquid nitrogen in the field and held at −70°C at the Louisiana State Univ. Museum of Natural Science (LSUMNS), where tissue vouchers remain (see Johnson et al. 1984 for details on collection and preservation methods).

Electrophoretic procedures basically followed Selander et al. (1971), Harris and Hopkinson (1976), and Johnson et al. (1984). Forty-two presumptive genetic loci were scored. For multiple isozymes at a locus, the most anodal one on a gel was scored as a "1" (i.e., sMDH-I). Alleles at each locus were coded by reference to their mobility from the origin. Acronyms for loci follow the International Union of Biochemistry Nomenclature Committee (IUBNC 1984). We entered individual genotypes into the computer program BIOSYS-1 (Swofford and Selander 1981), which generated a table of allelic frequencies, Nei's (1978) and Rogers' (1972) genetic distances, a UPGMA phenogram (Sneath and Sokal 1973), and several distance-Wagner trees (Farris 1972, 1981; Swofford 1981). Three monomorphic loci (two general proteins ["AB"] and mACOH [Enzyme Commission 4.2.1.3] were removed from the analysis to accommodate current program dimensions (this has very minor effects on estimates of genetic variation). Distance-Wagner trees were generated by specifying (in BIOSYS-1) the Multiple Addition Criterion and allowing for 30 partial networks to be used during each successive step. Prager and Wilson's (1976) "F" value was used to determine which partial networks would be saved. Distance-Wagner trees were rooted using the Fork-tailed Palm-Swift (Reinarda squamata) (Apodidae) as the outgroup. To evaluate the robustness of the distance-Wagner trees, we used the bootstrap procedure (Felsenstein 1985b) to resample with replacement phylogenetically informative loci 100 times. From each of the 100 bootstrapped replicates of loci, we produced a distance-Wagner tree. A majority-rule consensus tree was then produced from the 100 trees.

Much controversy surrounds the cladistic analysis of alleles (Patton and Avise 1983, Buth
1984, Swoford and Berlocher 1987). One can consider the locus as the character and alleles as (unordered) character states, or, consider each allele as a character and the states as present or absent. Buth (1984) strongly recommends the former approach, because coding alleles as present or absent can lead to ancestral nodes having "no" alleles. The coding of polymorphisms is also unresolved, and there are several alternatives. We coded each locus as a character and alleles at each locus as unordered states. In the case of polymorphism, the most frequent allele was considered the state; this approach, as most, ignores frequency information, which is a definite drawback. These data were analyzed using the computer program HENNIG86 (written by James S. Farris). HENNIG86 was used to find all most parsimonious trees. We present this analysis as a compromise of coding and analysis (see Dittmann et al. 1989 for a similar approach).

The use of genetic distance data to infer phylogenies is a much debated issue (see Farris 1985, 1986; Felsenstein 1986), as is the use of a phenetic vs a cladistic algorithm (Nei 1987). Thus, we present results of both of these methodologies.

RESULTS

Genetic variation. — Of 42 loci scored, 33 (79%) showed at least two allelic variants across all taxa (Table 1). Attempts at scoring and analyzing five other loci were unsuccessful (AK-1 [E.C. 2.7.4.3], ALDO [4.1.2.13] GLUDH [1.4.1.3], mGOT [2.6.1.1], mSOD-1 [1.15.1.1]). Nine loci were monomorphic and fixed for the same allele in all taxa: ACP (3.1.32), EST-2 (3.1.1.3), HK (2.7.1.1), LAP (3.4.1.3), LDH-1 (1.1.1.27), mSOD-2 (1.15.1.1), and the three loci listed above. One locus, ADH (1.1.1.1), was nearly fixed, except for a single variant allele. At 13 loci, the Trochilidae shared a single allele, but one different from that in the swift.

Because some measures of within-sample genetic variation are especially dependent on sample size, we considered only our largest samples (H. leadbeateri [N = 9] and H. xanthogonys [N = 5]). For these taxa, observed mean direct-count heterozygosity \( H(\text{obs}) = 0.017 \pm 0.013 \) [SD] and \( 0.015 \pm 0.007 \); percentage of polymorphic loci (95% criterion) is 10.26 and 7.69; and the average number of alleles per locus is 1.15 and 1.08, respectively.

Genetic distances. — The average Nei’s genetic distance among the 10 Trochilidae examined is \( 0.331 \pm 0.138 \) [SD] (N = 45) (Table 2). Within Heliodoxa interspecific genetic distances range from 0.025 (H. leadbeateri vs H. jacula) to 0.367 (H. rubinoides vs H. branickii); the average is 0.240 \( \pm 0.088 \) (N = 21). Within Heliodoxa including Polyplancta the average genetic distance is 0.241 \( \pm 0.080 \) (N = 28). Genetic distance values for Polyplancta vs Heliodoxa range from 0.128 (vs H. schreibersii) to 0.283 (vs H. xanthogonys).

Branching diagrams. — Dendrograms depicting hypothesized relationships (Figs. 1 and 2) reveal several common features. Three genetically defined subgroups exist within the brilliants, one consisting of H. leadbeateri, H. jacula, and H. rubinoides, one of H. schreibersii and P. au-
rescens, and the third of H. gularis, H. branickii, and possibly H. xanthogonys. Urosticte benjamini is placed adjacent to the Heliodoxa group; however, this warrants comment. The placement of Urosticte varies when two alternative, nearly equal-length distance-Wagner trees are compared. We portray the distance-Wagner tree that is consistent with the majority of our branching diagrams. The three subgroups of taxa discussed above were present in the consensus distance-Wagner tree (not shown) based on 100 bootstrapped replicates of loci, which corroborates the trees depicted in Figs. 1 and 2. Schistes geoffroyi is consistently placed as a sister taxon to all other hummingbirds.

Cladistic analysis.—Patterns of allelic distribution among taxa reveal the basic phylogenetic framework implied by our data. We found no shared alleles that unite the genus Heliodoxa as currently recognized into a monophyletic group. There are, however, alleles at two loci (DIA, PGM-1) shared by all Heliodoxa (including Polyplandta) except H. xanthogonys. Within the Heliodoxa, several sister groups were identified. One group has H. leadbeateri and H. jacula as sister taxa linked with H. rubinoides. Heliodoxa leadbeateri and H. jacula share apparently derived alleles at four loci (sMDHP, MPI, NP, PEPD) and there are only frequency differences between these taxa at other loci. Heliodoxa rubinoides shares alleles at two loci (AK-2 and G6PDH) with these taxa. The phenotypically similar H. xanthogonys shares one allele at GPT with the leadbeateri-jacula-rubinoides group. An allele at GPT supports H. schreibersii and P. aurescens as sister taxa; these taxa share an allele at sMDHP with U. benjamini (a possible example of parallelism).

Zimmer (1951) suggested that the allopatric taxa H. gularis and H. branickii were conspecific. Two alleles (at ADA, mMDH2) support the monophyly of this species pair. Six differences, however, were found between these taxa, four of which were apparently fixed (GPT, sIDH, NP, PEPD); these taxa are likely not conspecific. Two loci (sMDHP, SORD) support the grouping of H. branickii, H. gularis, and H. xanthogonys; the latter species has five autapomorphies. At G6PDH these three taxa share a derived allele with H. schreibersii.

In comparing Urosticte with Heliodoxa, we found 12 fixed differences and seven alleles that Urosticte shares with at least one other member of the Heliodoxa (relative to Schistes). Schistes exhibited 14 unique alleles and few shared with Heliodoxa, consistent with its designation as a sister taxon to the other hummingbirds.

Coding loci cladistically (Appendix II) resulted in 22 informative characters. HENNIG86 found 27 equally parsimonious trees (not shown); we do not know how many trees are one or a few steps longer. Of interest are groups that occur in high frequency: H. leadbeateri, H. jacula, and H.
**Table 1**

**Allelic Frequencies for Variable Loci. Numbers in Parentheses Are Frequencies of Alleles Not Fixed for That Locus. Allelic Designations by Letter Indicate Fixation at That Locus**

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<td>A</td>
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<td>0.124</td>
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<td>–</td>
<td>0.259</td>
<td>0.291</td>
<td>0.280</td>
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<td>0.137</td>
<td>0.249</td>
<td>0.422</td>
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<td>0.241</td>
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<td>0.312</td>
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<td>0.303</td>
<td>0.255</td>
<td>0.276</td>
<td>–</td>
<td>0.224</td>
<td>0.296</td>
<td>0.261</td>
<td>0.357</td>
<td>0.395</td>
<td>0.727</td>
</tr>
<tr>
<td>6 <em>H. schreifersii</em></td>
<td>0.213</td>
<td>0.204</td>
<td>0.207</td>
<td>0.234</td>
<td>0.238</td>
<td>–</td>
<td>0.203</td>
<td>0.133</td>
<td>0.363</td>
<td>0.329</td>
<td>0.731</td>
</tr>
<tr>
<td>7 <em>H. rubinoides</em></td>
<td>0.125</td>
<td>0.129</td>
<td>0.318</td>
<td>0.367</td>
<td>0.341</td>
<td>0.225</td>
<td>–</td>
<td>0.238</td>
<td>0.436</td>
<td>0.359</td>
<td>0.785</td>
</tr>
<tr>
<td>8 <em>P. aurescens</em></td>
<td>0.276</td>
<td>0.263</td>
<td>0.240</td>
<td>0.259</td>
<td>0.283</td>
<td>0.128</td>
<td>0.259</td>
<td>–</td>
<td>0.351</td>
<td>0.351</td>
<td>0.749</td>
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<tr>
<td>9 <em>S. geoffroyi</em></td>
<td>0.562</td>
<td>0.535</td>
<td>0.473</td>
<td>0.456</td>
<td>0.436</td>
<td>0.447</td>
<td>0.573</td>
<td>0.427</td>
<td>–</td>
<td>0.487</td>
<td>0.759</td>
</tr>
<tr>
<td>10 <em>U. benjami</em></td>
<td>0.429</td>
<td>0.429</td>
<td>0.432</td>
<td>0.530</td>
<td>0.494</td>
<td>0.395</td>
<td>0.445</td>
<td>0.427</td>
<td>0.668</td>
<td>–</td>
<td>0.810</td>
</tr>
</tbody>
</table>

**Table 2**

Matrix of Nei's (1978; below diagonal) and Rogers' (1972; above diagonal) genetic distances.
rubinoides (27 of 27 trees, 100%), H. schreibersii and P. aurescens (23 of 27 trees, 85%), and H. gularis and H. branickii (18 of 27 trees, 67%). There is little consensus among the 27 trees concerning other relationships. However, in 15 of 27 trees (56%), the P. aurescens-H. schreibersii clade and H. leadbeateri-rubinoides-jacula clade were sister taxa. The affinities of H. xanthogonys are uncertain, and different placements of this taxon contributed to the lack of strict consensus among the 27 trees; the relationships of this taxon require further research.

**DISCUSSION**

Genetic variation.—Two taxa (H. leadbeateri and H. xanthogonys) for which a sufficient number (see Nei 1978) of individuals was available for analysis exhibited low values of $H$(avg) (0.017, 0.015) relative to other birds ($H$[avg] = 0.05; Barrowclough 1980, Corbin 1983). Low heterozygosity estimates have been reported for some insular species (Selander 1976, Yang and Patton 1981). *Heliodoxa xanthogonys* is, in fact, an “insular” species in that populations inhabit islands of submontane vegetation (“tepuis”) in southeast Venezuela and therefore are almost certainly isolated from other populations. Insularity might explain the low $H$(avg) value of xanthogonys; however, these isolated populations often exist at high density (J. P. O’Neill pers. comm.). *Heliodoxa leadbeateri*, on the
other hand, is distributed from Colombia and Venezuela south to Bolivia (Meyer de Schauensee 1966). Nei et al. (1975) have shown that low values of $H$ are expected if the total population of a species has passed through a lengthy bottleneck or has existed at very low density for many generations. Although little is known of the natural history of many hummingbird taxa, $H. \text{leadbeateri}$ is not currently a low-density taxon (Davis 1986, J. V. Remsen pers. comm.). It is, therefore, unclear why $H$ is low in this taxon. It is unknown if low $H$ values are a general phenomenon in hummingbirds. In any event, heterozygosity levels at allozyme loci are dubious predictors of adaptive potential or "genetic health" (Lande and Barrowclough 1987). Past demographic events may leave a signature in patterns of heterozygosity, but discovering these events and their biological significance is difficult. Therefore, the significance, if any, of low levels of heterozygosity is unclear.

Genetic differentiation.—Genetic differentiation among avian taxa, particularly passerines, is low relative to other vertebrates (Barrowclough and Corbin 1978; Avise et al. 1980a, b; Barrowclough et al. 1981; Avise and Aquadro 1982; Zink 1982). Relatively few workers, however, have investigated genetic differentiation in nonpasserines (Guttman et al. 1980, Barrowclough et al. 1981, Gutiérrez et al. 1983, Johnson and Zink 1983,
Lanyon and Zink 1987, Zink et al. 1987, Hackett 1989). Although values of \( H \) may be low, genetic distance values at all taxonomic levels in the hummingbirds exceed those previously reported for other birds (see Barrowclough 1980). Our average value for congeners, 0.241, is four times higher than that observed between most congeneric species of oscines (Avise and Aquadro 1982). Also, Johnson et al. (1988) report an average D among species within \( Vireo \) and \( Hylophilus \) of 0.293 (see also Marten and Johnson 1986, Christidis 1987); they also argue that there are too few vireo genera, which inflates genetic distance values among congeners. Hackett (1989) estimated an average interspecific genetic distance of 0.103 ± 0.061 for the nonpasserine genus \( Sterna \). Our within-family value of 0.404 is similar to values obtained in studies of other nonpasserines (Gutiérrez et al. 1983, Lanyon and Zink 1987). Our between-family value of 1.45 (swift vs hummingbirds) is also high, but the number of independent comparisons at this level is small; this value is reported for future comparison.

Factors that could increase genetic differentiation in hummingbirds relative to temperate birds include (1) increased age of lineages; (2) aspects of social systems (e.g., polygyny; see Wilson et al. 1975); and (3) aspects of demography (fluctuating effective population sizes) thought to accelerate divergence for selectively neutral characters (Nei 1987). It is unknown which of these factors contributes most, if at all, to the increased levels of genetic differentiation observed in hummingbirds surveyed herein. If allelic substitutions in birds are selectively neutral (Barrowclough et al. 1985) and accrue at a constant rate (molecular clock hypothesis), then species of \( Heliodoxa \) are on average older than species of temperate birds. Regarding (2), some species of hummingbirds are lekking, a mating structure that reduces the variance effective population size and might increase rate of genetic drift. The magnitude of this effect is unknown in \( Heliodoxa \); most species exhibit loosely organized leks (T. A. Parker pers. comm.). In other hummingbirds (\( Phaethornis \)) a high level of genetic differentiation has been found between some lekking species (Gill and Gerwin unpubl. data). Concerning (3), some species of hummingbirds are known to be isolated and/or restricted in distribution, which might cause Ne to fluctuate, and at least one of these (\( H. xanthogonys \)) shows an increased level of genetic divergence relative to most of its congeners. Other evidence (Braun and Parker 1985, Capparella 1987) reveals that Neotropical birds show greater genetic differentiation than temperate birds, which argues for the “greater age” hypothesis because these taxa do not all share aspects (2) and (3). Disentangling alternative causal factors is difficult and all might contribute to increased genetic differentiation among hummingbirds.
Protein evolution and body temperature.—Avise and Aquadro (1982) suggested that high avian body temperature limits the number of tolerable alleles at enzyme loci. As a consequence, reduced genic diversity would lead to a smaller substrate for genetic divergence, accounting for the conservative nature of avian intertaxon genetic differentiation. Hummingbirds possess the highest body temperature among birds (Welty 1982), and hummingbirds surveyed genetically to date consistently exhibit low heterozygosity relative to other birds. However, genetic differentiation among hummingbird taxa exceeds that observed for most other birds. These observations illustrate the potential interaction of factors influencing protein evolution, such as high body temperature (reduced genetic variation) and greater antiquity of hummingbird clades (increased genetic differentiation). Avise and Aquadro’s (1982) interesting hypothesis deserves continued attention because our results seem partly consistent with their predictions. Experimental tests of enzyme kinetics also might reveal constraints on amino-acid substitutions in avian enzymes.

Relationships among taxa.—Relationships within the Trochilidae in general are uncertain, with only a few studies addressing phylogenetic or taxonomic relationships (see Zimmer 1951; Graves 1980, 1986; Stiles 1983; Schuchmann 1987, unpubl. data; Zusi and Bentz 1982; Gerwin unpubl. data). This problem is not unique to hummingbirds; that is, there are few studies investigating phylogenetic relationships for most Neotropical avian taxa. For Heliodoxa and its relatives, we referred to published checklists as a starting point for hypothesized relationships and our results are compared to Zimmer’s (1951) linear sequence.

Thirteen alleles are shared by the 10 trochilid members, uniting them into a monophyletic group when compared to R. squamata. Doubts about the hummingbirds’ nearest relative have existed for some time (Sibley and Ahlquist 1972, Zusi pers. comm.). DNA-DNA hybridization data support the placement of the Apodidae as the sister group, albeit a rather distant one (Sibley et al. 1988). Our electrophoretic data confirm only that the swift is a distant outgroup from the trochilid taxa surveyed (we would need to survey other taxa to confirm a swift-hummingbird sister-group relationship). We found, however, 10 alleles shared by both the hummingbirds and the swift.

In our analyses, several phylogenetic patterns emerged consistently. The well differentiated (from each other and other taxa) S. geoffroyi and U. benjaminii branch off first and second, respectively. Compared with members in the genus Heliodoxa, their average genetic distances are high (0.489 ± 0.059 and 0.448 ± 0.043, respectively), suggesting a relatively ancient connection with Heliodoxa. However, the placement of U. benjaminii varied when several alternative distance-Wagner trees were generated.
This ambiguity is the result of conflicting allelic distributions. *Urosticte benjami* shares common alleles with some member of *Heliodoxa* at five loci and an allele (at sMDHP) with *H. schreibersii* and *P. aurescens*. These results represent convergence of alleles or retentions of ancestral states. *Urosticte* has always been placed near *Heliodoxa* in taxonomic treatments and has been tentatively placed in a higher-level clade defined as “Andean” hummingbirds (R. Zusi, pers. comm.). Recently, Schuchmann (1987) proposed that *Urosticte* and *Ocreatus underwoodii* (Booted Racket-tail) are sister taxa, and that these plus *Eriocnemis* and *Haplophaedia* form a monophyletic group. The sharing of six common alleles by *Urosticte* with various *Heliodoxa* may reflect its inclusion in a group whose only members studied at this time were *Heliodoxa*. The high number (12) of genetic differences lead us to advocate its continued exclusion from *Heliodoxa- Polyplancta*. Protein comparisons with proposed relatives should clarify the relationships of *Urosticte* to other taxa. In addition the monophyly of *Heliodoxa* would be tested.

The genus *Heliodoxa*, as currently recognized, is paraphyletic because our results indicate that *Polyplancta* is a sister taxon to *H. schreibersii*. However, no synapomorphies unite the genus *Heliodoxa* as a monophyletic group, even when *Polyplancta* is included. Recent data on mating behavior and vocalizations also support the conclusion that *Polyplancta* is a member of the *Heliodoxa* assemblage (Schuchmann pers. comm.). We suggest that the monotypic genus *Polyplancta* be moved to *Heliodoxa*, and the monophyly of the resultant group studied further.

In sum, our phenetic and cladistic analyses of the protein data support the following groupings: (1) *H. jacula-leadbeateri-rubinoides*, (2) *H. branickii-gularis*, and (3) *H. schreibersii-P. aurescens*. We hypothesize that groups 1 and 3 are sister groups, and we are uncertain as to the placement of *H. xanthogony* and group 2. Comparing the genetic groupings with the patterns of resemblance in external morphology (frontispiece) reveals the difficulty in inferring phylogeny from the latter. Apart from the obvious synapomorphy (white crissum) linking *branickii-gularis*, systematic affinities are obscured, potentially by sexual selection for male plumage traits.

*Phenotypic evolution: a genetic perspective.*—In theory, sexual selection can yield rapid phenotypic differentiation and speciation (West-Eberhard 1983). The phenotypic diversity observed in hummingbirds, especially in male plumages, might be a result of sexual selection (Futuyma 1987). If so, then these speciation events were not recent, owing to the relatively high genetic differentiation observed among *Heliodoxa* sister-taxa, excluding *leadbeateri-jacula* ($D = 0.025$). In some north temperate species, such as *Dendroica* warblers, plumage differentiation, perhaps via sexual
selection, and speciation have occurred with little or no allozymic differentiation (Barrowclough and Corbin 1978). Additional comparisons of levels of allozymic divergence in sexually dimorphic species might clarify the role of sexual selection in avian speciation.

Classifications, by virtue of their linear sequences of taxa, have long reflected that throat color is evolutionarily plastic, or subject to parallel evolution, in hummingbirds. Classifications have not grouped all taxa with similar throat colors. Nonetheless, throat color, when used with other characters, could indicate systematic relationships. Within the Heliodoxa assemblage exist pink (rubinoides, branickii, gularis), blue (jacula, xanthogonys), green (leadbeateri), black (schreibersii) and green and black (P. aurescens) throat colors (see frontispiece). We hypothesize that these “states” are homologous, both in terms of “throat color” as a character, and in instances (pink, blue) when more than one species share the same character states. For instance, although we recognize that the pink throats of branickii, gularis, and rubinoides exhibit slight differences, we assume for argument that the pink throats are homologous.

The most closely related taxa in Heliodoxa are leadbeateri and jacula (\(D = 0.025\)), and they have distinct throat colors (green and blue, respectively). This contrasts with the situation in the sister taxa branickii and gularis, which have pink throats. Males of these taxa are overall very similar phenotypically (in addition to throat color they also share white undertail coverts, and their overall body plumage color is similar), and yet their genetic distance value (\(D = 0.090\)) is 3.5 times higher than leadbeateri vs jacula. The pink-throated rubinoides is placed adjacent to the leadbeateri-jacula cluster, and is genetically quite distinct from the other pink-throated forms. Although the body plumage colors of H. schreibersii and P. aurescens are strikingly different, the genetic data unite them as sister taxa. Perhaps most surprising is the placement of xanthogonys. Genetically, it is the most distinct member of the group (\(D[avg] 0.289\)). Phenotypically, however, its throat pattern closely resembles jacula. In our analysis xanthogonys is genetically similar to branickii-gularis, although we are not confident of a sister-group relationship. The high level of genetic differentiation, coupled with an apparent lack of phenotypic differentiation between xanthogonys and the leadbeateri-jacula cluster, highlights one aspect of this analysis—the complexity and plasticity of phenotypic change in hummingbirds relative to patterns of genetic affinities. If our phylogenetic hypothesis is correct, then the pink and blue throat colors appear to have arisen in parallel. One could not use throat color, per se, to unite taxa into a classification reflecting phylogeny, because parallel evolution prevents this (Wiley 1981, Christidis 1987). Although plasticity in throat color has been suspected in hummingbirds,
based on arrangements of past classifications, our data represent the first direct evidence.

Classification of brilliant and Gould's Jewelfront.—We advocate a phylogenetic classification (Wiley 1981), one which preserves the branching order (genealogy) of our phylogeny (Fig. 2). Within any level of the hierarchy we follow the "sequencing convention" of Wiley (1981) to reflect phylogenetic positions of taxa. Thus, phylogenetic patterns can be recovered fully from our classification.

Genus Heliodoxa

- **H. imperatrix incertae sedis**
  - Division 1
    - *H. xanthogonys*
  - Division 2
    - Subdivision 1
      - *H. gularis*
    - *H. branickii*
    - Subdivision 2
      - Section 1
        - *H. schreibersii*
        - *H. (Polyplancta) aurescens*
      - Section 2
        - *H. rubinoides*
        - *H. jacula*
        - *H. leadbeateri*

**ACKNOWLEDGMENTS**

We are grateful to numerous colleagues at the LSUMNS who collected the tissue samples used in this study. We thank J. S. McIlhenny and the late B. S. Odum for providing funds for those expeditions. We thank F. B. Gill and M. B. Robbins, of the Philadelphia Academy of Natural Sciences, for providing tissue samples. We thank J. P. O'Neill for painting the frontispiece. F. B. Gill, T. A. Parker, J. P. O'Neill, K.-L. Schuchmann, and C. G. Sibley provided unpublished data and fruitful discussions. D. L. Dittmann and K. Kennedy assisted with lab work. We are especially indebted to N. Tague and S. J. Hackett for preparing the figures. N. Tague and G. Kinney assisted with typing. K. W. Corbin kindly supplied a copy of his computer program GENESYS. Financial support for this research was provided by grants from the Wilson Ornithological Society (Fuertes Award), the American Museum of Natural History (Chapman Fund), and the LSUMNS. K. W. Corbin, S. J. Hackett, M. S. Hafner, J. V. Remsen, Jr., and two anonymous reviewers provided helpful comments on the manuscript.

**LITERATURE CITED**


## Appendix I

**Species Studied, Sample Sizes, and Regions for Specimens (Precise Localities Available from the Authors)**

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td>Violet-fronted Brilliant</td>
<td>9</td>
<td>Ecuador (8), Peru (1)</td>
</tr>
<tr>
<td><em>Heliodoxa leadbeateri</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green-crowned Brilliant</td>
<td>3</td>
<td>Peru (2), Ecuador (1)</td>
</tr>
<tr>
<td><em>H. jacula</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fawn-breasted Brilliant</td>
<td>1</td>
<td>Peru</td>
</tr>
<tr>
<td><em>H. rubinoides</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-throated Brilliant</td>
<td>3</td>
<td>Peru</td>
</tr>
<tr>
<td><em>H. schreibersii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rufous-webbed Brilliant</td>
<td>2</td>
<td>Peru</td>
</tr>
<tr>
<td><em>H. branickii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pink-throated Brilliant</td>
<td>1</td>
<td>Peru</td>
</tr>
<tr>
<td><em>H. gularis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Velvet-browed Brilliant</td>
<td>5</td>
<td>Venezuela</td>
</tr>
<tr>
<td><em>H. xanthogonys</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gould’s Jewelfront</td>
<td>4</td>
<td>Peru (2), Bolivia (1), Venezuela (1)</td>
</tr>
<tr>
<td><em>Polyplancta aurescens</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-tip</td>
<td>1</td>
<td>Peru</td>
</tr>
<tr>
<td><em>Urosticte benjamini</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wedge-billed Hummingbird</td>
<td>1</td>
<td>Ecuador</td>
</tr>
<tr>
<td><em>Schistes geoffroyi</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fork-tailed Palm-Swift</td>
<td>1</td>
<td>Peru</td>
</tr>
<tr>
<td><em>Reinarda (Tachornis) squamata</em></td>
<td></td>
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</tr>
</tbody>
</table>
## APPENDIX II

States of Loci Used as Input into the Computer Program HENNIG86. States for Polymorphic Loci Were Those Representing the Most Common Allele at a Locus. Characters Were Coded as Nonadditive. Only Phylogenetically Informative Loci Were Used, and the Two More Distant Outgroups (*U. benjamini* and *R. squamata*) Were Excluded.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locus&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td><em>H. leadbeateri</em></td>
<td>A</td>
</tr>
<tr>
<td><em>H. jacula</em></td>
<td>A</td>
</tr>
<tr>
<td><em>H. gularis</em></td>
<td>A</td>
</tr>
<tr>
<td><em>H. branickii</em></td>
<td>A</td>
</tr>
<tr>
<td><em>H. xanthogonys</em></td>
<td>B</td>
</tr>
<tr>
<td><em>H. schreibersii</em></td>
<td>A</td>
</tr>
<tr>
<td><em>H. rubinoides</em></td>
<td>A</td>
</tr>
<tr>
<td><em>P. aurescens</em></td>
<td>A</td>
</tr>
<tr>
<td><em>S. Geoffroyi</em></td>
<td>C</td>
</tr>
</tbody>
</table>

<sup>a</sup> 1 = *sCOH*, 2 = *ADA*, 3 = *ADK*, 4 = *ESTD*, 5 = *G6PDH*, 7 = *sGOT*, 8 = *GPT*, 9 = *GR*, 10 = *sDH*, 11 = *mDH*, 12 = *LA*, 13 = *LGG*, 14 = *mMDH*, 15 = *sMDH*, 16 = *MPI*, 17 = *NP*, 18 = *PGI*, 19 = *PGM*, 20 = *PPRO*, 21 = *SDH*, 22 = *DIA*. EC numbers in Table 1.

<sup>b</sup> Characters 3, 7, 9, 13, and 18 had polymorphisms (Table 1) which could be considered informative; however, these characters were coded as invariant here.
KIRTLAND'S WARBLERS ON THE NESTING GROUNDS DURING THE POST-BREEDING PERIOD

PAUL W. SYKES, JR.,1 CAMERON B. KEPLER,1 DAVID A. JETT,1 AND MICHAEL E. DECAPITA2

ABSTRACT.—Eighty-four Kirtland's Warblers (Dendroica kirtlandii) were caught 122 times during 8809 net-h at five study areas on the breeding grounds in northern lower peninsular Michigan during the post-breeding seasons (16 August–30 September) from 1984–1987. This more than quadruples the known number of post-breeding season records for the species at the nesting colonies. Combined with older records within and south of the breeding grounds, this information indicates that a substantial number of breeding birds remain in Michigan through September, and a few individuals probably remain into early October. Mean capture rate per 100 net-h was 1.4 warblers at the principal study area for the post-breeding period. Males were captured more frequently than females. Most hatching year (HY) birds had completed Prebasic I Molt by the end of August whereas Basic Molt occurred throughout the 16 August–30 September study period in after hatching year (AHY) birds. Subcutaneous fat deposition was low for both sexes in the two age classes prior to migration. Migration apparently consists of two waves—an early departure (mid-August to early-September) of HY birds, and late departure (late September) of AHYs. These late-season birds may face some man-induced stresses after the traditional 1 May–15 August breeding area closure. An extension of the closure through mid-September is recommended. Received 12 Jan. 1989, accepted 20 Feb. 1989.

Because the endangered Kirtland’s Warbler (Dendroica kirtlandii) breeds within a highly restricted range centered in a six-county region in northern lower peninsular Michigan (Walkinshaw 1983), great care has been taken to protect the bird and its habitat during the period it remains in the state. The Kirtland’s Warbler Recovery Team (Byelich et al. 1976, 1985) stressed the need to restrict human use of all state and federal forest lands used by the warbler for nesting (95–97% of current nesting areas; Ryel 1984, Weise 1987) from 1 May to 15 August each year, embracing the mid-May to mid-July nesting period (Mayfield 1960). These closure dates include time before and after the known nesting period to buffer the birds from undue stresses which might affect survival. The original recovery plan further indicated that a review of “all land use plans” should be made “in order to avoid conflicts which may be detrimental to the birds” (Byelich et al. 1976, p. 25).

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2 U.S. Fish and Wildlife Service, Manly Miles Building, 1405 South Harrison Road, East Lansing, Michigan 48823.
Biologists working with Kirtland’s Warblers have concentrated their efforts during the breeding period, when adult males are highly vocal and conspicuous and nests are easily found. By mid-July most singing has ceased, most chicks have fledged, and the birds become more cryptic in plumage and behavior, requiring increased effort to find them (Mayfield 1960, Walkinshaw 1983). By August, the first Kirtland’s Warblers have returned to the Bahamas (Hundley 1967, Wallace 1968, Robertson 1971). It has been widely assumed that most of the warblers leave the nesting areas in August (Mayfield 1960; Walkinshaw 1983; Byelich et al. 1976, 1985), as relatively few published records exist (11 for the second half of August and 13 for all of September); only one record is later than 1933 (Table 1).

In 1984 we began banding Kirtland’s Warblers in the post-breeding season. We were initially surprised to capture five birds in September in a modest banding effort. Since the presence of large numbers of Kirtland’s Warblers on the breeding grounds during the post-breeding season would alter our understanding of their post-breeding and migratory behavior, and also have major implications for their management, we decided to obtain information on the numbers, age, sex, and locations of these late-summer early-fall birds.

**STUDY AREAS AND METHODS**

Study areas in 1984 were east of Grayling in Crawford County, Michigan, and included: (1) “Bald Hill” (Sect. 20, T-27-N, R-1-W) north of North Down River Road, two net sites, 23 nets; and (2) “Bucks Crossing” (Sect. 8 and 9, T-27-N, R-2-W) along Lewiston grade on Camp Grayling Artillery Range (Michigan National Guard), three net sites, 39 nets. Study areas in 1986 included: (1) “Bald Hill,” four net sites, 48 nets; and (2) “McKinley” (Oscoda County, Sect. 10, T-26-N, R-4-E); 2 net sites, 14 nets. Study areas in 1987 were in the vicinity of Grayling and Mio and included: (1) “Bald Hill,” six net sites, 91 nets; (2) “Muskrat Lake” (Oscoda County, Sect. 13, T-27-N, R-1-E) north of County Road 608, three net sites, 26 nets; and (3) “Mack Lake” (Oscoda County, Sect. 21 and 22, T-25-N, R-3-E) west and east of U.S. Forest Service Road 4147 in the southcentral part of the 1980 Mack Lake Burn (Simard et al. 1983) on the Huron National Forest, two net sites, 27 nets. When a study area was used for more than one field season (Bald Hill) the same net sites and net lanes were used each year, with new net sites and lanes being added as needed.

Netting operations were conducted from 8 August–6 September 1984, 13 August–13 September 1986, and 1 July–29 September 1987. The post-breeding period in this paper refers to 16 August to 30 September. This 46-day period has been subdivided into three intervals for analysis: 16–31 August, 1–15 September, and 16–30 September. Birds were captured with black nylon ATX 4-shelf, 12 × 2.6-m tethered mist nets with 36-mm mesh stretched between two 3-m-high pieces of galvanized electrical thin-walled conduit. Each net had its own set of support poles. Net configurations, conforming to vegetative cover and topography, consisted of single nets, nets end to end in line, and in T and L configurations, right angle crosses, etc.

Netting was generally conducted during the morning, as winds and/or high temperatures
made afternoon or early evening netting impractical on most days. No netting was attempted during rainy weather. We generally did not operate the same net sites on consecutive days in an attempt to prevent birds from acclimating to the nets. Nets were checked and birds removed every 15–30 min. All Kirtland’s Warblers were released at the same net where captured after being banded, aged (adult = after hatching year—AHY; immature = hatching year—HY), sexed, and checked for molt. Birds were checked for subcutaneous fat using the system developed by Helms and Drury (1960) with the following fat classes: 0 = no fat, 1 = trace of fat in furculum, 2 = furculum lined with thin layer of fat, 3 = ¼ to ½ furculum full of fat, 4 = furculum full of fat but not bulging, 5 = furculum bulging and fat along sides, etc. If an individual was captured more than once, fat class for the latest date captured was the value used in this paper. Handling of the warblers was completed as quickly as possible. Birds were transported and held in soft white open mesh nylon delicate-fabric laundry bags (36 × 45 cm with 4 × 4 mm mesh) with zippers across one end. All birds were uniquely color banded, two bands per leg, with red, light green, light blue, or yellow plastic butt-end size 1 bands bonded with a drop of acetone in combination with a size 1 U.S. Fish and Wildlife Service band.

The sex and age ratios, and proportion of birds with fat were compared using contingency table analyses. Capture rates were assumed to follow a Poisson process and were compared among time periods using the normal approximation of Cox and Lewis (1978).

RESULTS

During the post-breeding season, 84 different Kirtland’s Warblers were caught 122 times. Twenty-five of these birds were recaptured a total of 38 times. Each bird was tallied only once in each of the three time intervals used in our analysis, even if caught more frequently. This resulted in the addition of 23 recaptures to our data set (Table 2). These 107 records are comprised of 57 males, 39 females, and 11 sex-undetermined HY birds.

There was a continuing drop in the number of individuals of both age classes (HY = 38 to 0 and AHY = 25 to 11) from late August to late September, with a significantly greater decrease ($\chi^2 = 13.65, P < 0.0002, df = 1$) for HYS than for AHYS during this period (Table 2). HY birds made up 49% (N = 52) of the total captures (includes recaptures) throughout the post-breeding season. HY birds constituted a majority (60%, N = 38) of birds netted during 16–31 August, decreasing to 42% (N = 14) from 1–15 September, and strikingly, to 0% from 16–30 September.

The netting effort (8809 net-h for the five study areas) is summarized in Table 3. Our effort increased each year of the study. Only at Bald Hill (with 76% of the total net-h) did we net in all three years; all other areas were netted during one year. Mean capture rate per 100 net-h at Bald Hill for the 16 August–30 September period was 1.4 (Table 4). This rate was variable from year to year with 3.7, 2.2, and 1.0 birds for 1984, 1986, and 1987, respectively. The annual decline of capture rate over the years at Bald Hill reflects an annual increase in our banding effort later in the season combined with coverage in more marginal sites in an attempt to capture dispersing birds.
<table>
<thead>
<tr>
<th>Date</th>
<th>Locality</th>
<th>Age</th>
<th>Sex</th>
<th>Type of record</th>
<th>Collector or observer</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 Aug 1903</td>
<td>Near junction of N. Branch Au Sable with Au Sable Riv., Crawford County</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>J. A. Parmalee</td>
<td>Wood and Frothingham 1905</td>
</tr>
<tr>
<td>20 Aug 1933</td>
<td>Red Oak, Oscoda County</td>
<td>U</td>
<td>M</td>
<td>Specimen UMMZ 97791</td>
<td>A. D. Tinker</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>25 Aug 1904</td>
<td>Roscommon County</td>
<td>U</td>
<td>M</td>
<td>Sighting</td>
<td>—</td>
<td>Frothingham 1906</td>
</tr>
<tr>
<td>26 Aug 1933</td>
<td>SE of Lovells, Crawford County</td>
<td>U</td>
<td>M</td>
<td>Specimen UMMZ 72366</td>
<td>A. D. Tinker</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>26 Aug 1933</td>
<td>SE of Lovells, Crawford County</td>
<td>U</td>
<td>M</td>
<td>Specimen UMMZ 155,431</td>
<td>A. D. Tinker</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>27 Aug 1915</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,703</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>30 Aug 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>I</td>
<td>F</td>
<td>Specimen UMMZ 125,705</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>30 Aug 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 125,706</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>30 Aug 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 125,707</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>30 Aug 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,708</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>31 Aug 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,709</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>1 Sep 1915</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,704</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>1 Sep 1930</td>
<td>3 mi. SE Lovells, Crawford County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 65993</td>
<td>A. D. Tinker</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>3 Sep 1904</td>
<td>Near junction of N. Branch Au Sable with Au Sable Riv., Crawford County</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>J. A. Parmalee</td>
<td>Wood and Frothingham 1905</td>
</tr>
<tr>
<td>4 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,710</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>5 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 125,711</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>6 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>I</td>
<td>M</td>
<td>Specimen UMMZ 125,712</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>6 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 125,713</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>7 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 125,714</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>8 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>F</td>
<td>Specimen UMMZ 125,715</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
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### Table 1
CONTINUED

<table>
<thead>
<tr>
<th>Date</th>
<th>Locality</th>
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<th>Sex</th>
<th>Type of record</th>
<th>Collector or observer</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,716</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>9 Sep 1916</td>
<td>Near Luzerne, Oscoda County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,717</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>28 Sep 1919</td>
<td>7 mi. S of Houghton Lake Village, Roscommon County</td>
<td>A</td>
<td>M</td>
<td>Specimen UMMZ 125,718</td>
<td>M. M. Peet</td>
<td>Wood 1951</td>
</tr>
<tr>
<td>29 Sep 1975</td>
<td>Mack Lake Mgt. Area, Oscoda County</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>P. F. Schempf</td>
<td>Schempf 1976</td>
</tr>
</tbody>
</table>

* A = adult, I = immature, U = unknown.

* F = female, M = male, U = unknown.

* Specimen data at the Univ. of Michigan Museum of Zoology (UMMZ) courtesy of Janet Hinshaw.

* Complete references listed in Lit. Cit. section.
Capture rates at Bald Hill for the late-breeding season (1 July–15 August) compared to the post-breeding season (16 August–30 September) are presented in Table 4. Using data for all three years, the capture rates during the late-breeding period were higher than during the post-breeding period \((Z = 4.11, \ P < 0.0001)\). Within the post-breeding period, data from all three years were used to compare late August with early September, but only 1987 data were available to make comparisons with late September. Capture rates did not differ between late August and early September \((Z = 0.51, \ P = 0.6080)\), but rates for both periods were higher than that of late September \((Z = 3.01, \ P = 0.0026 \text{ and } Z = 1.98, \ P = 0.0479)\). Sample sizes from other study areas in 1987 and earlier were too small for statistical analyses.

The late recaptures (1 September or later) in 1987 totalled 11 individuals (Fig. 1). These birds were assumed to be present in the vicinity continually at least until the last date shown, as all initial bandings of the 11 birds and all subsequent recaptures were within the same study areas. Some of these birds were probably present later than we recorded them. The late recaptures consisted of 18% HYs (1 male, 1 sex undetermined) and 82% AHYs (7 males, 2 females). All birds initially banded in September 1987 were subsequently recaptured in the same month. The last date on which a Kirtland’s Warbler was recaptured (29 September 1987 at Bald Hill) equals the latest published record (Schempf 1976) for the species on the breeding grounds.

The sex ratio of the captures when sex was determined (89%) was 1.4 males to 1 female, but this was not significantly different from 1:1 \((\chi^2 = \)
### Table 3

**Mist Netting Efforts and Kirtland's Warbler Capture Rates in Michigan during the Post-Breeding Period**

<table>
<thead>
<tr>
<th>Period</th>
<th>Bald Hill</th>
<th>Mack Lake</th>
<th>Muskrat Lake</th>
<th>Bucks Crossing</th>
<th>McKinley</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total net-h</td>
<td>Capture rate/100 net-h</td>
<td>Birds (N)</td>
<td>Total net-h</td>
<td>Capture rate/100 net-h</td>
</tr>
<tr>
<td>1984</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(16 Aug–6 Sep)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16–31 Aug</td>
<td>275</td>
<td>3.6</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1–15 Sep</td>
<td>78</td>
<td>3.8</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>353</td>
<td>3.7</td>
<td>13</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1986</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(16 Aug–13 Sep)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16–31 Aug</td>
<td>743</td>
<td>2.4</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1–15 Sep</td>
<td>557</td>
<td>1.8</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1300</td>
<td>2.2</td>
<td>28</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1987</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(16 Aug–29 Sep)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16–31 Aug</td>
<td>2246</td>
<td>1.4</td>
<td>31</td>
<td>340</td>
<td>0.3</td>
</tr>
<tr>
<td>1–15 Sep</td>
<td>924</td>
<td>1.3</td>
<td>12</td>
<td>671</td>
<td>0.3</td>
</tr>
<tr>
<td>16–30 Sep</td>
<td>1842</td>
<td>0.5</td>
<td>9</td>
<td>231</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>5012</td>
<td>1.0</td>
<td>52</td>
<td>1242</td>
<td>0.3</td>
</tr>
<tr>
<td>Study area total</td>
<td>6665</td>
<td>1.4</td>
<td>93</td>
<td>1242</td>
<td>0.3</td>
</tr>
</tbody>
</table>

*Dates in parentheses are inclusive for data used in this paper.*
Table 4
Comparison of Capture Rates of Kirtland’s Warblers by Years for Bald Hill Study Area for Late-Breeding and Post-Breeding Seasons

<table>
<thead>
<tr>
<th>Year</th>
<th>Late-breeding season</th>
<th>Post-breeding season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 July-15 August</td>
<td>16 August-30 September</td>
</tr>
<tr>
<td></td>
<td>Total net-h</td>
<td>No. birds captured</td>
</tr>
<tr>
<td>1984</td>
<td>201</td>
<td>8</td>
</tr>
<tr>
<td>1986</td>
<td>119</td>
<td>3</td>
</tr>
<tr>
<td>1987</td>
<td>1989</td>
<td>58</td>
</tr>
<tr>
<td>Total</td>
<td>2309</td>
<td>69</td>
</tr>
</tbody>
</table>

2.42, \( P = 0.1198, \text{df} = 1 \) (Table 2). This preponderance of males was found in both HY and AHY age classes and for each of the three post-breeding season intervals.

Our study of molt in this species during the post-breeding period has just commenced, so the results presented are preliminary. The Prebasic I Molt (Postjuvenal Molt, body plumage only; see Mayfield 1960) in HY birds (\( N = 37 \) different individuals) was generally completed by the end of August. However, there was a wide range of variability among individuals, as some had completed their Prebasic I Molt by 16 August, while others extended to the end of August (32%) and a few to 10 September. We did not observe any sign of molt in remiges and rectrices of HY birds after the end of August. The Basic Molt (Postnuptial Molt) in AHY birds (\( N = 38 \) different individuals) spanned the length of our study period, 16 August through 29 September. As with HY birds, the start and completion of molt was highly variable among individual AHYs. Two AHY males required more than 30 days, and that for an AHY female exceeded 28 days. Although the work presented in this paper does not extend long enough into the fall to encompass the entire Basic Molt, it may prove similar in length to the 39–42-day period that Nolan (1978) found for the Prairie Warbler (\( D. \) discolor).

Fat classes were determined for 26 Kirtland’s Warblers (12 HYs, 14 AHYs) in 1986 and 50 warblers (25 HYs, 25 AHYs) in 1987. In 1986, the percentages of individuals for the fat classes (0 [none], 1, 2, 3, 4, and 5 [highest value]) were 31, 50, 15, 4, 0, and 0, respectively and for 1987, the percentages were 40, 4, 24, 26, 6, and 0, respectively. Combining classes 0 and 1 into a low fat group and classes 2–5 into a high fat group showed that proportionally more high fat birds were caught in 1987 than in 1986 (\( \chi^2 = 9.41, \ P = 0.0022, \text{df} = 1 \)). This difference may be a result of more late captures in 1987.
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DISCUSSION

Our study reveals that a substantial portion of the Kirtland's Warbler population remains on the breeding grounds in Michigan at least through September. Also, from 18 August–12 September 1985, biologists with the Michigan Department of Natural Resources made eight observations of 10 unmarked (4 in September) Kirtland's Warblers on the breeding grounds (E. S. Carlson and J. A. Weinrich pers. comm.). We infer that a few birds may remain to the first half of October. The published records of migrant Kirtland's Warblers \( (N = 15) \) in areas south of the breeding grounds after 1 September support this hypothesis (Table 5). Five Kirtland's Warblers (33%) were located within 310–460 km of the breeding area from 2–25 October.

HY birds appear to leave the breeding grounds earlier than adults, because proportionally fewer young of the year are found in September. This apparent decrease could result from HY birds migrating earlier than AHY birds, from higher mortality of HY birds during this period, from post-breeding dispersal by HY birds, or from temporally based changes in capture probabilities. We feel that HY birds, in general, migrate earlier than adults. Nolan (1978) found this to be true with Prairie Warblers. Also, during the post-breeding period, HY birds complete their wing and tail molt by the end of August, while in adults this extends through

![Fig. 1. Late recaptures of Kirtland's Warblers in 1987. Each solid dot represents a recapture; dashed lines indicate the birds were probably present in the vicinity.](image-url)
<table>
<thead>
<tr>
<th>Region</th>
<th>Date</th>
<th>Locality</th>
<th>Age°</th>
<th>Sex°</th>
<th>Type of record</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern</td>
<td>24 Sep 1965</td>
<td>Bloomfield Hills, Oakland County</td>
<td>I</td>
<td>M</td>
<td>Sighting</td>
<td>Nickell 1965</td>
</tr>
<tr>
<td>Michigan</td>
<td>29 Sep 1951</td>
<td>Muskegon</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>Whelan 1952</td>
</tr>
<tr>
<td>Southern</td>
<td>14 Sep 1948</td>
<td>Pickering, Durham County</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>Walkinshaw 1983</td>
</tr>
<tr>
<td>Ontario</td>
<td>2 Oct 1915</td>
<td>Point Pelee, Essex County</td>
<td>I</td>
<td>M</td>
<td>Specimen</td>
<td>Harrington 1939</td>
</tr>
<tr>
<td>Northern</td>
<td>2 Sep 1948</td>
<td>Loves Park, Winnebago County</td>
<td>A</td>
<td>M</td>
<td>2 sightings</td>
<td>Smith and Parmalee 1955</td>
</tr>
<tr>
<td>Northern</td>
<td>2 Sep 1935</td>
<td>Near Hilliard Bridge, Cleveland</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>McQuown 1944</td>
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<tr>
<td>Indiana</td>
<td>8 Sep 1940</td>
<td>Cleveland</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>McQuown 1944</td>
</tr>
<tr>
<td>Northern</td>
<td>22 Sep 1929</td>
<td>Springfield Township, Lucas County</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>Campbell 1940</td>
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<tr>
<td>Ohio</td>
<td>26 Sep 1943</td>
<td>Rocky River Valley, Cuyahoga County</td>
<td>U</td>
<td>U</td>
<td>Sighting</td>
<td>Williams 1943a, b</td>
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<tr>
<td></td>
<td>28 Sep 1969</td>
<td>Bowling Green</td>
<td>U</td>
<td>U</td>
<td>Sighting of 2 birds</td>
<td>Clench 1973</td>
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<tr>
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<td>5 Oct 1941</td>
<td>Rocky River Valley, Cuyahoga County</td>
<td>U</td>
<td>U</td>
<td>2 sightings</td>
<td>Williams 1941a, b</td>
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<tr>
<td></td>
<td>7 Oct 1934</td>
<td>Near Hilliard Bridge, Cleveland</td>
<td>U</td>
<td>U</td>
<td>2 sightings</td>
<td>McQuown 1944</td>
</tr>
<tr>
<td></td>
<td>14 Oct 1886</td>
<td>Cleveland</td>
<td>U</td>
<td>U</td>
<td>Found dead</td>
<td>Davies 1906</td>
</tr>
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</table>

° A = adult, I = immature, U = unknown.
° M = male, U = unknown.
° Complete reference listed in Lit. Cit. section.
September. Furthermore, Berger (1968) found migratory restlessness in captive (hand reared) HY Kirtland’s Warblers (N = 9) between 25 August–8 September.

Of the August records in the Bahamas, one Kirtland’s Warbler was listed as an adult female (Wallace 1968), two males and a female were listed with age unspecified (Hundley 1967), and another was listed with age and sex unspecified (Robertson 1971). Our experience with Kirtland’s Warblers leads us to question the reliability of aging and sexing this species at this time of year unless examined in hand. The more subdued plumages of the two age groups in the fall made it difficult to distinguish between age/sex classes. However, a few (but not all) adult males retain some trace of black in the region of the lores, and these individuals can be aged and sexed in the field if seen at close range under good lighting conditions. Given these conditions, the age and sex for the August sight records in the Bahamas may not be reliable.

Our data suggest that Kirtland’s Warblers tend to migrate alone in the fall rather than in groups. This is supported by published accounts of migrating individuals with no mention of conspecifics (Mayfield 1960, Clench 1973, Walkinshaw 1983). Hence, most HY birds probably make their first southward migration alone in the absence of adults with prior experience.

Subcutaneous fat deposition was surprisingly low for the 76 individuals (1986 and 1987 combined) examined. Many of the birds during 16 August–29 September showed no fat deposition (31% in 1986 and 40% in 1987). There were no birds in 1986 in the two highest fat classes (4 and 5) and only 6% in fat class 4 and none in fat class 5 in 1987. This small sample suggests that most Kirtland’s Warblers have not accumulated a large energy reserve by late September prior to initiating migration. Data for HY and AHY birds were similar in this regard. Migratory birds are known to build up fat just prior to migrating (Wolfson 1945, Cherry 1982, Pettersson and Hasselquist 1985, Moore and Kerlinger 1987). The apparent lack of fat accumulation in Kirtland’s Warblers prior to migration needs further investigation.

Probst and Hayes (1987) suggested the possibility of an imbalance in the sexes. Although the sex bias in favor of males that we found supports Probst and Hayes, the sex ratio is not significantly different from 1:1. Although there could be higher female mortality, due to incubating the eggs and brooding the young in ground nests, we note here that capture probabilities for males and females may have differed and led to biased sex ratios in the capture data. However, with the Kirtland’s Warbler population hovering near 200 singing males for the last 17 years (Ryel 1984, Weinrich 1987), a possible skewed sex ratio in favor of males is cause for concern and should be carefully monitored in the future.
The first posted closure of Kirtland’s Warbler breeding grounds on public land was implemented in 1964 at Mack Lake (Huron National Forest), and this management procedure was followed on state forest lands several years later (G. W. Irvine, J. A. Weinrich pers. comm.). The time of closing was set to encompass the entire breeding season. An opening date in mid-August was based upon the supposition that all breeding activities were completed and that most of the warblers had left the nesting areas by late August or early September (Mayfield 1960; Walkinshaw 1983; Byelich et al. 1976, 1985). The mid-August opening date for the warbler areas was further supported by the early Bahama records (Hundley 1967, Wallace 1968, Robertson 1971). Published data would logically lead one to conclude that by late August most of the warblers would have left the Michigan breeding grounds. Aside from the unpublished Michigan DNR records, only one Kirtland’s Warbler has been reported on the breeding grounds after 16 August in the last 50 years (Schempf 1976). Males sing only from early May to early July, and the birds become extremely difficult to find by the end of July; it is easy to conclude erroneously that most birds have left by this time or shortly thereafter.

We (pers. obs.) have seen five recently fledged young from three nests being actively fed between 14 and 17 August. Kirtland’s Warblers generally care for their young from 29 to 44 days after they leave the nest (Mayfield 1960), so these late young would not be independent until well into September.

We have observed various potentially harmful activities in occupied Kirtland’s Warbler habitats following their opening to the public on 15 August. Included were: recreational use of all-terrain vehicles (ATVs), dirt bikes, pickup trucks, and automobiles; firewood cutting and gathering; field training and conditioning of dogs for hunting; cutting, stacking, and hauling of pulpwood; seismic exploration for petroleum deposits; and, starting in mid-September, hunting of snowshoe hares (Lepus americanus) and Ruffed Grouse (Bonasa umbellus). While there may be little chance of direct harm to individual Kirtland’s Warblers from these activities, mortality to the birds could occur. More serious is the threat of fire from people (discarding hot matches, smoking, open camp fires, etc.) and mechanized equipment (hot exhaust systems, sparks, etc.) in jack pine areas that are adapted to burn, particularly in dry years. As an example, in 1987 43% of the Kirtland’s Warbler population was found in two areas, and loss of this habitat could have been a disaster to a species with such low numbers.

Because the Kirtland’s Warbler is endangered and is a breeding species unique to Michigan, it would seem reasonable to keep the few areas occupied by them closed while the birds are present and while fire danger is still high. The total habitat occupied by the warbler (parts of 54 sections
in six counties, Weinrich 1987) is miniscule compared to the Federal and State forest lands in northern lower peninsular Michigan available for recreational activities enjoyed by the public.

Our efforts indicate that many Kirtland’s Warblers remain on the breeding ground longer than previously thought, with a few birds possibly remaining into October. We recommend that all breeding areas having more than ten singing males remain closed until mid-September. This would protect the warblers from human activity as much as possible. The extension would encompass all late nesting activities, provide added protection for late hatched HY birds not yet fully independent, minimize disturbance to molting adults (AHYs), and provide added protection during the critical period when migratory energy reserves are being acquired. Since we do not know what factors are suppressing the population of this endangered species or where these factors occur in the annual cycle, this small modification to present management procedures might prove beneficial to the future survival of this unique parulid.

ACKNOWLEDGMENTS

C. I. Bocetti, E. S. Carlson, C. A. Faanes, D. J. Munson, J. R. Probst, R. L. Refsnider, T. K. Ruth, S. Savage, C. M. and L. H. Walkinshaw, and J. A. Weinrich helped with the field work. We particularly extend our appreciation to M. L. Suplinskas for her assistance with the study. We thank D. D. Brooks, M. M. Waltz, and other staff members of the Grayling Field Office of Michigan Department of Natural Resources for logistical support. J. G. Hinshaw provided data on Kirtland’s Warbler specimens at University of Michigan Museum of Zoology. Reviews by P. H. Albers, W. Link, H. F. Mayfield, G. W. Pendleton, and J. R. Probst were most helpful in improving the manuscript. We thank B. J. Fancher for typing the drafts and final of the manuscript.

LITERATURE CITED

NECTAR AVAILABILITY AND HABITAT SELECTION BY HUMMINGBIRDS IN GUADALUPE CANYON

WILLIAM H. BALTOSSER

ABSTRACT.—The importance of nectar availability and habitat selection to the seasonal occurrence, abundance, and nesting of Black-chinned (Archilochus alexandri), Broad-billed (Cyananthus latirostris), Violet-crowned (Amazilia violiceps), and Costa’s (Calypte costae) hummingbirds was investigated. Periods of seasonal and daily nectar abundance were interspersed with periods of limited availability. Areas that contained greater quantities and more predictable nectar supplies tended to have more nests. Habitats selected for nesting differed among species, but were most alike for Black-chinned and Violet-crowned hummingbirds and for Broad-billed and Costa’s hummingbirds. Results support the hypothesis that guilds are not always at resource-defined equilibrium. Hummingbird populations appeared to be above sustainable long-term levels in 1976, nearer such levels in 1977, and below these levels in 1980. Received 19 Sept. 1988, accepted 23 March 1989.

The relative importance of factors influencing the abundance of species and how shared resources are utilized have been the subject of numerous debates. Menge and Sutherland (1976), for example, have viewed predation, competition, and temporal heterogeneity as all being potentially important. Connell (1975, 1980) stressed that predation is frequently the major selective force organizing natural communities, while others such as Diamond (1978) have maintained that competition was perhaps more significant. In contrast, Wiens (1974, 1977, 1983) has proposed that many communities are often below saturation levels for the available resource, and thus competition is perhaps only important intermittently. Still others, such as Strong et al. (1979), have questioned whether observed community organization really differs from random assemblages (i.e., if patterns exist, are they the result of closely interwoven relationships between organisms, or do species occupy suitable available space without regard to the presence or absence of other species?).

Spatial and temporal heterogeneity, with respect to nectar availability and habitat selection, is examined in the present manuscript to determine the impact of these factors upon the seasonal occurrence, abundance, and nesting of each hummingbird species (see Baltosser 1986 for discussion of predation). Hummingbirds were selected for study because they depend on nectar sources that generally occur in discrete patches that are readily

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identified and quantified. They were also selected for study because of their small size and high mass-specific daily energy requirements, which make hummingbirds respond quickly to changes in their environment.

STUDY AREA

Guadalupe Canyon lies along the United States-Mexico border in extreme southwestern New Mexico and extreme southeastern Arizona. From its source in the Peloncillo Mountains of New Mexico, the canyon drains to the southwest, passing through Arizona before entering Mexico. Within Mexico the canyon joins the Río de San Bernardino, a tributary of the Río Yaqui. Data were generally collected from the 150-m-wide canyon bottom that rises from the International Boundary northeast into New Mexico, a distance of 8500 m (total area approximately 106 ha). Elevation of the canyon bottom ranges from 1305 m in the Arizona portion to 1366 m in the New Mexico segment. Guadalupe Canyon is surrounded by Chihuahuan Desert scrub vegetation that interdigitates with riparian vegetation in the creek bottom. On the basis of topography, exposure, and vegetation, I recognized three major habitats: riparian creek bottom, precipitous north-facing slopes, and xeric south-facing slopes. The creek bottom is characterized by numerous open areas interspersed with clumps of mature Arizona sycamores (Platanus wrightii) and Fremont cottonwoods (Populus fremontii), with understories of seepwillow (Baccharis glutinosa) and burro-brush (Hymenoclea monogyna) in central portions, and honey mesquite (Prosopis glandulosa), red barberry (Berberis haematocarpa), and netleaf hackberry (Celtis reticulata) near the edges. North-facing slopes rise abruptly from the canyon floor and are characterized by open areas interspersed with netleaf hackberry, one-seed juniper (Juniperus monosperma), oaks (Quercus arizonica and Q. grisea), soapberry (Sapindus saponaria), and agaves (Agave schottii and A. parryi), with dense shrub thickets composed of red barberry, honey mesquite, gray-thorn (Condalia lycioides), woolly buckthorn (Bumelia lanuginosa), and poison ivy (Rhus radicans). South-facing slopes rise gradually from the canyon bottom and are characterized by open areas with scattered agaves and ocotillo (Fouquieria splendens), or thickets of mixed species that include honey mesquite, little-leaf sumac (Rhus microphylla), and white-thorn (Acacia constricta).

METHODS

Local distribution of hummingbirds and the dispersion of resources were monitored biweekly from April through September using spot-map techniques (Williams 1936, Kendeigh 1944). For the purpose of field surveys, Guadalupe Canyon was divided into 51 segments of equal size spaced linearly throughout the canyon. However, these segments were grouped into ten units for data analysis (Fig. 1).

Floral censuses designed to determine the phenology of nectar-producing plants and the relative abundance of nectar were conducted in 1976 and 1977 (Baltosser 1978). The phenology, location, and abundance (rare, common, abundant) of each species were measured every 7–10 days. Similar censuses, modified to obtain the actual number of flowers blooming, were conducted biweekly in 1980. Data for important species were obtained directly by counting the number of open flowers. When it was impractical to count all open flowers within a patch, flowers in smaller plots were counted and these data were used to extrapolate values for the entire patch. The above procedures were repeated in occasional cases in which the phenology of a species spanned more than one biweekly census.

Energy yields of important nectar-producing plants, based on the number of mg of sugar in each flower, were measured using methods of Roberts (1979) and Hainsworth and Wolf
(1972). The amount of sugar per flower was measured using Roberts’ method of spectrophotometric assays. Similar data were obtained using Hainsworth and Wolf’s method by use of microcapillary tubes in conjunction with a pocket refractometer (see Bolten et al. 1979). The results obtained for each plant species using both methods were averaged and used in conjunction with those of floral censuses to measure biweekly standing crop nectar values, measured in joules, for each segment of the canyon.

Vegetation of nesting habitats was sampled in plots at randomly selected nests of each species. Selected nests were used as the center points of circular plots 30 m in diameter (707 m²). Within each plot, frequency, density, and cover values were measured for the following vegetation classes: height class III (trees > 3.5 m), height class II (trees and shrubs > 1 m ≤ 3.5 m), height class I (shrubs ≤ 1 m), and herbaceous plants.

Cover in each height class was estimated directly above and below a randomly selected point within each quarter of each nest plot. Density was estimated by counting all woody species occurring within the three height classes of each nest plot. Cover of small shrubs and herbaceous plants was estimated using a gridded 1-m² quadrat. When possible, height class II cover was measured by the same procedures. Cover of small trees and shrubs too tall for this method was projected onto the grid by a pole placed perpendicular to the grid. Cover produced by tall trees was estimated using two ocular tubes similar to the one described by James and Shugart (1970). Each tube provided a visual field of 1 m² at a known distance: 3.5 m for the shorter tube and 10 m for the longer tube.

Hummingbird nesting habitats were sampled from randomly selected nest plots of each species. Habitat descriptions and analyses were based on topography, dominant plant species, and 23 composite vegetation parameters (Baltosser 1978, 1983). Statistical analyses of these data included both univariate and multivariate vegetation analyses of the nest plots of each species. Univariate analyses (UNIVAR—D. M. Power, unpubl. data) of these parameters were used to test for differences between the habitats of the various hummingbirds. Multivariate discriminant function analyses (Dixon 1973) were then used to examine differences between the various habitats by considering intercorrelations between several variables, which resulted in reducing the number of significant variables from 14 in univariate analyses...
to six. The discriminant analysis also computed a posterior probability for each nest plot that showed its chances of belonging to each bird species, i.e., just how similar each plot was to all others and how similar the nesting habitat of each hummingbird species (i.e., overall mean) was to other nesting hummingbird species.

Data on intra- and interspecific hummingbird interactions with respect to nectar availability were obtained from casual observations of encounters at floral resources, and from an experiment in 1980 designed to monitor the response and subsequent interactions of hummingbirds to reductions and spatial shifts in nectar supplies. Several hypotheses were established a priori to predict hummingbird behavior: (H0) hummingbirds will show no measurable response; (H1) hummingbirds will show measurable responses. Given that the former alternative hypothesis (H1) was accepted, then: (H0) each species will respond in the same manner; (H1) species will respond differently. Given that the former alternative hypothesis (H1) was accepted, then (H0) reductions in nectar supplies will have no effect on nesting success; (H1) nectar reductions will have an effect on nesting success.

Six Parry agave plants, all within 77 m of each other and the nests of three of the four hummingbird species present within Guadalupe Canyon at the time, were manipulated in the experiment. Additional agaves were present, but these were considerably farther from active hummingbird nests than were those chosen for study. I first observed hummingbird foraging behavior during selected periods for one day prior to each manipulation. At dusk of the control day, flowers that were open or ready to open were removed from all but one plant to ensure that flowers on only a single agave contained nectar the following day. The number of flowers removed and the number remaining were counted each time to calculate total energy values and the percent reduction. The same agaves were manipulated in the same manner during subsequent weeks; the only change was that the unmanipulated agave was arbitrarily changed. Hummingbirds quickly discovered, however, which agave contained nectar.

RESULTS

Hummingbirds. — The Guadalupe Canyon hummingbird guild consisted of four nesting species (all at the periphery of their breeding ranges), two transient species, and a single vagrant. Black-chinned (Archilochus alexandri), Broad-billed (Cyananthus latirostris), Violet-crowned (Amaryllis violiceps), and Costa’s (Calypte costae) hummingbirds all nested, whereas Broad-tailed (Selasphorus platycercus) and Rufous (S. rubis) hummingbirds were common seasonal transients. A single vagrant Lucifer Hummingbird (Calothorax lucifer) was observed only once.

The seasonal occurrence and abundance of hummingbirds in Guadalupe Canyon are shown in Table 1. Black-chinned and Broad-billed hummingbirds were present from April to September, while other guild members were present for shorter periods. The abundance of each species was similar among years, with the exception of the Black-chinned in 1980. The reduction in Black-chinned numbers in 1980 apparently resulted from an unusual and extreme freeze that occurred in December 1978. Foliage in segments A–E during 1980 was still, after nearly 17 months, reduced by 75%, based on gridded overlays of photographs from former years. Frost damage in lower segments (F–J) was not as extreme and vegetation had recovered to a greater extent by 1980.
The effects of the freeze were reflected in the distribution and number of Black-chinned nests during 1980. The number of Black-chinned nests in segments A–E in 1980 was only five, as compared to 21 and 17 in 1976 and 1977, respectively. Broad-billed and Violet-crowned hummingbird nest numbers during 1980 were not affected by the freeze. Presumably, this was because the Violet-crowned was never common in upper portions of the canyon (more affected segments), and plant species used for nesting by the Broad-billed were not damaged by the frost to the same degree as were the Arizona sycamores used for nesting by the Black-chinned.
The term “nesting season” as used in the present context refers to those months female hummingbirds were attending nests. The Black-chinned had the longest nesting season, followed in order by Broad-billed, Violet-crowned, and Costa’s (Baltosser 1986). The first nesting period for the Black-chinned, which each year attempted to raise at least two broods, began in mid-April and terminated for many birds in mid- to late June. The second nesting period for the Black-chinned began in early July and extended into mid-August, although a few individuals were occasionally still feeding nestlings in early September.

Many Black-chinned females were engaged in feeding fledglings and in nest construction during the break between nesting periods. I observed four Black-chinned females constructing second nests in early July 1976 while still feeding large nestlings in their first nests. This did not, however, appear to be a universal trait. In 1977 only a single instance of overlapping nesting was observed for this species and no instances were recorded in 1980.

Broad-billed Hummingbirds nested during the same months as the Black-chinned and generally had two broods. In 1976 I observed a female of this species constructing a second nest near to her first, which still contained large nestlings. No other observations of overlapping nesting by this species were documented.

A single Violet-crowned Hummingbird occasionally arrived in Guadalupe Canyon in early May, but most did not occur until mid-June. Nesting for the Violet-crowned began the second week of July in 1976, in mid-June in 1977, and late June in 1980; each year nesting extended into September.

Costa’s Hummingbirds have occurred in Guadalupe Canyon as early as March (Deuel and Parker 1972), but during my study they did not arrive until April. In 1976 and 1977 members of this species attempted to nest in May and early June, while in 1980 attempts were made only in May.

Availability of arthropods and nectar.—Foliage arthropods never appeared to be a limiting food supply, nor were they used to any extent. Even when there were “super abundant” numbers of planthoppers (Insecta: Homoptera) during 1980, hummingbirds did not alter their foraging to take advantage of this surplus. The only arthropods consistently consumed, other than those concealed in flower corollas, were flying Diptera and Ephemeroptera.

A tape-measure was used in 1980 to determine the biweekly availability of surface water throughout Guadalupe Canyon, because in 1976 and 1977 the occurrence of Ephemeroptera and Diptera appeared to be positively correlated with surface water availability. Precise measurements
of surface water were not made in 1976 and 1977, but its spatial-temporal occurrence was similar to that of 1980. Surface water was not abundant during late June, July, and early August 1980, and thus insects of both orders persisted only in segment C. Hummingbirds in this area continued to supplement their diet with these insects, but birds in other segments were not seen feeding on arthropods.

Nectar availability in Guadalupe Canyon exhibited two distinct seasonal peaks that were basically the same in 1976, 1977, and 1980 (Baltosser 1978, 1986). Each year the two flowering periods were separated by a conspicuous decline in nectar production in mid-June. Peak production of many plant species tended to be temporally distinct from peaks of other species, and each year was similar to the 1980 data shown in Table 2. As a result of temporally and spatially shifting nectar supplies, all hummingbirds were often forced to utilize the same plant species and many hummingbirds the same flower patches.

The first flowering period in 1976, 1977, and 1980 extended from late April through mid-June, with peak production between early and mid-May (Table 3, Baltosser 1978). During this period as many as 1005 kJ (standing crop) were available. Had this total been evenly distributed throughout the canyon, there would be approximately 100.5 kJ available in each 10.6-ha segment. However, as Table 3 shows, nectar supplies during this period were not evenly distributed, nor was nectar production equal among the 12 plant species in flower (Table 2). Hummingbirds foraged from all plant species in bloom during the first period, but 78% of the total energy was produced by Penstemon pseudospectabilis (Table 2).

The second flowering period in 1976, 1977, and 1980 extended from late June through early September, with peak production occurring from mid-July through early August (Table 3, Baltosser 1978). During this time as many as 747 kJ (standing crop) were available. If this were evenly distributed throughout the length of the canyon, there would be approximately 74.7 kJ available in each 10.6-ha segment. Nectar supplies during the second period were more evenly distributed than in the first (Table 3). The figure of 74.7 kJ is therefore a reasonably accurate assessment of nectar supplies in most segments during the second period. Thirteen plant species were in bloom and used by hummingbirds during the second flowering period, but 90% of the total production was by Agave parryi (Table 2).

Nectar requirements.—The relationship between available nectar and hummingbird abundance is shown in Table 4. Limited data from covered flowers of Penstemon superbus, Penstemon pseudospectabilis, Anisacanthus thurberi, Agave parryi, and Epilobium canum indicate that daily
Table 2
Phenology of Important Nectar-Producing Plants Showing the Biweekly Contribution of Each Species to Standing Crop Values and the Relative Dispersion of Each Throughout Guadalupe Canyon

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Flowering phenology (date and number of kJ)</th>
<th>Segments present (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Penstemon superbus</td>
<td>Apr. 25: 18.11, May 7: 14.96, May 21: 6.04, June 3: 1.75, June 17: 0.37, July 3: 0.03, Aug. 2: 0.01, Aug. 16: 0.03, Sep. 2: 0.03</td>
<td>55</td>
</tr>
<tr>
<td>Cirsium neomexicanum</td>
<td>5.66, 38.67, 34.58, 9.66, 5.16</td>
<td>92</td>
</tr>
<tr>
<td>Penstemon pseudopectabilis</td>
<td>137.51, 546.85, 306.74, 62.61</td>
<td>4</td>
</tr>
<tr>
<td>Castilleja spp.</td>
<td>0.12, 0.24, 0.06, 0.02, 0.01, 0.01, 0.01, 0.01, 0.01</td>
<td>14</td>
</tr>
<tr>
<td>Fouquieria splendens</td>
<td>0.56, 91.49, 16.06</td>
<td>57</td>
</tr>
<tr>
<td>Anisacanthus thurberi</td>
<td>0.75, 27.96, 14.20, 2.63</td>
<td>16</td>
</tr>
<tr>
<td>Chilopsis linearis</td>
<td>1.50, 4.56, 0.67</td>
<td>6</td>
</tr>
<tr>
<td>Bouvardia glaberina</td>
<td>0.32, 0.03</td>
<td>8</td>
</tr>
<tr>
<td>Agave schottii</td>
<td>0.65, 14.70, 48.35, 36.57, 13.40, 0.05, 0.16, 0.05</td>
<td>67</td>
</tr>
<tr>
<td>Caesalpinia gilliesii</td>
<td>3.72, 5.51, 2.39, 0.11, 0.03, 0.03</td>
<td>8</td>
</tr>
<tr>
<td>Penstemon barbatus</td>
<td>0.08, 0.51</td>
<td>8</td>
</tr>
<tr>
<td>Erythrina flabelliformis</td>
<td>1.22, 0.93, 0.21</td>
<td>18</td>
</tr>
<tr>
<td>Agave parryi</td>
<td>16.85, 486.27, 343.35, 288.35, 89.92, 96</td>
<td>4</td>
</tr>
<tr>
<td>Epilobium canum</td>
<td>0.03, 0.03</td>
<td>4</td>
</tr>
<tr>
<td>Stachys coccinea</td>
<td></td>
<td>8</td>
</tr>
</tbody>
</table>
production varied, but was frequently four times that of standing crop values of flowers exposed to natural levels of exploitation. During each of the two flowering periods, minimum nectar requirements of hummingbirds in Guadalupe Canyon were on occasion met by available supplies (Table 4), but these data show that periods of seasonal abundance were interspersed with periods of limited availability.

The relationship between nectar supplies and their predictability of occurrence to nest dispersion and nesting success is shown in Table 5. A positive correlation between nectar abundance and the number of nests in each segment occurred during both nesting periods, but was statistically significant only during the second period ($r = 0.39, P < 0.19$ and $r = 0.87, P < 0.01$). An inverse correlation between the number of nests in each segment and nectar predictability (i.e., the greater the variability the fewer nests) occurred during the first nesting period but this difference was not statistically significant ($r = -0.49, P < 0.09$); there was virtually no relationship during the second period ($r = 0.01, P > 0.95$). Fledging success was not correlated with either amount of nectar or its predictability during the first period ($r = 0.23, P < 0.47$ and $r = -0.25, P < 0.45$, respectively), nor was there any correlation between fledging success and predictability during the second period ($r = -0.14, P > 0.68$). There was, however, significant correlation during the second nesting period between fledging success and the amount of nectar ($r = 0.61, P < 0.03$).

**Nest sites.**—Plant species used for nest sites by hummingbirds in Guadalupe Canyon are shown in Table 6. Black-chinned, Broad-billed, and to a certain extent Costa's hummingbirds utilized trees and shrubs in roughly the same proportions in which the various species occurred. In

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### Table 3

**Biweekly Energy (kJ) Availability Throughout Guadalupe Canyon During 1980**

<table>
<thead>
<tr>
<th>Date</th>
<th>Standing crop</th>
<th>Percent of total by segment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x}$ SD</td>
<td>A  B  C  D  E  F  G  H  I  J</td>
</tr>
<tr>
<td>April 25</td>
<td>161 106</td>
<td>86 5 1 5 1 1 1 1 1 1</td>
</tr>
<tr>
<td>May 7</td>
<td>602 403</td>
<td>91 3 1 1 1 1 1 1 1 1</td>
</tr>
<tr>
<td>May 21</td>
<td>469 306</td>
<td>73 3 3 5 3 3 2 3 2 2</td>
</tr>
<tr>
<td>June 3</td>
<td>113 74</td>
<td>68 4 3 1 2 2 1 9 2 8</td>
</tr>
<tr>
<td>June 17</td>
<td>31 17</td>
<td>17 2 3 3 4 16 4 23 6 23</td>
</tr>
<tr>
<td>July 3</td>
<td>69 35</td>
<td>16 7 8 4 2 10 8 12 7 26</td>
</tr>
<tr>
<td>July 15</td>
<td>523 224</td>
<td>5 5 10 13 6 12 4 6 19 20</td>
</tr>
<tr>
<td>August 2</td>
<td>357 151</td>
<td>9 5 10 16 8 12 3 6 12 21</td>
</tr>
<tr>
<td>August 16</td>
<td>289 121</td>
<td>6 5 12 11 6 13 3 3 22 18</td>
</tr>
<tr>
<td>September</td>
<td>91 38</td>
<td>2 3 6 17 10 10 4 2 23 23</td>
</tr>
</tbody>
</table>
Table 4
AVAILABLE NECTAR SUPPLIES AND HUMMINGBIRD NECTAR REQUIREMENTS

<table>
<thead>
<tr>
<th>Date</th>
<th>Total available nectar</th>
<th>Minimum nectar requirementsa</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>April 25</td>
<td>644</td>
<td>902</td>
<td>847</td>
<td>621</td>
<td></td>
</tr>
<tr>
<td>May 7</td>
<td>2408</td>
<td>1047</td>
<td>1290</td>
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<td>452</td>
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<td>1234</td>
<td>488</td>
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<td>124</td>
<td>799</td>
<td>1073</td>
<td>695</td>
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<tr>
<td>July 3</td>
<td>276</td>
<td>1736</td>
<td>1438</td>
<td>863</td>
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<tr>
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<td>2092</td>
<td>1651</td>
<td>1408</td>
<td>1054</td>
<td></td>
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<tr>
<td>August 2</td>
<td>1428</td>
<td>1931</td>
<td>2001</td>
<td>1219</td>
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<tr>
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<td>1156</td>
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<td>1523</td>
<td>1321</td>
<td></td>
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<tr>
<td>September 2</td>
<td>364</td>
<td>1383</td>
<td>1031</td>
<td>993</td>
<td></td>
</tr>
</tbody>
</table>

a Total available nectar = 4 x standing crop (kJ).

Minimum energy (kJ) required based on the number of birds present × 8.02 kJ/day for each 1 g body weight (Powers and Nagy 1988, Weathers and Stiles 1989); Black-chinned = 3.3 g, Broad-billed = 3.0 g, Violet-crowned = 5.7 g, Costa’s = 3.0 g, Broad-tailed = 3.6 g, Rufous = 3.2 g, and Lucifer = 2.9 g.

Contrast, Violet-crowned Hummingbirds selected plants for nest sites in a more specialized manner, selecting only one of the many available species.

Nest heights (m) of all hummingbird species, which included additional nests from other years (e.g., 1975 and 1978), were significantly different when compared using an analysis of variance (F = 26.11, P < 0.01). All species comparisons except Black-chinned vs Violet-crowned showed significant differences (P < 0.05). Broad-billed nest heights were extremely consistent, despite nests being in a variety of plant species. Mean, standard deviation, and sample size for each species are as follows: Black-chinned \( \bar{x} = 5.8 \pm 2.8 \) [SD], N = 116; Broad-billed \( \bar{x} = 1.1 \pm 0.5 \), N = 33; Violet-crowned \( \bar{x} = 7.1 \pm 2.7 \), N = 14; and Costa’s \( \bar{x} = 1.7 \pm 1.1 \), N = 11.

Nest plot classifications based on the posterior probabilities calculated from six significant vegetation parameters (i.e., Height Class III Cover, Height Class II Cover, Height Class II Density, Height Class I Cover, Herbaceous Cover, and Foliage Height Diversity for Height Class III) of 46 plots resulted in 78% of the plots being grouped correctly. Mistakes in classification were made for all species, but seven of ten incorrectly classified plots were grouped incorrectly for the same reason. These seven plots were near margins of typical habitat for each species, and because of the large plot size (15-m radius), included portions of atypical habitat. The remaining three incorrectly grouped plots included two Broad-billed plots classified as Costa’s and one Costa’s classified as a Broad-billed.
### Table 5

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td></td>
<td>First nesting period</td>
<td>Second nesting period</td>
</tr>
<tr>
<td></td>
<td>No. nests</td>
<td>No. successful nests</td>
</tr>
<tr>
<td>A</td>
<td>13</td>
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<td>5</td>
<td>0</td>
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<tr>
<td>C</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>D</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
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<td>3</td>
<td>2</td>
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<tr>
<td>I</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>J</td>
<td>19</td>
<td>7</td>
</tr>
</tbody>
</table>

Plant species found in Costa’s plots, however, differed from those in Broad-billed plots by 72%, and thus even though both species had similar numerical values for many vegetation measurements, most were based on different species of plants.

Black-chinned Hummingbirds usually nested in relatively open areas interspersed with clumps of mature Arizona sycamore trees centrally located within the canyon, over or adjacent to the bare sandy bottom (Fig. 2). Most Black-chinned nests were in Arizona sycamores, 5–6 m above the bare creek bottom. As a result, many nests had relatively few small trees and shrubs immediately nearby. However, since plots had a radius of 15 m they occasionally included small trees and shrubs such as netleaf hackberry, one-seed juniper, seepwillow, and burro-brush near plot perimeters.

Violet-crowned Hummingbirds nested in areas with vegetation similar to that in Black-chinned plots. Instead of being centrally located within the riparian vegetation, Violet-crowned nests were at the edge of this vegetation in relatively open areas next to xeric hillsides (Fig. 2). Those portions of Violet-crowned plots nearest the creek bottom usually contained several Arizona sycamore trees underlain by seepwillow and burro-brush. Portions of Violet-crowned plots adjacent to open areas bordered by xeric hillsides had high densities of honey mesquite, red barberry,
Table 6

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Black-chinned</th>
<th>Violet-crowned</th>
<th>Broad-billed</th>
<th>Costa’s</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plant density</td>
<td>No. of nests</td>
<td>Plant density</td>
<td>No. of nests</td>
</tr>
<tr>
<td><em>Platanus wrightii</em></td>
<td>118</td>
<td>100</td>
<td>200</td>
<td>14</td>
</tr>
<tr>
<td><em>Celtis reticulata</em></td>
<td>32</td>
<td>11</td>
<td>19</td>
<td>7</td>
</tr>
<tr>
<td><em>Fraxinus velutina</em></td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>40</td>
</tr>
<tr>
<td><em>Quercus spp.</em></td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><em>Juniperus monosperma</em></td>
<td>14</td>
<td>1</td>
<td>6</td>
<td>37</td>
</tr>
<tr>
<td><em>Prunus persica</em></td>
<td>—</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Berberis haematocarpa</em></td>
<td>77</td>
<td>104</td>
<td>156</td>
<td>6</td>
</tr>
<tr>
<td><em>Clematis ligusticifolia</em></td>
<td>0</td>
<td>11</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td><em>Senecio salignus</em></td>
<td>57</td>
<td>55</td>
<td>48</td>
<td>1</td>
</tr>
</tbody>
</table>

*Unsampled nest plots.*

little-leaf sumac, gray-thorn, and large amounts of herbaceous cover composed primarily of grasses. All Violet-crowned nests were located in Arizona sycamore trees, their height above the ground averaging 7 m.

Broad-billed Hummingbirds nested in thickets near the edge of the canyon in areas primarily of northern exposure bordered by rock outcrops and typical Black-chinned habitat (Fig. 2). Dominant plant species within Broad-billed plots were small trees and shrubs, including netleaf hackberry, one-seed juniper, red barberry, honey mesquite, gray-thorn, little-leaf sumac, poison ivy, and woolly buckthorn. A few plots also contained small numbers of Arizona sycamore, Fremont cottonwood, and soapberry trees. Nests were in a variety of plant species, most were about 1 m above the ground, and many were within 1 m of rock outcrops.

Costa’s Hummingbird nests were in the dry arroyo tributaries adjacent to the main canyon bottom or in areas of southern exposure (Fig. 2). The majority of plants within Costa’s plots were xeric shrubs such as honey mesquite, little-leaf sumac, and white-thorn. Large trees were not present in plots of this species nor were many small ones. Nests tended, however, to be located 1–2 m above the ground in the few small trees (usually netleaf hackberry) that were present.

Foraging and experimental nectar reductions.—Virtually every hummingbird species in Guadalupe Canyon at one time or another was displaced from nectar sources by members of all other species. The trend, however, was for the larger Violet-crowned Hummingbird to be dominant, followed in order of decreasing dominance by Rufous, Broad-billed,
Fig. 2. Diagrammatic cross section of Guadalupe Canyon based on univariate and multivariate discriminant analyses showing the distributional patterns (horizontal axis), and mean nest heights (vertical axis) of Black-chinned (BC), Violet-crowned (VC), Broad-billed (BB), and Costa’s (CO) hummingbirds.

Broad-tailed, Black-chinned, and Costa’s hummingbirds. The data in Table 7 are based on only 12 hours of observation, but show typical interactions at unmanipulated agaves during the period of experimental nectar reductions.

The single greatest factor responsible for the disruption of female Black-chinned foraging was conspecific females. Rufous Hummingbirds were also a major source of disruption for Black-chinned and Broad-billed females. Interactions with Broad-billed and Violet-crowned hummingbirds also interfered with Black-chinned foraging. Rufous were interrupted in their foraging by conspecifics and by Violet-crowned and Broad-billed hummingbirds, although the latter were more frequently interrupted by Rufous Hummingbirds.

Sample size was insufficient for a statistical interpretation of the 1980 nectar reduction experiment because only three Black-chinned, two Broad-billed, one Violet-crowned, and five Rufous hummingbirds were present in the immediate vicinity of the experiment. Nevertheless, the amount of time (%) individuals spent feeding under natural and manipulated
### Table 7

**Interactions Between Hummingbirds in Guadalupe Canyon While Foraging at *Agave parryi* Plants During July and August 1980**

<table>
<thead>
<tr>
<th>Species displaced</th>
<th>Species effecting displacement</th>
</tr>
</thead>
<tbody>
<tr>
<td>B-C</td>
<td>B-C</td>
</tr>
<tr>
<td>B-C</td>
<td>10</td>
</tr>
<tr>
<td>B-B</td>
<td>0</td>
</tr>
<tr>
<td>R</td>
<td>0</td>
</tr>
<tr>
<td>V-C</td>
<td>2</td>
</tr>
</tbody>
</table>

* Number of occasions a given species was displaced by another; abbreviations are as follows: B-C (Black-chinned), B-B (Broad-billed), R (Rufous), and V-C (Violet-crowned).

conditions was of interest. Standing crops of the six agaves within a 77 m radius (1.9 ha) of each other and single nests of Black-chinned, Broad-billed, and Violet-crowned hummingbirds were experimentally reduced on average (all plants combined) from 22.8 kJ to 7 kJ. Female Black-chinned Hummingbirds accounted for 38% of all foraging under natural conditions, but under conditions of reduced nectar supplies this dropped to only 5%. Male Black-chinned were not affected by reductions, nor were Rufous Hummingbirds of either sex or age in terms of the total proportion of time spent at flowers. In contrast, the Broad-billed increased its use of the single unmanipulated agave from 28% under natural conditions to 38%, while the Violet-crowned went from 9% to 28%, respectively. The increase in usage under experimental conditions by the Broad-billed and Violet-crowned is in part an artifact of sampling (i.e., decreased use by the Black-chinned), but each did in fact increase the length of time spent at the single unmanipulated agave under conditions of reduced nectar availability. Black-chinned and Violet-crowned hummingbirds nesting in the immediate vicinity (within 77 m) of nectar manipulations had complete nesting success. Broad-billed Hummingbirds, which generally succeeded in fledging young once they had hatched, lost one nestling early to predation and the other at a later date.

**DISCUSSION**

**Breeding seasons and temporal occurrence.**—The timing of avian breeding seasons has often been explained in terms of food availability, the eggs being laid during a period that anticipates the energetic costs of brooding and feeding young (Moreau 1950, Thomson 1950, Lack 1954, Perrins 1970, Immelmann 1971). Recent experimental studies by Ewald and Rohwer (1982), Davies and Lundberg (1985), Knight (1988), and Wimberger (1988) add support to this hypothesis. The nesting seasons of
hummingbirds in Guadalupe Canyon also seem to be related to the availability of food. Before mid-April and after mid-September there were very few nectar sources available to hummingbirds. Coincidentally, Black-chinned and Broad-billed hummingbirds nested only from mid-April through early September, whereas Violet-crowned and Costa’s nested during only a portion of this period.

The nesting of Costa’s Hummingbirds in Guadalupe Canyon is believed to be a recent phenomena (Baltosser 1983). The fact that the species nests earlier to the west, and later in areas of sympatry (Stiles 1973, present study), may be due in part to competition as suggested by Cody (1974) for birds in general. Delayed nesting in Guadalupe Canyon may also result from the absence of nectar supplies prior to mid-April and the fact that subfreezing temperatures occasionally persist into April.

Violet-crowned Hummingbird nesting did not begin until mid-June, despite the fact that an occasional bird was present earlier. Late nesting by this species is believed to be related to its larger size (5.7 g) and subsequent need to perhaps specialize on more productive and predictable nectar resources, which did not become available until the second flowering period.

The occurrence of transient Broad-tailed and Rufous hummingbirds coincided with seasonal peaks in nectar abundance. Nectar availability in Guadalupe Canyon was highly contingent (Colwell 1974), i.e., nectar levels varied widely throughout the season but in a consistent temporal pattern each year. The result was that transients occurred during specific periods when nectar supplies happened to be greatest. Similar responses of hummingbirds to seasonal flushes in resource abundance have been shown by Gass (1979), DesGranges and Grant (1980), and Feinsinger (1980).

Spatial distribution of nesting species.—Segregation into different habitats is one of the most common means by which ecologically similar species partition resources (Schoener 1974). Nesting habitat selection by hummingbirds in Guadalupe Canyon was associated with the structure and exposure of the vegetation, with each species utilizing slightly different habitats for nesting. Black-chinned and Violet-crowned hummingbirds nested in habitats with many similar features, as did Broad-billed and Costa’s hummingbirds.

The dispersion of hummingbird nests in Guadalupe Canyon was also associated with the spatial and temporal distribution of nectar supplies. When nectar supplies were not as evenly distributed throughout the canyon (i.e., during the first nesting period), segments having more abundant nectar supplies tended to have more nests. However, when nectar supplies were more evenly distributed (i.e., during the second nesting period),
segments having nectar supplies that were more predictable tended to have more nests. These results support the hypothesis that spacing patterns of species with altricial young should be correlated with the spatial and temporal distribution of food sources (Orians 1971).

Foraging and nectar availability. — Results of floral manipulations conducted on nectar supplies nearest the nests of Black-chinned, Broad-billed, and Violet-crowned hummingbirds in Guadalupe Canyon were similar to those conducted by Pimm (1978), from which the former were patterned. In Pimm’s study, the Black-chinned was better able to cope with unpredictable nectar supplies than were larger Blue-throated Hummingbirds (Lampornis clemenciae). Black-chinned Hummingbirds (two adult females) in my study shifted their foraging to more distant agaves when nectar supplies were experimentally reduced. Whether this shift was in response to Broad-billed and Violet-crowned hummingbirds is not clear, as there were far more occasions in which individuals seemed to ignore the presence of another bird than instances that resulted in confrontation (e.g., a chase or calling). Violet-crowned and Broad-billed hummingbirds appeared to become somewhat more specialized when nectar was experimentally reduced, but nectar supplies nearest their nests were not sufficiently abundant so both also foraged at more distant agaves. For all three species, however, nectar supplies at outlying agaves seemed to be sufficiently abundant and yet close to have offset the effects of nectar reductions at the six agaves nearest nests.

Manipulations designed to reduce nectar availability during my study produced results that conform to a priori predictions in that hummingbirds: (1) showed measurable responses to reductions in nectar supplies, and (2) responded differently to these reductions. However, the final null hypothesis (i.e., reductions in nectar supplies will have no effect on nesting success) cannot be rejected. Foraging behavior of each hummingbird species in areas where nectar supplies nearest nests were reduced appeared to depend on the quantity, dispersion, and predictability of alternative nectar sources. As long as alternative supplies were nearby, predictable, and of sufficient quantities Black-chinned, Broad-billed, and Violet-crowned hummingbirds foraged from the same nectar sources. Only when nectar supplies were experimentally reduced did the Black-chinned make an obvious switch to alternative supplies and only during this period did the larger Violet-crowned appear to consistently dominate nectar sources nearest its nest.

Guild organization.—Patterns of seasonal occurrence, distribution, abundance, and interactions among guild members were not maintained indefinitely by any single factor, but were the result of several interdependent factors (Baltosser 1983). Unusual weather fluctuations, such as the record freeze that resulted in reduced foliage for nesting in 1980, may
on occasion have a substantial impact upon guild organization. In areas like Guadalupe Canyon, where each of the nesting species is at the periphery of its range, major weather fluctuations may assume added significance because these areas may experience “ecological crunches” (Wiens 1977) more frequently.

Small-scale differences in habitat selection and a partial seasonal separation of breeding seasons, the latter almost certainly predicated in part upon nectar availability, were important to guild organization. Periods of seasonal and daily abundance of nectar were interspersed with periods of limited availability. A major decline in availability during mid-June apparently influenced the number of individuals of each species that nested.

Patterns of organization in the Guadalupe Canyon hummingbird guild were similar to those in other studies of hummingbirds (e.g., Stiles 1973, Feinsinger 1976, DesGranges 1978, Feinsinger and Colwell 1978, Pimm 1978), and to nectarivorous guilds in general (e.g., Gill and Wolf 1975, Johnson and Hubbell 1975, Ford 1979). In Guadalupe Canyon the larger and more specialized Violet-crowned Hummingbird tended to utilize only the most productive and accessible nectar supplies, which it also tended to dominate, especially when these supplies were experimentally reduced. Smaller and more generalized species such as the Black-chinned and Broad-billed utilized many of the same nectar resources as the Violet-crowned, but unlike the Violet-crowned, both species also routinely utilized less productive and more highly dispersed sources. The potential effect on nesting of competition for nectar became apparent only when nectar supplies were experimentally decreased.

Thomson (1980) has suggested that evolutionary responses to competition may determine the attributes of species, while their numbers may respond to other pressures such as predation. The present study shows that nectar availability and habitat selection are each associated with, and important to, the organization of the Guadalupe Canyon hummingbird guild. Results support works such as Rotenberry (1978, 1980), Rotenberry et al. (1979), and Wiens (1974, 1977, 1983) that suggest that guilds are often not at resource-defined equilibrium. Guadalupe Canyon hummingbird populations appeared to be above equilibrium levels in 1976, nearer to such levels in 1977, and below these levels in 1980. The results of the present study, when coupled with other factors such as predation (Baltosser 1986), suggest that a variety of factors influence, perhaps intermittently, the structure of the Guadalupe Canyon hummingbird guild.

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LITERATURE CITED


NEST DEFENSE BEHAVIOR OF LESSER GOLDEN-PLOVERS

INGVAR BYRJKJEDAL

ABSTRACT.—The responses of incubating Lesser Golden-Plovers (*Pluvialis dominica dominica*) to a human observer and to avian nest predators were studied at Churchill, Manitoba. Golden-plovers typically left their nest when a human approached to within about 100 m. Usually, birds walked from their nests and vocalized loudly while in full view. As the intruder continued to approach, birds sometimes gave distraction displays, involving “tail down run,” “rodent run,” and “broken wing” behaviors. Only a few cases of “sitting tight” and “early surreptitious departure” were seen. Some birds flew or ran to a position between the intruder and the nest before performing a distraction display. Both sexes responded similarly toward human intruders. When the observer remained stationary 0.5 m from a nest, about 50% of the males, but none of the females, returned and approached the observer to within a few meters and then performed distraction displays. Reactions toward avian predators were cryptic. With Northern Harriers (*Circus cyaneus*) golden-plovers typically left their nests and stood quietly 100–200 m away; with Herring Gulls (*Larus argentatus*) and Parasitic Jaegers (*Stercorarius parasiticus*) they assumed either an erect, alert position on the nest ( predator at a distance) or squatted ( predator nearby). Aggressive mobbing of avian predators by golden-plovers was not observed. Low abundance of corvids and humans, and presence of other birds that efficiently drive off avian predators, may account for the golden-plovers’ apparent paradoxical combination of conspicuous responses to ground predators and cryptic responses to avian predators. Received 11 Aug. 1988, accepted 6 March 1989.

To avoid nest predation, birds may respond to an approaching predator with behavior which is either cryptic (sitting tight, departing stealthily) or conspicuous (e.g., scolding, circling, injury-feigning, attacking). The potentials of the various behaviors differ according to the kind of predator involved. Thus, birds may react differently to predators that are ground-living or flying, visually or scent oriented, and large or small (Sordahl 1981, McCaffery 1982, Gochfeld 1984, Byrjkjedal 1987). Conspicuous behavior successfully carried out against one predator species may attract the attention of another which the bird is unable to drive or lure away (McCaffery 1982, Byrjkjedal 1987). This may cause constraints on conspicuous antipredator behavior. None of 32 Palearctic shorebirds for which information was available had conspicuous ground predator strategies in the incubation period (scolding, circling, attacking) unless they had aggressive avian predator strategies (10 species, Cramp and Simmons 1983, pers. obs.).

Lesser Golden-Plovers (*Pluvialis d. dominica*) attack avian nest pred-

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1 Museum of Zoology, Univ. of Bergen, N-5007 Bergen, Norway.
ators only in parts of the breeding range, yet their ground predator responses are highly conspicuous (Drury 1961, Parmelee et al. 1967, Sordahl 1981, McCaffery 1982). I studied antipredator behavior of incubating Lesser Golden-Plovers in subarctic Canada in order to identify the species' strategies against ground-living and avian nest predators. The studied population did not attack avian predators, and I discuss whether conflicting cryptic and conspicuous strategies have influenced their antipredator behaviors.

MATERIALS AND METHODS

The study was performed 24 June–20 July 1986 at Churchill, Manitoba, in a 3.75-km² area of lichen and sedge tundra (further details, Byrkjedal 1989). The most common potential nest predators were Herring Gulls (Larus argentatus) (44% of 36 individual avian predators seen while I watched four golden-plover nests, see below), Parasitic Jaegers (Stercorarius parasiticus) (31%), Northern Harriers (Circus cyaneus) (17%), and Northern Shrikes (Lanius excubitor) (8%). Common Crows (Corvus brachyrhynchos) nested on the forest edge; one pair was sometimes seen on the tundra, as were a few Common Ravens (Corvus corax). However, no corvids were seen during the nest watches. Red foxes (Vulpes vulpes) are the chief mammalian predators at Churchill (Skeel 1983); I saw them 3–4 times in the study area. Arctic foxes (Alopex lagopus) and small mustelids may also occur (J. C. Davies pers. comm.).

I found 23 golden-plover nests in the study area. Twenty were found during or just after the egg-laying phase. I individually color-banded seven males and three females. Sexing was easily done in the field by plumage characters, males being more contrast-rich than females (Hayman et al. 1986).

I regarded reactions to humans as comparable to reactions to other ground predators (see Armstrong 1956), and recorded the behavior of golden-plovers to my own intrusions (N = 97) at 22 nests. On these intrusions I walked steadily straight toward the nest while dictating on a tape recorder the reactions of the incubating bird and also of its mate, if present. I also recorded my own and the bird's distance to the nest each time the bird changed behavior. I estimated bird–nest distances visually and recorded my own distances to the nest by pacing. I started the straight approaches 200–300 m from the nests at a point where the sitting bird most likely could see me. These nest visits are referred to as "intrusions." On 63 of the intrusions, I continued to record behavior for 5 min as I sat down 0.5 m from the nest. These observations are analyzed separately.

I found about 12 h incubation stints for each sex, the females sitting at night and the males during the day (unpubl.). Off-duty females were far beyond the territory, while off-duty males were on the territory about 50% of the time. Accordingly, I made intrusions at different times in order to obtain data on both mates and of the males' possible functions as sentinels.

The plovers' reactions to aerial predators were recorded during distant watches (sometimes from a parked car) of four nests (1685 nest min). I also was alert for aggressive predator-mobbing at all times during the field work.

I use Gochfeld's (1984) terminology of antipredator behavior. Definitions of postures are given in Fig. 1. The term "distraction display" refers to behaviors signalling "physical incapabilities" (drawings H through N, Fig. 1).

RESULTS

Reactions to humans.—When I approached golden-plover nests, the sitting bird typically left in an upright walk to one side, often after having
circled the nest at <2 m distance (Fig. 1; data are presented for males only, but data for females were similar). The upright walk often developed into a distraction display, most commonly "tail down run" and "rodent run." As I reached the nest the birds ended their departure and usually stood alert or started circling the nest at about 60 m distance. On 28% (N = 16) of the intrusions (10 nests) the birds, after having departed from the nest, returned and entered a position between the intruder and the nest ("intercepting") before starting a distraction display to one side. In a few cases the birds left their nest surreptitiously. They did so at longer distances (median 175 m) from the intruder than when leaving in full view (males; median 99.5 m, P < 0.01, Wilcoxon's Sum of Ranks Test; Fig. 2). Distraction displays started when the birds were at median distances of 17.5 m (males) from the nest and 25 m from the intruder (Fig. 3).

On 17 of 88 intrusions (12 of 22 nests) the birds (males) started to vocalize loudly while they were less than 2 m from the nest, in 6 of these cases (6 nests) even before leaving the nest. Usually the birds started to vocalize 5–10 m from the nest. Golden-plovers always vocalized in "upright walk" and when "standing alert" or "circling at a distance," but they were silent when performing distraction displays and when departing surreptitiously.

To clarify the essential features I classify the responses to humans (from Fig. 1) in four main categories: (1) leaving the nest stealthily with no distraction display, and finally hiding; (2) leaving the nest in full view (walking or flying), no distraction display, finally hiding; (3) leaving the nest in full view, no distraction display, remaining in full view; and (4) leaving the nest in full view, giving distraction display, remaining in full view. The highly conspicuous behaviors (3) and (4) were by far the most common (Fig. 4; the graph includes some intrusions that were not included in Fig. 1 due to loss of details). The birds responded with early surreptitious departure (category 1) in only 10% of the intrusions.

Males and females did not differ in the frequencies of behavioral categories (1)–(4) (χ²-tests, Fig. 4) or in reaction distances (Wilcoxon's Sum of Ranks Tests; Fig. 2). Off-duty birds contributed little to nest defense. On only six of 19 intrusions did off-duty males warn their incubating mate of my approach, and on one of three intrusions did off-duty females warn. Off-duty birds of either sex stood vocalizing 50–60 m from the nest but never engaged in distraction displays.

On 63 intrusions (20 nests), I remained near the nest (0.5 m distance) for 5 min. Males incubated on 50 of these occasions (20 nests) and females on 13 (11 nests). On 27 of these intrusions (11 nests), the attendant males approached me and then departed in distraction display. None of the females did so (significant difference between mates; Fisher's Test, P =
Fig. 1. Reactions of incubating male Lesser Golden-Plovers to a human approaching nests (58 intrusions, 22 nests). O–R are the behaviors seen when the intruder reached nest site. Figures on arrows give the number of approaches on which a behavior was recorded, and thicker arrows represent higher frequencies of occurrence.

A = Incubating male sees intruder
B = Close circling of nest (<2 m distance)
C = Upright run or walk, in full view
D = Flight
E = Surreptitious departure (bird sneaking between tussocks)
0.004, two-tailed). Such behavior ("... returning toward a recalcitrant intruder as if to recapture its attention") was termed "re-entrapment" by Gochfeld (1984). Re-entraps were repeated up to 11 times during a 5-min period. The birds started re-entrapment displays at a median distance of 3 m from the intruder and ended their display at a median distance of 6 m, whereupon they started to scold and circle, or returned for another re-entrapment. Several types of distraction displays were usually performed during each re-entrapment (Table 1). Elaborate displays ("broken wing" and "stationary wing-spread" displays) were more common during re-entraps than during a bird's initial display bout.

Response distances, and the frequencies of behavioral categories (1)-(4) and re-entraps, did not change significantly over the season (Wilcoxon's Sum of Ranks Tests both on date and on time since egg laying).

Reactions to avian predators.—Distant watches at four nests (1685 min) showed that the responses of incubating birds varied with the species of predator (Fig. 5). The observations concern golden-plover males only, as they incubated during the day, when avian predators were active. The most numerous potential nest predators were Herring Gulls, but incubating plovers showed only slight reactions to them—at most, alertness (<150 m distance) and "semi-squatting" (<70 m distance; the bird sank deeply into the nest but did not stretch the neck along the ground). Four golden-plover nests were situated 85-150 m from Herring Gulls' nests. The birds reacted far more to Parasitic Jaegers, usually by squatting entirely flat on the nest when jaegers came within about 150 m. The plovers

---

F = Bird enters position between intruder and nest  
G = Crouched run, in full view  
H = Tail down run (tail canting, head lowered, bird in full view)  
I = Rodent run (tail canting and half spread, wings drooping and quivering, back feathers more or less ruffled)  
J = Mobile broken wing display (bird moves along ground with one or both wings flapping)  
K = Stationary broken wing display (similar to J but display performed on the same spot)  
L = Stationary wing-spread display, bird facing intruder  
M = False brooding (bird sits on the ground as if incubating)  
N = Impeded flight  
O = Distant circling (with false feeding; about 60 m from nest)  
P = Standing alert  
Q = Continued display when intruder reached nest site  
R = Standing concealed behind tussock or bush

Three different types of J and K were seen.
also squatted in the presence of a Northern Shrike perched in tree-tops 50–70 m from their nests. Incubating birds left the nest when Northern Harriers were 50–100 m away, flew 100–200 m and stood silently until the harrier was out of sight.
The plovers never were seen mobbing any avian predators during 185 hours of field work in the area. However, breeding Whimbrels (*Numenius phaeopus*) were abundant in the area and mobbed frequently. While I watched the four golden-plover nests, jaegers intruding in the golden-plover territories were successfully driven away by Whimbrels on six of 11 observed intrusions and harriers on two of five intrusions.

**DISCUSSION**

When approached by a ground predator, many shorebirds either leave the nest early and surreptitiously or they sit tight and do not perform any distraction display until flushed almost from underfoot. By “intermediate” responses a bird would “lose the benefits of both behavioral extremes” (Gochfeld 1984). Lesser Golden-Plovers show “intermediate”
behavior, as they leave early and highly conspicuously. In the case of human intruders, they depart from the nest at about 100 m distance, usually with loud vocalizations and no attempts to conceal themselves. The effect of this behavior is probably to disturb the search of an approaching predator long before it has come within "detectability distance" of the nest. The birds resort to "injury feigning" behavior only if the intruder continues to approach the nest. Usually such behavior was elicited when the intruder was considerably less than 50 m from the nest.

The ground predator responses of Lesser Golden-Plovers are completely different from those of Greater and Pacific (Lesser) golden-plovers (*Pluvialis apricaria, P. [dominica] fulva [probably a separate species (Connors 1983)]) and Black-bellied Plovers (*P. squatarola*), all of which practice an early surreptitious departure. The latter two often reappear after the departure and distract or chase the ground predator (Drury 1961, Sauer 1962, Flint and Kondratjew 1977), while the former remains cryptic. In addition, Greater, and sometimes Pacific (Lesser), golden-plovers sit tight as an alternative to early departure (Williamson 1948, Sauer 1962, Ratcliffe 1976, Byrkjedal 1987).

Early conspicuous departure was not a specific reaction to humans, as
Byrkjedal • NEST DEFENSE OF LESSER GOLDEN-PLOVERS 587

Table 1
Distraction Displays Given by Lesser Golden-Plover Males during 71 Re-Entrapments*

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Number of displays observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail down run (H)</td>
<td>39</td>
</tr>
<tr>
<td>Rodent run (I)</td>
<td>30</td>
</tr>
<tr>
<td>Mobile broken wing display (J)</td>
<td>50</td>
</tr>
<tr>
<td>Stationary broken wing display (K)</td>
<td>60</td>
</tr>
<tr>
<td>Stationary tail down/wing-quiverc</td>
<td>6</td>
</tr>
<tr>
<td>Stationary wing-spread display, facing intruder (L)</td>
<td>43</td>
</tr>
<tr>
<td>False brooding (M)</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>229</td>
</tr>
</tbody>
</table>

* Displays given at close range while observer sat 0.5 m from nest (N = 20 nests).

The letters in parentheses refer to description of the postures given in Fig. 1.

c Posture similar to “tail down run,” but bird stationary with wings quivering.

a bird dog elicited the same behavior (tested at four nests; see also Armstrong 1956). In fact, early conspicuous departure would be a poor adaptation to human predation, as humans could easily use such behavior to locate nests. Lesser Golden-Plover nests are probably among the easiest shorebird nests to find, while nests of Pacific (Lesser) Golden-Plovers, Black-bellied Plovers, and in particular Greater Golden-Plovers, can only be found with considerable effort (Williamson 1948, Ratcliffe 1976, Por-tenko 1981, Byrkjedal 1987). The Lesser Golden-Plover may be less well adapted to human nest predation than the other Pluvialis plovers due to a virtual lack of humans over much of its breeding range (Lee and DeVore 1968, Godfrey 1979, Hayman et al. 1986).

The Lesser Golden-Plovers at Churchill showed markedly cryptic responses to flying predators in spite of their conspicuous ground predator reactions. Being visually oriented, avian predators could be attracted to a nest site by conspicuous responses to ground predators by the attending bird. In the other Pluvialis plovers, reactions during the incubation period to both ground-living and flying predators are either strongly cryptic (Greater Golden-Plovers: Byrkjedal 1987) or conspicuous (Black-bellied Plovers: Drury 1961, Flint and Kondratjew 1977; Pacific (Lesser) Golden-Plovers: Sauer 1962). Aggressive mobbing of flying predators has been reported from some Lesser Golden-Plover populations (Drury 1961, Sordahl 1981, McCaffery 1982) but was not seen at Churchill. The apparent paradoxical combination of cryptic and conspicuous strategies of these golden-plovers might result from: (1) differences in diurnal activities of avian and ground-living predators, (2) low abundance of avian predators,

Many ground predators (e.g., red, but not Arctic, foxes) tend to be crepuscular while avian predators operate during the day. This difference in diurnal rhythm may ease the conflict between cryptic and conspicuous behaviors, but probably less so in high latitudes where nights are shorter and lighter than at low latitudes. At Churchill, I repeatedly saw foxes active in the middle of the day. Avian predators were abundant at Churchill. On average golden-plover territories were overflown about once per 45 min. Nevertheless, the chances that avian predators should detect conspicuous ground predator responses might have been slight. The species that were most abundant (Herring Gulls, Parasitic Jaegers, Northern Harriers) usually search in swift flight. Their presence over a golden-plover territory is therefore very short, and the chances are small that it should coincide with an intruding ground predator. Although Common Crows and Common Ravens were observed, they were relatively scarce on the Churchill tundra. Corvids are extremely potent nest predators, likely to capitalize on conspicuous ground predator behaviors due to their persis-
tent search (fairly slow flight, frequent use of vantage points, watching from concealment; pers. obs.), and high mental abilities (e.g., Simons 1976, Montevcechi 1978, Sonerud and Fjeld 1987). Corvids are severe nest predators on the breeding grounds of Greater Golden-Plovers (Ratcliffe 1976; Parr 1980; Langslow 1983; Byrkjedal 1980, 1987) and may have put constraints on conspicuous antipredator behavior in this species. The tundra-nesting P. squatarola, P. fulva, and P. d. dominica may have experienced less constraints from corvids. Corvids need trees or cliff-ledges for nesting and are therefore less abundant on the flat and bare tundra (Dement’ev and Gladkov 1954, Godfrey 1979).

Aggressive predator-mobbers at Churchill were Whimbrels, Hudsonian Godwits (Limosa haemastica), and Bonaparte’s Gulls (Larus philadelphla) (Hagar 1966, Jehl and Smith 1970, Skeel 1983, pers. obs.). Most golden-plover territories overlapped with Whimbrel territories. Whimbrels efficiently chased away flying predators, attacking from a distance of 100–200 m. This could have decreased the possibilities for flying predators to take advantage of the golden-plovers’ conspicuous ground predator responses and also have reduced the need for golden-plovers to aggressively mob avian predators.

Summing up, the study shows that incubating Lesser Golden-Plovers use conspicuous ground predator responses in spite of relying on cryptic behavior against flying predators. Low nest predation pressure from corvids and humans, as well as the presence of other birds that efficiently chase avian predators, are likely factors accounting for this.

ACKNOWLEDGMENTS

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LITERATURE CITED


NEST HABITAT USE OF RIO GRANDE WILD TURKEYS

JOEL A. SCHMUTZ,1 CLAIT E. BRAUN,2 AND WILLIAM F. ANDELT1

ABSTRACT.—Nest habitat use of Rio Grande Wild Turkeys (Meleagris gallopavo intermedia) was studied along the South Platte River in northeast Colorado in 1986–87. Thirty-three of 35 nests were in riparian habitats. Nests were either in western snowberry (Symphoricarpos occidentalis) (67%) or mixed forbs and grasses (33%). Early season nests were more likely to be in snowberry than late season nests. Nest sites were characterized by greater overstory canopy cover, more shrubs, fewer grasses, and greater understory cover and height than surrounding areas. These areas had more shrubs, fewer large trees, and greater understory cover and height than riparian habitats throughout the study area. Phenology of understory vegetation and the effect of such vegetation on nest predation may influence temporal patterns of nest habitat use. Received 19 Dec. 1988, accepted 25 March 1989.

Avian nest habitat selection may be influenced by many factors including predation (Martin and Roper 1988), inter- and intraspecific competition (Orians 1980), and the thermal environment (Walsberg 1985). To understand habitat selection and the effect of such factors, patterns of nest habitat use must first be documented. For Wild Turkeys (Meleagris gallopavo), several investigators have recently reported quantitative data on nest habitat use (Lazarus and Porter 1985, Ransom et al. 1987, Wertz and Flake 1988). The varied habitats used for nesting and low sample sizes of these studies precluded elucidation of what criteria Wild Turkeys may use in choosing nest sites. Nest predation has been implicated as a major limiting factor of Wild Turkey populations (Reagan and Morgan 1980, Speake 1980, Ransom et al. 1987), but the influence of predation on habitat choice is not clear.

The objective of our study was to document quantitatively nest habitats used by an introduced population of Rio Grande Wild Turkeys (M. g. intermedia). We investigated nest-site selection by: (1) comparing nest sites to random sites at several levels or scales, and (2) comparing the chronology and success of nests in different vegetative types.

STUDY AREA

The study was conducted along the South Platte River in Logan, Morgan, and Washington counties in northeast Colorado. This riverbottom community extended to 1.0 km in width

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and was dominated by an open-canopied plains cottonwood (*Populus sargentii*) forest. Boxelder maple (*Acer negundo*), red ash (*Fraxinus pennsylvanica*), and Russian-olive (*Eleagnus angustifolia*) occurred in low but increasing frequencies. Common forbs included pepperweed (*Lepidium latifolium*), poison hemlock (*Conium maculatum*), ragweed (*Ambrosia spp.*), sunflower (*Helianthus spp.*), and thistle (*Cirsium spp.*). Common grasses included cheatgrass brome (*Bromus tectorum*), prairie cordgrass (*Spartina pectinata*), inland saltgrass (*Distichlis stricta*), sand dropseed (*Sporobolus cryptandrus*), and wheatgrass (*Agropyron spp.*). Shrubs occurred in discrete patches and were predominately western snowberry, although willows (*Salix spp.*) were common in mesic areas (plant names follow Scott and Wasser [1980]). Lindauer (1983) provided a complete vegetative description of this particular community.

Private lands adjacent to the riverbottom were primarily used for production of alfalfa, corn, wheat, and other small grains and row crops. Cattle were grazed at varying intensities both in and adjacent to the riverbottom. The Colorado Division of Wildlife owned approximately one-third of the riverbottom in the study area. These lands were not grazed and were used for both consumptive and nonconsumptive recreation.

Sixty Rio Grande Wild Turkeys from Kansas and Texas were introduced into the study area during 1980–83. No Wild Turkeys had previously existed in northeast Colorado.

**METHODS**

Wild Turkeys were trapped in February 1986–87 with drop-nets and clover traps. Captured birds were classified as yearlings (< one year of age) or adults (> one year of age) based on characteristics of primaries IX and X (Petrides 1942). Females were fitted with transmitters mounted on ponchos (Amstrup 1980) or attached to the central pair of rectrices (Bray and Corner 1972). Poncho and tail-clip transmitters weighed 29–32 and 26–29 g, respectively, and had expected battery lives of six months.

*Habitat measurements.*—Hens were monitored daily, when possible, to ascertain nest initiation. Date of initiation was estimated by calculating number of eggs laid and incubation period (Schmutz and Braun 1989). Nest habitat variables were measured within two days after eggs hatched or were abandoned or depredated. Measurements of random habitat plots were distributed over the same periods as measurements of nest plots to minimize phenological differences. Eight nest plots and 31 associated random plots from 1986 were remeasured in April 1987 at the approximate date of nest initiation the previous year.

All plots were 0.04-ha circles with 22.5-m diameters. Nest plots were centered on nest sites. Up to four adjacent random (AR) plots were selected within 79 m of each nest at random distances and directions. Study area random (SAR) plots were spaced at 2.5-km intervals throughout the linear study area. At each interval, SAR plots were established in the riverbottom at a random percentage of the riverbottom’s width from the river at that interval. No SAR plots were within 300 m of a nest.

Variables measured at nest and random plots were: overstory canopy cover, understory cover, understory height, amount of shrubs, forbs, grasses, and bare ground, distance to nearest tree >30 cm in diameter at breast height (DBH), and basal area of all trees and small (<25 cm DBH), medium (25 cm and <45 cm DBH), and large (≥45 cm DBH) trees. Canopy cover was measured with a densiometer. A vegetation profile board (Nudds 1977) was used to estimate percent understory cover to one of six classes (<2.5, 2.5–25, 25–50, 51–75, 75–95, and >95%) in each of three height categories (<0.5, 0.5–1.0, and 1.1–2.0 m). The profile board was placed at the plot center and read from the plot perimeter in the four cardinal directions. Understory height was measured at these four perimeter locations and the plot center. Both understory height and basal area were measured in 5-cm increments.
Coverage of shrubs, forbs, grasses, and ground was estimated in meters along two perpendicular, but randomly oriented, transects, each equal to the plot diameter of 22.5 m.

In 1987, egg visibility was measured concurrent with habitat measurements at all 22 nests of radio-marked hens. Ten Wild Turkey eggs were placed in the nest bowl. The number of visible eggs was counted while standing above the nest, and while standing and crouching 2 and 5 m away in the four cardinal directions. The four directional measurements were then averaged.

Statistical analyses.—Habitat measurements in AR plots for each nest site were averaged and then paired with associated nest plot data for analysis with Wilcoxon signed ranks tests. If <2 AR plots were measured at a nest site, then the nest and associated AR plots were excluded from this analysis. Likewise, the eight nests measured in April 1987 were paired with 1986 habitat data and analyzed with Wilcoxon signed ranks tests. Habitat differences between nest and SAR plots were tested with median tests because the distributional differences between these two groups prevented analysis with more powerful Mann-Whitney tests (Conover 1980). Habitat and egg visibility differences between nests of different age hens, fates (successful vs unsuccessful), and vegetation types (snowberry vs other) were tested with Mann-Whitney tests as were differences between AR and SAR plots. Nesting in snowberry versus other vegetation as a function of nest initiation date was examined with logistic regression. Wilcoxon signed ranks tests were conducted using SPSS (Norusis 1986). The Statistical Analysis System was used for all other analyses (SAS 1987).

RESULTS

Thirty radio-marked hens initiated a known total of 35 nests. Thirty nests were in ungrazed riverbottom, three were in riverbottom lightly grazed within the past year, and the two latest initiated nests (>1.5 months after median nest initiation date [Schmutz and Braun 1989]) were approximately 200 m from the riverbottom edge in currently grazed pastures. For first nest attempts (including an unmarked adult), early nesting hens were more likely to nest in snowberry than late nesting hens (P = 0.067) (Fig. 1). Three hens were known to renest once and one hen renested twice. Excluding the hen that renested after laying a single egg, all four renests were in the opposite vegetation type (snowberry vs other) from the hens’ previous attempts.

Nest plots measured at hatch (late May–Jun 1986) had greater canopy and understory cover in all three height classes than the same plots measured the following year during the nest initiation period (mid-Apr 1987) (P < 0.05 for all tests). Live grasses and forbs were much shorter at nest initiation (\( \bar{x} = 9 \pm 1 \) [SE] cm) than at hatch (\( \bar{x} = 56 \pm 3 \) cm; P < 0.001), but height of live shrubs did not vary between nest initiation (\( \bar{x} = 100 \pm 8 \) cm) and hatch (\( \bar{x} = 106 \pm 9 \) cm; P = 0.722). Adjacent random plots also had greater canopy and understory (\( \leq 1 \) m) cover at hatch than at nest initiation (P < 0.05 for all tests).

Thirty-one nest plots (including one nest of an unmarked adult) were compared with their associated AR plots. Nest plots were characterized by greater canopy cover, more shrubs, fewer grasses, and greater under-
Fig. 1. Probability of Wild Turkeys nesting in snowberry as a function of nest initiation date in northeast Colorado, 1986–87. Logistic regression was used to predict values ± SE from $y = 0.041x - 6.051$, where initiation date was the Julian date.

story cover (≤1 m) and height than AR plots ($P < 0.01$ for all tests) (Table 1). Distance to large tree, basal area of trees, amount of forbs and bare ground, and understory cover > 1 m did not differ ($P > 0.05$) between nest and AR plots. Comparing the 31 first nest attempts to the SAR plots (N = 36), the same characteristics were different except that canopy cover and grass abundance did not differ. Additionally, AR plots had greater understory cover (>0.5 and ≤1.0 m) and height, more shrubs, and fewer large trees than SAR plots ($P < 0.05$). Other habitat variables did not differ ($P > 0.10$), but understory cover ≤0.5 m tended to be greater at AR plots ($P = 0.068$).

Nest plots centered in snowberry (N = 24) were closer to a large tree and had greater canopy cover, more large trees, more shrubs, and fewer forbs than nests in other vegetation (Table 2). Many snowberry clumps contained 1–5 large cottonwoods resulting in many of these differences. Nest failure due to predation was independent of habitat type (snowberry vs other) when examined across entire seasons ($G$ test, $G = 0.502$, $P = 0.479$). After dividing the data set into early (N = 16) and late (N = 17) seasons and excluding three abandonments, early nests in snowberry tend-
ed to be more successful than late nests in snowberry ($P = 0.027$) (Table 3). Among late nests, those in snowberry were less successful than those in forbs and grasses ($P = 0.026$). A greater proportion of nests in 1986 (11 of 13) were in snowberry than in 1987 (13 of 23). Nests in 1986 had greater understory cover ($>0.5$ and $\leq 1.0$ m) than 1987 nests ($P = 0.041$), but other habitat variables did not differ.

Habitat variables within adult nest plots ($N = 14$) did not differ ($P > 0.05$) from those of yearlings ($N = 22$) nor did successful nests ($N = 18$) differ from unsuccessful nests ($N = 16$, excluding two observer-induced abandonments). Egg visibility from all angles did not differ between age classes, nest fates, or vegetation types. An average of 5.4 eggs was visible from above the nest, $<$3 eggs were visible from a distance of 2 m, and $<$1 egg was visible from 5 m.

**DISCUSSION**

Whereas floristic composition at nest sites varies greatly across the Wild Turkey’s geographic range, most investigators have observed similar
Table 2
Habitat Variables at Wild Turkey Nests in Snowberry and Other Vegetation in Northeast Colorado, 1986-87

<table>
<thead>
<tr>
<th>Variable</th>
<th>Snowberry (N = 24)</th>
<th>Other (N = 12)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \bar{x} )</td>
<td>SE</td>
</tr>
<tr>
<td>Canopy, %</td>
<td>40.2</td>
<td>7.2</td>
</tr>
<tr>
<td>Shrubs, m</td>
<td>9.3</td>
<td>1.0</td>
</tr>
<tr>
<td>Forbs, m</td>
<td>4.4</td>
<td>0.9</td>
</tr>
<tr>
<td>Grasses, m</td>
<td>7.9</td>
<td>1.2</td>
</tr>
<tr>
<td>Ground, m</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>Understory cover, %</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;0.5 m</td>
<td>97.0</td>
<td>0.2</td>
</tr>
<tr>
<td>0.5–1.0 m</td>
<td>61.7</td>
<td>5.1</td>
</tr>
<tr>
<td>1.1–2.0 m</td>
<td>7.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Understory height, cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot center</td>
<td>92</td>
<td>6</td>
</tr>
<tr>
<td>Total plot</td>
<td>70</td>
<td>5</td>
</tr>
<tr>
<td>Distance to large tree, m</td>
<td>11.5</td>
<td>2.2</td>
</tr>
<tr>
<td>Basal area, m²/ha</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small trees</td>
<td>0.9</td>
<td>0.4</td>
</tr>
<tr>
<td>Medium trees</td>
<td>3.3</td>
<td>1.1</td>
</tr>
<tr>
<td>Large trees</td>
<td>8.6</td>
<td>2.3</td>
</tr>
<tr>
<td>Total trees</td>
<td>12.8</td>
<td>2.5</td>
</tr>
</tbody>
</table>

* \( P < 0.05 \).

Structural patterns in nest site vegetation. Nests are characterized by concealment in dense herbaceous or woody vegetation, both around and above the nest (Williams et al. 1968, Lazarus and Porter 1985, Wertz and Flake 1988). Similarly, we found that nests of Rio Grande Wild Turkeys were in understory vegetation denser and taller than the surrounding environment. Low visibility of eggs and incubating hens substantiated the concealing effect of these understory characteristics.

The relative cover value of snowberry strongly influenced temporal and spatial aspects of nest-site selection. Many of the observed differences (e.g., distance to large tree, grass abundance) were likely artifacts of their correlation with the presence of snowberry clumps. In mid-April, when hens were first initiating nests, the amount of cover provided by snowberry was much greater than that provided by herbaceous vegetation, and thus, snowberry was probably more effective at deterring nest predators (Bowman and Harris 1980). As the season progressed, the cover value of forbs and grasses approached that of snowberry, and correspondingly, these types were used more as nesting cover. Why nesting success between these
Table 3

Numbers of Successful and Depredated Wild Turkey Nests in Snowberry and Mixed Forbs and Grasses in Early and Late Season in Northeast Colorado, 1986–87

<table>
<thead>
<tr>
<th>Season</th>
<th>Fate</th>
<th>Snowberry</th>
<th>Forbs and grasses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>Successful</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Depredated</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Late</td>
<td>Successful</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Depredated</td>
<td>6</td>
<td>3</td>
</tr>
</tbody>
</table>

Two habitats changed with respect to time is not as clear. The greater abundance of forbs and grasses (as compared to shrubs) may result in lower probabilities of nest predation in these habitats due to the increased amount of area (potential nest sites) a predator would need to search (Martin and Roper 1988). The observation that all renests after nest depredation occurred in the opposite vegetation type further suggests that reducing potential nest predation influenced nest-site selection by these Wild Turkeys.

Although these data support the belief that Wild Turkeys select nest sites in dense, concealing understory vegetation, definition of what specific structural characteristics they may cue on is not yet possible. Differences between the two spatial scales of random plots (SAR vs AR) and between both types of random plots and nest plots suggests that without an experimental approach, it is difficult to interpret at what scale(s) nest habitat selection is operating. Interpretation of descriptive studies that compare use with non-use or random sites is potentially biased by the spatial scale(s) one chooses for measurement.

Tall, dense understory vegetation, possibly because of its moderation of nest predation, may be a primary cue used by Wild Turkeys in northeast Colorado for selecting nesting habitat. Whether or not potential nest sites can be defined by specific structural variables awaits further study. This study demonstrates the need for avian nest habitat studies to consider both spatial and temporal (phenological) scales of habitat measurement.

Acknowledgments

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LITERATURE CITED


DO BROWN-HEADED COWBIRDS LAY THEIR EGGS AT RANDOM IN THE NESTS OF RED-WINGED BLACKBIRDS?

GORDON H. ORIANS, EIVIN ROSKAFT, AND LES D. BELETSKY

ABSTRACT.—We tested the hypothesis that female Brown-headed Cowbirds (Molothrus ater) deposit their eggs randomly in nests of Red-winged Blackbirds (Agelaius phoeniceus) by analyzing the weekly distributions of numbers of eggs in the nests of potential hosts with Poisson distributions including and excluding the zero-class. The hypothesis that females laid randomly could not be rejected in any weekly period when either all nests were included or when only parasitized nests were used. However, when all data were pooled, a random hypothesis using all nests could be rejected because there were more nests without cowbird eggs than expected. Among parasitized nests, a random hypothesis could also be rejected because there were more nests with a single cowbird egg or with 3–5 cowbird eggs than expected. Our results illustrate the importance of examining distributions with respect to the opportunities actually available to laying cowbirds. Pooling data from entire seasons may give misleading results. Received 10 Aug. 1988, accepted 25 March 1989.

The Brown-headed Cowbird (Molothrus ater) has been reported to parasitize more than 200 different North American bird species (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). Some information is available on how cowbirds locate nests (Robertson and Norman 1977, Payne 1977), but little is known about how laying females choose from among available nests. If females do not discriminate among nests, but simply lay randomly in the nests they find, the proportions of nests with 0, 1, 2, 3, 4, . . . i cowbird eggs should approximate a Poisson distribution (Preston 1948, Mayfield 1965). Some authors have found non-random distributions of parasitized nests (Elliott 1977, Linz and Bolin 1982, Lowther 1984, Preston 1948), whereas others have found support for a random model (Mayfield 1965). From these analyses authors have drawn conclusions about choices of nests by female cowbirds.

It is difficult, however, to infer patterns of laying behavior from such statistics because deviations from random egg laying can be caused by many factors. Some, such as: (1) partial non-overlap between laying dates of parasites and hosts, (2) combining data from different acceptor species that are heavily or lightly parasitized, (3) inclusion of rejector species in the sample (Mayfield 1965, Rothstein 1975), and (4) desertion of parasitized nests, making them less likely than active nests to be found by

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human observers, result in artifacts that do not reveal anything about choices by laying female parasites. Others, such as: (5) unequal ease in finding nests by parasites, (6) effective nest defenses by hosts (Robertson and Norman 1976), (7) an excess of nests to parasitize, and (8) an avoidance of already parasitized nests by laying females reveal aspects of choices by female parasites and their interactions with potential hosts. In this paper we show how the ways in which data are pooled for analysis may affect interpretation of field data on patterns of brood parasitism.

It is important to be able to identify how parasitic females choose the nests in which they lay, because the success of parasites may depend, in part, upon the types of discriminations they perform and because the evolution of responses by hosts may be related to the ways in which parasites choose hosts. To examine these choices more closely, we studied cowbird parasitism of the Red-winged Blackbird (*Agelaius phoeniceus*) in an area where redwings were by far the most abundant host for cowbirds. By concentrating on a single, abundant host species, we were able to assess laying behavior of cowbirds in relation to the availability of host nests at the time the females were making their choices. Thus we were
able to control for many of the potential causes of nonrandom distribution patterns of parasitic eggs listed above, even if parasitic females actually laid their eggs randomly.

**STUDY AREA AND METHODS**

We studied Red-winged Blackbirds in a series of marshes located in the Columbia National Wildlife Refuge in central Washington State. The area and general ecology of blackbirds are described by Orians (1980). Observations were made each year from 1977 through 1983, from mid-March, before nesting began, to mid- to late-June, when at least 95% of annual breeding was completed. Marshes were searched for new nests and nests were checked for progress usually every three days. Because redwing nests are easy to find, all nests on the study area were located. The first cowbird eggs were laid in redwing nests during the last week of April, roughly one month after the first redwing nests were started. Thus, early nesting redwings escaped cowbird parasitism entirely. Because the intensity of parasitism (percent of nests parasitized) and number of nests available to be parasitized changed dramatically during the breeding season, we divided each month into four periods (7, 8, 7[8] and 8 days, respectively), long enough to yield samples large enough for statistical analysis, but short enough that nest availability and number of laying female cowbirds did not change very much.

We performed analyses both using all redwing nests, whether or not they were parasitized, and just the sample of parasitized nests. Analysis of the complete sample can reveal whether cowbirds find it more difficult to locate some nests than others. Analysis of the sample of parasitized nests can reveal whether female cowbirds avoid laying in already parasitized nests. Redwings are not known to eject cowbird eggs or to desert their nests when they are parasitized (Rothstein 1975).

Because weekly sample sizes are often small and because the seasonal pattern of egg laying of Red-winged Blackbirds and Brown-headed Cowbirds were similar among years (Fig. 1), except for 1979, data from different years are pooled by week in our analyses.
Table 2
The Observed and Expected Distribution of Brown-headed Cowbird Eggs in the Nests of Red-winged Blackbirds by Weekly Periods

<table>
<thead>
<tr>
<th>Period</th>
<th>Distribution of cowbird eggs (N)</th>
<th>Chi-square*</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>IV Apr.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>465</td>
<td>2</td>
<td>—</td>
</tr>
<tr>
<td>Expected₁</td>
<td>465</td>
<td>2</td>
<td>—</td>
</tr>
<tr>
<td>Expected₂</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>I May</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>439</td>
<td>8</td>
<td>—</td>
</tr>
<tr>
<td>Expected₁</td>
<td>439</td>
<td>8</td>
<td>—</td>
</tr>
<tr>
<td>Expected₂</td>
<td>8</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>II May</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>439</td>
<td>21</td>
<td>—</td>
</tr>
<tr>
<td>Expected₁</td>
<td>439</td>
<td>21</td>
<td>—</td>
</tr>
<tr>
<td>Expected₂</td>
<td>21</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>III May</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>312</td>
<td>31</td>
<td>3</td>
</tr>
<tr>
<td>Expected₁</td>
<td>309</td>
<td>36</td>
<td>2</td>
</tr>
<tr>
<td>Expected₂</td>
<td>30</td>
<td>5</td>
<td>—</td>
</tr>
<tr>
<td>IV May</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>204</td>
<td>37</td>
<td>7</td>
</tr>
<tr>
<td>Expected₁</td>
<td>197</td>
<td>47</td>
<td>5</td>
</tr>
<tr>
<td>Expected₂</td>
<td>35</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>I June</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>87</td>
<td>27</td>
<td>6</td>
</tr>
<tr>
<td>Expected₁</td>
<td>84</td>
<td>32</td>
<td>6</td>
</tr>
<tr>
<td>Expected₂</td>
<td>26</td>
<td>9</td>
<td>—</td>
</tr>
<tr>
<td>II June</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>80</td>
<td>16</td>
<td>6</td>
</tr>
<tr>
<td>Expected₁</td>
<td>72</td>
<td>28</td>
<td>5</td>
</tr>
<tr>
<td>Expected₂</td>
<td>15</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>III June</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Observed</td>
<td>17</td>
<td>13</td>
<td>3</td>
</tr>
<tr>
<td>Expected₁</td>
<td>15</td>
<td>16</td>
<td>6</td>
</tr>
<tr>
<td>Expected₂</td>
<td>11</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>IV June</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>6</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Expected₁</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Expected₂</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

* Chi-square calculated with Yates' correction.
### Table 2
**Continued**

<table>
<thead>
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<th>Period</th>
<th>Distribution of cowbird eggs (N)</th>
<th>Chi-square*</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>Observed</td>
<td>2039</td>
<td>156</td>
</tr>
<tr>
<td></td>
<td>Expected₁</td>
<td>1991</td>
<td>235</td>
</tr>
<tr>
<td></td>
<td>Expected₂</td>
<td>145</td>
<td>42</td>
</tr>
<tr>
<td>Successful nests</td>
<td>Observed</td>
<td>650</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>Expected₁</td>
<td>632</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>Expected₂</td>
<td>35</td>
<td>13</td>
</tr>
</tbody>
</table>

* Significant differences between observed and expected values are indicated: * \( P < 0.05 \), *** \( P < 0.001 \).

\[ \text{Expected}_1 = \text{expected values when zero class is included.} \]

\[ \text{Expected}_2 = \text{expected values using a truncated Poisson distribution excluding the zero class.} \]

### RESULTS

The number of cowbird eggs in weekly samples increased to a maximum the last week of May and thereafter decreased to the last week of June (Table 1). However, because the number of redwing nests started each week decreased steadily during the same period, the proportion of nests parasitized increased throughout the breeding season (Fig. 1).

A random distribution model could be rejected in only one of the weekly samples, during which there were more nests without cowbird eggs than expected by chance (Table 2). This may be an artifact of the differences in parasitism rates in 1979 because if 1979 is excluded from the analysis the random distribution model cannot be rejected \( (x^2 = 4.7, 0.05 < p < 0.10) \). The truncated Poisson distribution using only parasitized nests could not be rejected in any of the weekly samples (Table 2). However, with the entire sample, a random model could be rejected: (1) if the zero class was included because there were more nests without or with several cowbird eggs and fewer nests with a single cowbird egg than expected (both for the total sample and for successful nests only), and (2) for parasitized nests, because there were more nests with a single cowbird egg or with 3–5 cowbird eggs and fewer nests with two cowbird eggs, than expected (for the total sample for successful nests the random distribution model could not be rejected).

Most of the nest failures were due to predation. However, there was no significant difference between the rate of nest failures (percent of nests lost prior to fledging) in parasitized and unparasitized nests within any
weekly period or for the total sample ($\chi^2 = 1.71, P > 0.3, \text{df} = 1$). The proportion of successful nests was 31.9% for unparasitized nests and 25.8% for parasitized nests, respectively. Thus, predators found unparasitized nests as readily as they found parasitized nests.

**DISCUSSION**

Our data support the hypothesis that female cowbirds lay their eggs randomly in nests of Red-winged Blackbirds. There is no evidence that they avoided already parasitized nests or that the nests they failed to parasitize were more difficult to find or more heavily defended than the nests in which they did lay eggs. Although predators do not search for redwing nests in the same manner as female cowbirds, the fact that predation rates were not statistically different on parasitized and unparasitized nests suggests that unparasitized nests were not more difficult to find.

However, if we had analyzed our data by pooling them over the entire breeding season, we would have concluded that cowbirds tried to lay in already parasitized nests. The apparent excess of unparasitized nests would have been due to inclusion of nests started before the first cowbirds laid their eggs. The apparent excess of nests with more than one cowbird egg in the pooled sample was due to the fact that the number of suitable host nests relative to the number of laying female cowbirds varied temporally. Actually, however, when the intensity of parasitism was high, there were as many cases of multiple parasitism as expected under the assumption of random laying.

The nine marshes used in our study ranged from an average of 19 to 93 redwing nests per year. Parasitism rates varied strikingly among marshes, but they were not related to number of redwing nests ($N = 9, r = 0.06, P = 0.44$). Robertson and Norman (1977) found that rates of parasitism by cowbirds on redwings were inversely proportional to redwing nesting density, suggesting that the presence of more adults made it more difficult for cowbirds to gain access to the nests. Our failure to find such an effect may be due to the fact that our study marshes are mostly strip marshes only one territory in depth. Consequently, most territories abut only two others, regardless of marsh size, and it should not be more difficult for cowbirds to approach nests in the large marshes than in the smaller ones.

We do not expect our results necessarily to be characteristic of all interactions between cowbirds and their hosts. For some host species, unlike redwings, incubation periods differ from those of cowbirds. Also the redwing is a relatively large host. Male cowbirds are larger than female redwings, but female redwings are slightly larger than female cowbirds. Therefore, if a female encountering an already parasitized nest is able to
remove another host egg and substitute for it her own egg, her offspring has a good chance of experiencing less nestling competition than if she had laid in an unparasitized nest (Roskaft, Orians and Beletsky, unpubl. data). However, if the host is smaller than a cowbird, a nestling cowbird is a stronger competitor than a host nestling. Multiple parasitism of these species should be avoided. This would be especially true if parasitic females maintained exclusive laying territories because, in that case, a parasitic egg in a nest is highly likely to be hers. If there is overlap in laying areas of different parasitic females, so that a female may not know if a parasitic egg she finds in a nest is her own, ejection of a parasitic egg would be risky. A statistical study such as ours could reveal avoidance of already parasitized host nests if that were occurring.

ACKNOWLEDGMENTS

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BIRD–WINDOW COLLISIONS

DANIEL KLEM, JR. ¹

Abstract.—Collisions of birds with windows were studied by reviewing the literature, collecting data from museums and individuals, monitoring man-made structures, and conducting field experiments. Approximately 25% (225/917) of the avian species in the United States and Canada have been documented striking windows. Sex, age, or residency status have little influence on vulnerability to collision. There is no season, time of day, and almost no weather condition during which birds elude the window hazard. Collisions occur at windows of various sizes, heights, and orientations in urban, suburban, and rural environments. Analyses of experimental results and observations under a multitude of conditions suggest that birds hit windows because they fail to recognize clear or reflective glass panes as barriers. Avian, man-made structural, or environmental features that increase the density of birds near windows can account for strike rates at specific locations. A combination of interacting factors must be considered to explain strike frequency at any particular impact site. Received 28 Oct. 1988, accepted 17 April 1989.

The earliest account of a bird hitting a window in North America is by Nuttall (1832:88). He described a Sharp-shinned Hawk (Accipiter striatus) which, in the pursuit of prey, flew through two panes of greenhouse glass only to be stopped by a third. Townsend (1931) described a series of five fatalities of the Yellow-billed Cuckoo (Coccyzus americanus). His paper was the first to suggest that avian vulnerability to windows may be more marked in some species than in others and that specific windows claim a succession of victims. He termed the victims “tragedies” and apparently regarded them as rare, self-destroying incompetents. Picture windows were relatively uncommon through the end of World War II, and there was little reason for concern about their threat to birds. In the postwar period, a building boom stimulated the rapid expansion of the sheet glass industry, and large glass windows were incorporated into the designs of new and remodeled structures. Today, it is not uncommon to find modern buildings that are entirely surfaced with glass.

I found 88 papers reporting bird-window collisions, primarily after the mid-1940s (Klem 1979). They document strikes in North America, South America, West Indies, Europe, and Africa, and, with few exceptions are cited in annotated bibliographies on man-caused mortality to birds (Weir 1976, Avery et al. 1980). However, most textbooks and encyclopedia treatments of ornithology present little, if any, description of the fatal hazards that windows pose to birds. The sheet glass industry and its

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commercial allies appear to be unaware of the problem. On the other hand, I found avian fatalities resulting from window strikes to be common knowledge among the general public.

Birds have been reported to strike two general types of windows as classified according to their visual effects on the human eye. These are transparent windows which appear invisible and reflective windows which mirror the facing outside habitat. Two general types of collisions have been described (Wallace and Mahan 1975:456) and both reveal the ability of glass to misinform and misguide at least some birds. One primarily involves birds such as Northern Cardinal (*Cardinalis cardinalis*) that commonly flutter against picture windows and harmlessly peck the glass during the spring and summer. These birds seldom, if ever, stun or injure themselves or shatter the glass and usually are males defending their territories against their reflected images. In the second type, birds fly into transparent or reflective windows as if unaware of their presence. These collisions often have fatal consequences, and are the subject of this paper.

In this paper my objectives are: (1) to propose an explanation for why birds collide with windows, (2) to describe and analyze species, environmental and man-made structural characteristics associated with bird–window collisions in the United States and Canada, and (3) to suggest how these select characteristics account for the differential frequency with which birds strike windows in various man-made structures.

**METHODS**

I collected data for this study from 1974 to 1986 from personal observations, records of cooperating individuals, and a series of field experiments. A form letter was sent to 466 curators of museums and 11 individuals in the United States and Canada. They were asked to identify birds salvaged as window-kills or noted as surviving window strikes in 1975 and 1976; a few respondents included additional data from 1963 to 1977. Of those surveyed, 208 responded: 125 listed species known or reported to have collided with windows and 13 estimated the number of collision casualties brought to them each year, although they did not indicate the species. I obtained data from: (1) salvaged window-kills that were placed in the Dept. of Zoology Bird Collection at Southern Illinois University at Carbondale (SIUC) between 1971 and 1974 (currently in the Dept. of Biology bird collection at Muhlenberg College, Allentown, Pennsylvania), (2) Jack and Muriel Hayward’s house in the Union Hill community located 5.7 km southwest of Carbondale, Jackson County, Illinois, and (3) several private homes and university and commercial buildings within a 52,300-ha area in and around Carbondale, Illinois. The Hayward house was the only building at which bird strikes were recorded systematically in southern Illinois. The home was checked by the occupants, often several times a day, from September 1974 through December 1976. The house stands on a slope and is surrounded by shrubs, mixed conifer and deciduous trees, fields and lawn. It has 52 windows ranging in size from 0.6 m wide by 0.9–2.2 m high with a total outer glass surface area of 114.3 m². Each window was individually numbered to accurately register the location of bird strikes. As with the Hayward home, detailed data were obtained from the residence of Polly Rothstein in southeastern New York, 1.6 km southeast of Purchase,
Westchester County. Except for short periods, a few hours to 1–2 days, she collected data from August 1975 through December 1976. The Rothstein house is located in a suburban setting on level ground and is surrounded by trees, shrubs, and lawn. Bird collisions were documented whenever a strike was heard or seen, or a specimen was found beneath a window. Although most reports lacked some information, the data recorded were species, temporal, and habitat variables. Specimens salvaged at the Rothstein house were given to the Bruce Museum, Greenwich, Connecticut.

Four field experiments were conducted to determine if birds can recognize transparent obstructions or reflections. All experiments were conducted on the farm of W. G. George in the Shawnee Hills, 1.7 km north of Cobden, Union County, Illinois. Typical of small farms in this area, the land has patches of woods and fields, a small apple orchard, a sizeable lawn around the farmhouse, a corn field, and two water impoundments. Two preliminary experiments, conducted over 8- and 13-day periods (8–15 November and 19 November–1 December 1976), were designed to determine if birds would strike clear and reflective glass not associated with man-made structures. A strike was registered when a specimen was found beneath a window or a feather, body smudge or blood smear was found on the glass. In the first experiment, six clear storm windows, 0.4 m wide by 1.2 m high, having a combined surface area of 2.9 m² were placed on the ground adjacent to one another (separated by 0–15.2 cm) and on the periphery of a woody thicket facing an old field habitat. When viewed from the field or the thicket, habitat was visible behind each pane. In the second experiment, a mirror, 0.6 m × 1.7 m high, simulated a reflective glass pane. It was placed in the same locality as the clear panes and appeared to reflect perfectly the field habitat and sky. During both experiments the glass was checked daily.

The third experiment, conducted over a 20-day period (19 March–7 April 1977), was designed to determine if birds would strike clear picture windows simulating those in new houses and erected in a habitat where no other man-made structure previously existed. Five identical wood-framed windows, 1.4 m × 1.2 m high, with their bases 1.2 m above ground, having a combined surface area of 8.5 m² were constructed on the edge of a wooded area and corn field (Fig. 1). Windows were placed along a tree line running east to west and facing north-south. Distance between windows from east to west (right to left in Fig. 1) were 12.9 m, 16.5 m, 15.7 m, and 23.8 m. Depending on the light conditions and angle of view, habitat was seen behind or reflected from the glass, or a combination of these effects was visible. Trays were placed under each window to catch collision casualties. Each window was checked daily.

The fourth experiment, conducted over a 1-year period (21 February 1977–21 February 1978), was designed to determine if birds would strike clear and reflective windows that were placed in an existing structure (a century-old barn) that previously had no windows. Two clear and two gray-tinted panes, 1.4 m wide by 1.2 m high, having a combined surface area of 6.8 m², were installed with their bases 3.8 m above the ground on the north and east sides of the barn. From outside, wooded habitat was visible on the other side of the barn when looking through both clear panes. When viewed from an angle that did not permit a view through both panes, the clear windows reflected the facing wooded habitat. The tinted panes were adjacent to the clear panes, and they appeared to reflect perfectly the facing wooded habitat. Trays were placed under each window to catch collision casualties. Each window was checked daily.

Data were compared and analyzed with binomial and Chi-square tests (Siegel 1956). In some analyses, the data were subdivided to determine if they showed chronological trends.

RESULTS

Species.—My survey revealed 225 species belonging to 42 families are known to have struck windows. This number represents 25% of the 917
species that occur in the two countries (A.O.U. 1983). Table 1 lists the 20 most frequently reported species in the survey. In general, the diversity of collision victims include species that occupy every major habitat type. Absent from the list are birds that rarely occur in habitats containing man-made structures. They include most waterbirds, soaring hawks, and terrestrial species occupying unpopulated or sparsely populated desert, grassland, and forest. Species accounting for most strikes at single residences were similar to those in the survey. Exceptions were relatively large numbers of Yellow-billed Cuckoo collisions at the Hayward house and Blue Jay (Cyanocitta cristata) and House Sparrow (Passer domesticus) strikes at the Rothstein house.

Age and sex.—Window casualties were analyzed for age and sex differences by comparing pooled species data for all of southern Illinois, at a single residence (Hayward house), and for select species with sample sizes of ten or more (Table 2). Passerine ratios of immature (hatching-year, HY) to adult (after-hatching-year, AHY) birds were expected to be 3:1 if the samples were representative of populations immediately after the breeding season (Lack 1954, Peterson 1963). Except for the Purple Finch (Carpodacus purpureus), there were no significant differences from the expected ratio (Binomial test, \( P > 0.05 \)). Counts for the Purple Finch differed significantly from the 3:1 ratio (Binomial test, \( P < 0.03 \)), but adults and immatures were killed with equal frequency; adults of this

Fig. 1. Field experiment study site in Cobden, Union County, Illinois.
Table 1
Species* Most Frequently Reported Striking Windows in United States and Canada

<table>
<thead>
<tr>
<th>Species</th>
<th>Geographic Region</th>
</tr>
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<tbody>
<tr>
<td>American Robin (Turdus migratorius)</td>
<td>White-throated Sparrow (Zonotrichia albicollis)</td>
</tr>
<tr>
<td>Dark-eyed Junco (Junco hyemalis)</td>
<td>Ruby-throated Hummingbird (Archilochus colubris)</td>
</tr>
<tr>
<td>Cedar Waxwing (Bombycilla cedrorum)</td>
<td>Tennessee Warbler (Vermivora peregrina)</td>
</tr>
<tr>
<td>Ovenbird (Seiurus aurocapillus)</td>
<td>Yellow-bellied Sapsucker (Sphyrapicus varius)</td>
</tr>
<tr>
<td>Swainson's Thrush (Catharus ustulatus)</td>
<td>Purple Finch (Carpocaptes purpureus)</td>
</tr>
<tr>
<td>Northern Flicker (Colaptes auratus)</td>
<td>Common Yellowthroat (Geothlypis trichas)</td>
</tr>
<tr>
<td>Hermit Thrush (Catharus guttatus)</td>
<td>Rose-breasted Grosbeak (Pheucticus ludovicianus)</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (Dendroica coronata)</td>
<td>Gray Catbird (Dumetella carolinensis)</td>
</tr>
<tr>
<td>Northern Cardinal (Cardinalis cardinalis)</td>
<td>Wood Thrush (Hylocichla mustalina)</td>
</tr>
<tr>
<td>Evening Grosbeak (Coccothraustes vespertinus)</td>
<td>Indigo Bunting (Passerina cyanea)</td>
</tr>
</tbody>
</table>

* Species reported most often in a survey of 125 museum curators and individuals; most frequent is listed first.

species may be more vulnerable than immatures or they may have occurred in proportionately greater numbers at this particular site. These data suggest that adults and immatures are at least equally vulnerable to windows. Male and female strike rates did not differ significantly from the expected 50:50 ratio for pooled or individual species data (Binomial test, \( P > 0.24 \)).

Seasons.—Strike data from several buildings in southern Illinois and

Table 2
Age* and Sex* of Window Casualties

<table>
<thead>
<tr>
<th>Pooled†/individual†</th>
<th>Age</th>
<th>Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>M</td>
</tr>
<tr>
<td>Southern Illinois</td>
<td>72</td>
<td>17</td>
</tr>
<tr>
<td>Hayward House</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>American Robin</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Northern Cardinal</td>
<td>18</td>
<td>7</td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>Purple Finch</td>
<td>18</td>
<td>9</td>
</tr>
</tbody>
</table>

* Age was determined by skull pneumatization and limited to AHY (after hatching year) and HY (hatching year) passerines killed in fall (September to December).

† M = male; F = female.

* Southern Illinois data obtained from casualties at several buildings around Carbondale, Jackson County; Hayward house data obtained from single residence.

† Species with sample sizes of 10 or more.
at single residences of the Hayward and Rothstein houses were analyzed by season (Fig. 2). The frequency of strikes per month were not uniformly distributed for southern Illinois in 1975 ($\chi^2 = 27.6$, $P < 0.01$) or 1976 ($\chi^2 = 50.0$, $P < 0.001$), for the Hayward house in 1975 ($\chi^2 = 35.5$, $P < 0.001$), or the Rothstein house in 1976 ($\chi^2 = 32.9$, $P < 0.001$). Seedeaters attracted to feeders near windows accounted for high numbers of strikes in winter (December–February). Migrants, especially nocturnal migrants, active around dwellings during the day, accounted for high strike rates in spring (March–May) and fall (September–November). Breeding birds, especially the Yellow-billed Cuckoo, accounted for summer (June–August) strikes. These data suggest that birds strike windows in every season of the year, that collision rates may vary greatly from month to month, and except for a reduction during summer breeding, no marked seasonal differences are evident.

**Times of day.**—To compare diurnal collision rates, a day was divided
into four 3-h time periods: early morning (first light–09:00), late morning (09:01–12:00), early afternoon (12:01–15:00), and late afternoon (15:01–last light). Early morning and late afternoon periods ranged from 2 to 5.5 h due to varying daylight periods throughout the year.

Times of impact were known for 45 (73.8%) of 61 strikes at the Hayward house in 1975; they were: 31 (50.8%) in early morning, 8 (13.1%) in late morning, 5 (8.2%) in early afternoon, and 1 (1.6%) in late afternoon. Times of impact were known for 41 (87.2%) of 47 strikes at the Rothstein house in 1976. They were: 10 (21.3%) in early morning, 19 (40.4%) in late morning, 8 (17.0%) in early afternoon, and 4 (8.5%) in late afternoon. Only two accounts of impacts at night were recorded. Both occurred at the Hayward house in 1976 and were by Black-throated Green (Dendroica virens) and Blackpoll warblers (D. striata). These data indicate that, at least for single homes, birds strike windows almost exclusively during daylight hours, and that collisions occur more often in the morning.

Weather.—Weather variables examined were: presence or absence of direct sunlight, presence or absence of precipitation, wind speed, wind direction, and ambient temperature. All weather variables were recorded for 36 (59.0%) strikes at the Hayward house. Of 47 strikes at the Rothstein house, 32 (68.1%) included lighting condition, 31 (66.0%) precipitation and wind speed, 2 (4.3%) wind direction, and 30 (63.8%) temperature. The percentages used in the weather analysis refer to these documented records.

Strike rates were substantial at both houses during both sunny and overcast conditions; under sunny conditions, 24 (66.7% and 75.0%) collisions were recorded at both the Hayward and Rothstein houses. All but one strike, during rain at the Rothstein home, occurred in the absence of precipitation. In southern Illinois, three additional strikes were documented in rain. During a severe snowstorm approximately 50 non-fatal bird strikes were recorded when a flock of Dark-eyed Juncos (Junco hyemalis) flew into a window of a rural home in Makanda, Illinois, in 1976. Birds struck windows under varying wind speeds, but collisions were recorded most often during calm conditions; 33 (91.7%) and 23 (74.2%) collisions occurred in winds of 0–11.3 kph (0–7 mph) at the Hayward and Rothstein houses, respectively. At the Hayward house five or more strikes occurred at windows facing all major compass directions. Similarly, for both houses, collisions occurred in temperatures ranging from −9.4–31.1°C (15.1–88.0°F). Comparison of the frequency of strikes in four equal categories of the temperature range for each house revealed that three (10.0%) or more occurred in each category. The overall weather data indicate that, with the exception of certain severe conditions affecting visibility, strike rates are higher during favorable weather.
Windows and man-made structures. — Bird strikes occurred at windows with clear transparent panes and at those with tinted reflective panes. When clear windows are installed one behind the other, such as in corridors, stairways, or rooms, they create an illusion of an unobstructed passageway (Fig. 3). Tinted windows create an illusion of unobstructed habitat which is mirrored on the glass surface. Clear panes mimic tinted mirror-like panes when little or no light is visible behind them (Fig. 4). Except for a seemingly related incident of frightened individuals hitting the side of a home, I found or collected no records of strikes at opaque, translucent, or stained glass windows which present other visual effects. At one site, over a 5-year period (1975–79), one account documented a strike at a reflective glass door but none at the adjacent stained glass windows of a church in Madison, Illinois (V. Lecko pers. comm.).

Strikes occurred at windows of various sizes, in structures of many different sizes and shapes ranging from those installed in stationary motor vehicle doors and telephone booths, to large plate glass walls around multistory buildings. Collisions were documented at windows of buildings located in urban, suburban, and rural environments. These data qualitatively indicate that collisions are likely at any outside clear or tinted window installed in any structure located in any type of habitat.

Quantitatively, 1975 data from the Hayward house were used to analyze strikes at windows of different sizes, heights from the ground, and orientation. Window size was known for 53 (86.9%) and window height for
49 (80.3%) strikes (Table 3). These data indicate that collisions occur at windows of different sizes and heights from the ground. Collisions may be more frequent at large windows (> 2 m² [21.6 ft²]) placed at ground level and above 3 m (10 ft). Window orientation was known for 49 (80.3%) strikes. Strikes per square meter of glass for each facing direction were: 0.5 northeast, 0.1 southeast, 0.9 south, 0.4 southeast, and 0.7 west and northwest. During fall and spring, windows that cut across and faced migratory flightpath directions, north and south respectively, were suspected of posing a greater hazard to migrants than windows facing east or west. To test this hypothesis, only migrants in southern Illinois were considered and consisted of 14 fall and three spring migrants at the Hayward house in 1975 and 1976. As might be expected for fall migrants, eight (57.1%) struck windows oriented northwest, but five (35.7%) hit southwest, and one (7.1%) struck a west facing window (Binomial test, \( P = 0.79 \)). Only one (33.3%) spring migrant hit a window oriented southwest while two (66.7%) others struck windows facing northwest. Comparison of strikes per square meter of glass showed no marked tendency for south or north bound migrants hitting north or south facing windows, respectively. These data indicate that windows facing general migratory directions of north and south are no more hazardous than windows oriented in other directions.
Table 3

<table>
<thead>
<tr>
<th>Height (m)</th>
<th>Small (&lt;1 m²)</th>
<th>Medium (1-2 m²)</th>
<th>Large (&gt;2 m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N  Area (m²)</td>
<td>N/ m²</td>
<td>N  Area (m²)</td>
</tr>
<tr>
<td>0.0-0.3</td>
<td>0  0.0</td>
<td>0.00</td>
<td>22 43.4</td>
</tr>
<tr>
<td>0.3-3.0</td>
<td>2  6.3</td>
<td>0.32</td>
<td>2  11.7</td>
</tr>
<tr>
<td>&gt;3.0</td>
<td>0  6.9</td>
<td>0.00</td>
<td>23 29.0</td>
</tr>
</tbody>
</table>

* Data from a single residence, the Hayward house, Carbondale, Jackson County, Illinois.

Experiments. — Two experiments tested the hazards of clear and reflective glass not associated with man-made structures. Over an 8-day period, four birds died after colliding with clear windows; they were: two Northern Cardinals, a Red-bellied Woodpecker (*Melanerpes carolinus*), and a White-throated Sparrow (*Zonotrichia albicollis*). Over a 13-day period, two birds died after hitting a mirror simulating a reflective pane, a White-throated Sparrow and a Dark-eyed Junco. Strikes at the mirror were probably minimal due to ice covering the surface during early morning hours throughout the experiment. These results indicate that windows need not be associated with man-made structures to kill birds.

The third experiment, monitoring five clear picture windows simulating those in new houses, resulted in 13 strikes over a 20-day period. Eight (65%) were fatal, the birds killed were: Northern Cardinals, two; Dark-eyed Juncos, four; Fox Sparrow (*Passerella iliaca*); and Swamp Sparrow (*Melospiza georgiana*). These data further suggest that birds may fail to detect transparent windows in man-made structures.

In the fourth experiment, seven strikes were recorded over a 1-year period at clear and reflective windows installed in a century-old barn. Bay-breasted Warbler (*Dendroica castanea*) and three unidentified birds hit clear windows; American Robin, Dark-eyed Junco and one unidentified bird hit reflective windows. These results further document that glass panes become hazardous for birds once installed in man-made structures, regardless of how long the structure may have been a part of the surrounding environment.

DISCUSSION

*Why birds strike windows.* — The literature contains several hypotheses attempting to explain how windows may be rendered functionally invisible to birds. If we exclude the harmless collisions resulting from territorial residents fighting their mirror images, all other hypotheses can be grouped
into two causal categories. One group consists of defective, impaired, or deceived hypotheses. Several authors have speculated that birds hit windows because of: (1) defective eyes (Willet 1945), (2) impaired vision due to smoke (Langridge 1960), blinding glare (Sinner unpubl. data), mist (Konig 1963), alcohol (Rogers 1978), or diverted attention (Dunbar 1949, Giller 1960, Bent 1968:231, Raible 1968, Valum 1968). None of these explanations are supported by my results. Field experiments revealed that birds collide with: (1) clear and reflective windows not installed in man-made structures, (2) clear windows installed in structures simulating those in new houses and placed in habitats where no other human dwellings previously existed, and (3) clear and reflective windows installed in an existing structure which had been a part of the habitat for more than a century. Individual accounts further document that birds strike windows of various sizes, heights from the ground, and orientation in man-made structures of various shapes and sizes that are set in urban, suburban, and rural environments. These data suggest that windows are not recognized as obstacles by birds, whether installed in man-made structures or placed in their accustomed haunts.

The second group of hypotheses emphasize perception. A number of authors have speculated that inexperienced birds strike windows (Bauer 1960, Giller 1960, Morzer-Bruijns and Stwerka 1961, Löhrl 1962, Raible 1968, Valum 1968, Schmitz 1969, Harpum 1983). There is no evidence indicating that physical deficiencies of the young or learning in adult or immature solely determines the ability of birds to detect glass barriers. Immatures and adults were found to be equally vulnerable, and the diversity of window-kills suggest no species is immune from the hazards of glass. Although indirect, available evidence supports the interpretation that the avian visual system is incapable of perceiving clear and reflective glass (Gibson and Walk 1960, Walk and Gibson 1961, Emlen 1963, Tallarico and Farrell 1964).

My observational data indicate that there is no exclusive avian vulnerability to windows based on age or sex, season, time of day, weather, window type or setting. Experiments further document that birds do not discriminate between unobstructed habitat and habitat seen behind clear glass or mirrored in reflective panes. Overall, these findings indicate that birds are likely to strike windows wherever they mutually occur. In general, glass is an invisible and potentially lethal hazard for all birds, but especially for those in flight. Other animals (insects, fish, mammals) are known to frequently strike stationary windows or other glass barriers, but the momentum at which they impact usually does not cause serious injury. In contrast, even the smallest flying bird can generate fatal momentum.

Factors influencing collision frequency. — Since glass is invisible to birds,
various bird, window, and environmental characteristics may explain the frequency with which certain species become casualties at particular localities. Strike rates at specific sites are unique and require attention to a combination of contributing factors. However, some factors can substantially influence the species and frequency of collisions. Considering the importance of single factors is a means of dealing with a complex problem, and knowing the importance of a factor can help assess and suggest measures to reduce or eliminate strikes at a particular site.

Bird-related factors include density and behavior. Although other factors were examined in their analysis, Graber and Graber (unpubl. data) found that the total number of birds in the area was correlated with the number of collisions at their rural Pope County home in southern Illinois ($r = 0.83$, $N = 10$, $P < 0.005$). Flight habits of birds accustomed to man-made structures may provide some protection by reducing the force with which the strike occurs. House Sparrow, European Starling (*Sturnus vulgaris*), and Rock Dove (*Columba livia*) seem to avoid windows by hovering in front of or slowly flying to nearby perches. However accustomed these species are to human dwellings, they are killed frequently at some sites. R. F. Johnston (pers. comm.) reports Rock Dove flying against small, cave-like windows at the Museum of Natural History, Univ. of Kansas. Hummingbirds learned to avoid the glass sides of cages (Bent 1940:386), and individuals accustomed to living near buildings may benefit from non-fatal collisions by learning to avoid the space that windows occupy. If this type of learning occurs in the wild, it may serve to protect at least some individuals, but it is likely to be of limited consequence for most species. Some birds are reported to be at high risk due to their habit of flying through restricted passageways in heavy cover (Ross 1946, Snyder 1946); they are killed while attempting to reach lighted areas behind or reflected in glass and often consist of *Accipiter* hawks, grouse, thrushes, and waxwings. Others habitually fly through open doors and windows, thus increasing their vulnerability (Löhr 1962). Many accounts document distracted individuals as frequent victims: individuals chasing one another (Dunbar 1949), individuals escaping danger (Valum 1968, Schmitz 1969), predators pursuing prey (Klem 1981), and individuals under the influence of alcohol (Rogers 1978), or spatially disoriented due to a combination of adverse weather and artificial lighting (Herbert 1970).

Window-related factors influencing strike rate include type, size, placement of glass, and the presence of bird attractants. I found birds more vulnerable to clear or reflective large ($>2 \text{ m}^2$) windows at ground level and at heights above 3 m. With respect to location, birds hit windows wherever they occur, but strike rates were highest in suburban and rural environments, which, in most cases, typically contain the largest densities.
Similarly, bird attractants were found to influence the frequency of strikes by increasing bird density near windows. Attractants are feeders, fruiting trees and shrubs, water supplies in the form of bird baths and impoundments, nesting or perching sites in vegetation, and areas that offer protection from adverse weather conditions. The frequency with which finches, blackbirds, chickadees, titmice, nuthatches, woodpeckers, and hummingbirds were reported as victims is probably best explained by their regular and abundant occurrence at feeders.

Environmental factors influencing strike rate include season, time of day, and weather. The frequency of strikes in different seasons is probably best explained by the seasonal abundance of birds in human-modified environments. I found seasonal strike rates to be highly variable in southern Illinois and New York. Higher winter collision rates at single houses in these regions, compared to those reported elsewhere, are probably best explained by local site differences, the major one being the presence of feeding stations which attract large numbers of winter residents. Seed eaters predominated as strike casualties during the winter in both regions and included: Dark-eyed Junco, White-crowned (Zonotrichia leucophrys), and White-throated sparrow, and Northern Cardinal. Strikes in fall and spring consisted mainly of migrant warblers, thrushes, waxwings, and finches. Few birds hit windows in summer, probably because their movements are largely restricted to breeding territories. Southern Illinois species killed in summer were Ruby-throated Hummingbird (Archilochus colubris), fledgling White-eyed Vireo (Vireo griseus), Nashville Warbler (Vermivora ruficapilla, an early migrant), and Yellow-billed Cuckoo. The cuckoos were known breeders, determined by eggs in the oviduct. Although few in number, summer window-kills may result in the added loss of dependent eggs and young. Those species which occur in the greatest numbers during any one season will most likely comprise the greater number of window casualties for a particular site.

In Indiana, strike rates during daylight hours of sunrise to 13:00 were reported to be four times greater than at any other time of the day (Witzler et al. unpubl. data). In this study, most strikes occurred in early and late morning. Graber and Graber (unpubl. data) reported collisions throughout the daylight hours (06:00–17:00) in southern Illinois, but more strikes occurred between 10:01–12:00 and 13:01–14:00 than at other times. At some localities strikes probably occur more often in early morning because birds are actively searching for food, and as most feeder watchers will testify, the largest concentration of birds at feeding stations usually occurs in early morning. Alternatively, during winter when large numbers of birds congregate at feeding stations, high strike rates can be expected throughout the day as local flocks periodically visit specific feeding stations.
Various weather conditions have been hypothesized to increase strikes by enhancing the deceptive effects of glass, hampering visibility, or accounting for the increased abundance of birds in the vicinity of man-made structures (Valum 1968, Konig 1963, Carpenter and Lovell 1963, Hall 1972). Most strikes occur under generally favorable weather, and probably are due to the clarity with which habitat is visible behind or reflected in glass. As my data further support, under conditions of poor visibility, during day or night, birds may experience spatial disorientation and become especially vulnerable if they descend to the vicinity of man-made structures and are attracted to lighted areas behind windows.

In summary, it is clear that: (1) birds fail to see windows as barriers and are vulnerable to them wherever they mutually occur, (2) any factor that increases the density of birds near windows will account for strike frequency, and (3) for any specific collision site, a combination of interacting factors must be considered to explain strike rates.

ACKNOWLEDGMENTS

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LITERATURE CITED


Breeding biology of Muscovy Ducks using nest boxes in Mexico.—The Muscovy Duck (Cairina moschata) is a cavity-nesting species widely distributed in the neotropics, ranging throughout much of Mexico and Central and South America (Johnsgard 1978). Despite its extensive range, however, the Muscovy Duck is among the least studied of all New World waterfowl. Most information is historical and sparse (Phillips 1922, Delacour 1959, Leopold 1959, Wetmore 1965), and even recent literature discusses the species only in general terms (Johnsgard 1978, Bolen 1983).

The Muscovy Duck has disappeared or declined throughout much of Mexico, presumably because of year-round hunting and extensive agricultural clearing of its riparian habitat (Leopold 1959, Saunders and Saunders 1981). This decline prompted Woodyard and Bolen (1984) to study selected aspects of Muscovy Duck ecology during 1980 and 1981. Their investigation was the first direct effort to examine nesting biology of the Muscovy Duck, and was the first time nest boxes designed specifically for the Muscovy Duck were erected in Mexico (1981). Only 18 boxes were erected, of which four were used by Muscovy Ducks; however, the study confirmed that nest boxes were a viable tool for managing populations of Muscovy Ducks.

Since 1981, over 4000 nest boxes have been placed in Mexico by Ducks Unlimited of Mexico, A.C. (DUMAC), but no systematic effort has been made to gather additional data on nest-box use or nesting biology of the Muscovy Duck. The objectives of this study were to document basic aspects of the nesting biology of Muscovy Ducks using the DUMAC boxes and to provide baseline information for future research and conservation efforts.

**Study area and methods.**—Initial box searches were conducted at nine sites in the state of Tamaulipas, Mexico, and involved checking >700 boxes. Subsequent box checks then were confined to three localities where Muscovy Duck nests were found. The northernmost location was at Laguna la Nacha, which is a 4000-ha freshwater lake 30 km east of San Fernando, Tamaulipas, and 110 km south of Brownsville, Texas (Fig. 1). The surrounding area has been described as mesquite scrub (Leopold 1950), where irrigated agriculture is the predominant land use pattern, and sorghum is the principal crop. Many temporary and permanent lagoons and other wetlands (the Tamaulipas Lagoons) are located nearby, and the Laguna Madre and Gulf of Mexico are 10 km to the east. A total of 168 nest boxes was available on three islands in Laguna la Nacha. These islands ranged in size from 4.3–15.8 ha and were located 450–750 m from shore. A total of 126 boxes were available during the 1985 and 1986 nesting seasons; 42 additional boxes were added prior to the 1987 season. All boxes were placed on metal or wood poles, but none was protected with predator guards. Woodyard and Bolen (1984) describe the basic design of the nest boxes used by Muscovy Ducks during this study.

The second study site was located about 120 km south of Laguna la Nacha on the Coltrisa and Palmas ranches, approximately 15 km southeast of Soto la Marina, Tamaulipas (Fig. 1). The general physiography and vegetation of this area were described by Ojeda and Medrano (1977). The primary land use on the ranches was cattle grazing and hay production. There were 135 boxes available on the Coltrisa Ranch, all in or near a 5–10 ha shallow (<3 m) lagoon. Boxes were located on flooded dead trees, living acacia (Acacia spp.) and mesquite (Prosopis spp.) trees and on wooden poles along the shore; boxes on wood poles were protected with predator guards. There were 69 boxes on the Palmas Ranch. Ten boxes were located in trees along the banks of a heavily wooded arroyo, and another 10 were placed on similar habitat along the Palmas River. Eleven boxes were located on wooden poles.
around a <1-ha farm pond, whereas the remaining 38 boxes were attached to dead trees around a 2-ha pond. Only those boxes on wooden poles were protected with predator guards. Boxes on both ranches were first available during the 1987 nesting season. The southernmost area was located 100 km south of the Coltrisa and Palmas ranches on the Santa Florinda ranch, about 15 km northeast of Manuel (Fig. 1). This region also was described by Ojeda and Medrano (1977); the primary land use was cattle ranching. A total of 35 boxes was located on metal or wooden poles in or around four 1–2-ha farm ponds. Again, only boxes on wooden poles were protected with predator guards. Twenty of the 35 boxes had been available during the 1985 and 1986 nesting seasons.

Nest boxes were checked at 1–2 week intervals from 1 April–8 August 1987, but road and weather conditions occasionally precluded box checks for up to four weeks. Data recorded at each nest were number of eggs, egg length and diameter (calipers, nearest 0.05

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**Fig. 1.** Location of Muscovy Duck nest-box study areas in Tamaulipas, Mexico.
mm), and weight (Homs spring scale, nearest 0.5 g). Date of nest initiation was calculated by backdating, assuming a laying rate of one egg/day (Sowls 1955). Dump nests (i.e., nests containing eggs from > 1 female) were identified as having a laying rate of > 1/day and/or an exceptional final clutch size (in one instance, 21 eggs). Incubation was assumed to begin on the day following clutch completion and hatching date was determined by actual observation of ducklings in the box. A nest was considered successful when ≥ 1 egg(s) hatched. Data recorded for each nest box were general habitat type, overhead canopy cover, box condition, box height, orientation of box entrance, and distance to water.

Two Muscovy Duck females initially were captured and banded at the nest box after two weeks of incubation as recommended by Grice and Rogers (1965) for Wood Ducks (Aix sponsa); however, banding was discontinued because both females deserted the nest. A third Muscovy Duck female was banded when captured on a nest with ducklings. Overall, 29 ducklings were web-tagged to provide birds of known age and origin for future studies.

Results and discussion.—Thirteen (3.2%) of 407 nest boxes checked at the three study areas were used by Muscovy Ducks. The highest box use occurred at Santa Florinda (9 of 35, 25.7%). Box use at other sites was <1% with only three of 204 and one of 168 boxes used at the Coltrisa/Palmas and Laguna la Nacha sites, respectively. However, box use by Muscovy Ducks at Laguna la Nacha had been 8.3 and 11.3% during the 1985 and 1986 nesting seasons, respectively, although all boxes were not checked in 1986 (DUMAC unpubl. data). Nest boxes appeared to be the only suitable nest sites in the area (i.e., few natural cavities were observed), thus the decline in nesting at Laguna la Nacha suggests that Muscovy Ducks are not as philopatric as are other cavity-nesting waterfowl (Bellrose 1980) or that illegal shooting had occurred in the area (Muscovy Ducks are protected in Mexico). Regardless, 1987 results from Santa Florinda and 1985–86 results at Laguna la Nacha demonstrate that nest boxes are acceptable to Muscovy Ducks.

We did not systematically assess the availability of natural cavities in the area of nest boxes, but large trees were sparse. Thus, the low incidence of box use suggests that populations of the Muscovy Ducks in this area of Mexico are low, and thus boxes are underutilized. Therefore, it may be more beneficial for management of Muscovy Ducks to place fewer boxes at more locations rather than concentrate large numbers of boxes on a given site. Additional boxes could then be added if the nesting population increases.

The first nest was initiated on or before 24 April 1987 and the last on 24 July 1987. The frequency of nest starts remained constant during this time and showed no discernable peak. For example, of the 12 nest initiations, one occurred/week (N = 7) from 3 May through 21 June, excepting two nests initiated during the week of 10 May. Only four nests were visited more than once during laying, but verified a laying rate of one egg/day as was assumed in calculating initiation dates. The first hatch occurred on 6 June and the last on 6 September. Woodyard and Bolen (1984) reported July and August hatching dates for two Muscovy Duck nests in Veracruz, Mexico.

Nesting phenology data were complete for 7 of 10 successful nests and indicated an average incubation period of 30 days (range = 30–31 days). This contradicts the generally accepted incubation period of 35 days as determined from captive or domestic birds (Delacour 1959, Bolen 1983).

Overall, the 1987 nesting season for the Muscovy Duck (first initiation to last hatch) in Tamaulipas lasted about 135 days (24 April–6 September). Leopold (1959) reported a few cases of nesting during June and July in Mexico and evidence of one female nesting in October, whereas Wetmore (1965) considered the nesting season in Panama to be June. In contrast, Phillips (1922) cites records of Muscovy Ducks nesting in South America during December, February, and May. Johnsgard (1978) has suggested a correlation between nesting and the rainy season. Long-term records on time of nesting are needed to determine if any
such relationship exists and to accurately establish the nesting season of the Muscovy Duck throughout its range.

Egg length and diameter were measured for 110 Muscovy Duck eggs from 10 nests. These measurements averaged 61.25 ± 0.17 [SE] × 44.55 ± 0.12 mm, which were smaller than the 67 × 44 mm average reported from Mexico by Leopold (1959). However, the range in egg measurements was 55.5–65.5 × 41.7–46.9 mm, which was similar to the 56.5–67.5 × 42.7–48.0 mm range found in Panama by Wetmore (1965).

Weight was measured for 31 eggs from four nests and averaged 66.4 g ± 0.71 SE (range 58.0–75.0 g). Comparable weights of wild Muscovy Duck eggs have not been reported. Eggs were glossy white in color, although some had a slight green or buff sheen.

Average clutch size of all nests was 13.6 ± 3.7 [SE] eggs/nest (N = 13) with a range of 9–21 eggs. Normal (i.e., not dump nests) Muscovy Duck nests had 9–15 eggs (x = 12.6 ± 1.9; N = 9). This is somewhat higher than the average 8–10 eggs/nest reported previously (Leopold 1959, Wetmore 1965); however, no sample size was presented by these authors. Woodyard and Bolen (1984) recorded nine eggs in the 2 normal nests of the Muscovy Ducks they observed in Mexico.

Four (31%) nests were classified as dump nests. Although dump nesting by Muscovy Ducks was presumed to occur (Phillips 1922, Wetmore 1965), it had not been documented. Average clutch size of dump nests was 17.7 ± 3.2 eggs/nest (N = 4) and ranged from 15–21 eggs. Two dump nests contained two Black-bellied Whistling Duck (Dendrocygna autumnalis) eggs each; a third nest with a normal clutch of Muscovy Duck eggs also contained two Black-bellied Whistling Duck eggs. Two of four Muscovy Duck nests observed by Woodyard and Bolen (1984) also contained mixed clutches, one of which was incubated successfully by a Muscovy Duck. In this study, all the mixed clutches were incubated by a Muscovy Duck female.

Ten of 13 (77%) Muscovy Duck nests were successful, which was similar to the 75% nest success observed by Woodyard and Bolen (1984) for four Muscovy Duck nests in boxes in Veracruz. McCamant and Bolen (1979) found that average nest success for Black-bellied Whistling Ducks nesting in boxes over a 12-year period also was 75%. Bellrose (1980) summarized the results of 22 Wood Duck nest box studies and found that nest success ranged from 32–95% but was typically between 65–75%.

Of the three (23%) Muscovy Duck nests that failed to hatch during this study, two were deserted during incubation, presumably because of observer disturbance; a third nest was deserted when the box was flooded. Three of four dump nests were successful; the one nest failure was caused by observer disturbance. Among mixed clutches, two of three nests incubated successfully by a Muscovy Duck female and one Black-bellied Whistling Duck egg was hatched within each clutch. In one case, the Black-bellied Whistling Duck egg hatched at least one day before the Muscovy Duck eggs, but all ducklings left the box. The incubation period of Black-bellied Whistling Duck eggs is 25–30 days (Bellrose 1980). Thus, regardless of which species incubates a mixed clutch there is potential for Muscovy Duck eggs not to come to full term or for Muscovy Duck ducklings to remain in the box.

During this study one of two marked females that deserted nests subsequently was observed to incubate successfully a second clutch. Renesting is common among many waterfowl species, and although presumed to occur among Muscovy Ducks, it had not been verified previously.

A total of 177 muscovy eggs were laid, of which 96 (54%) hatched. Of these, 142 eggs were laid in successfully incubated nests from which 97 (68%) hatched (Table 1). Hatchability of eggs from normal nests was greater than dump nests (73 vs 59%) because many eggs were added to dump nests after the onset of incubation, and thus did not come to full term before
other eggs hatched. Woodyard and Bolen (1984) observed three successful Muscovy Duck nests and found hatching success to be 88%. McCamant and Bolen (1979) found 63% hatching success among successful Black-bellied Whistling Duck nests and also concluded that dump nesting was responsible for reduced hatching success. Clawson et al. (1979) reported similar findings for Wood Ducks (77% for normal nests; 63% for dump nests).

There were 96 Muscovy Duck and three Black-bellied Whistling Duck ducklings produced from the 10 successful Muscovy Duck nests. Dump nests produced a slightly higher number of ducklings/nest (11.0, N = 3) than did normal nests (9.0, N = 7) (Table 1). However, the impact of dump nesting on productivity of cavity-nesting waterfowl is debatable (Clawson et al. 1979, Jones and Leopold 1967) and will require further study in the Muscovy Duck.

The small number of boxes used by Muscovy Duck females, their wide distribution, and the lack of variability among box and habitat characteristics at specific study areas did not allow for meaningful tests of nest-site preference. However, some general observations of nest-box selection were made.

Muscovy Duck females used boxes in a variety of habitat types. There were nine nests in small farm ponds (<2 ha), two in flooded dead timber, one along a heavily wooded creek, and one on a flooded island in Laguna la Nacha. Canopy cover at used boxes varied from 0–75%, but 10 of 13 (87%) had no overhead cover. However, 9 of these nests were at Santa Florinda where all 35 boxes were located in open habitat. Wooded streams traditionally have been regarded as Muscovy Duck habitat, but it appears that they will use many habitat types provided a suitable cavity is present. The same flexibility in nest-box selection has been demonstrated for the Wood Duck (Grice and Rogers 1965).

Box condition was classified subjectively as good (little evidence of deterioration), fair, and poor (showing major cracks and holes), but condition did not appear to influence box use. Height of used boxes varied from 0.8–3.5 m, which covered the range of available box heights. Nine nests were found in boxes facing southeast (85–175°) and three in boxes facing southwest (220–230°); only one used box faced north. Distance to water also may have influenced nest box use as 11 (85%) nests were found in boxes directly over water. The remaining nests were in boxes within 3 m of water, however, most available boxes were within 5 m of water.

Overall, this study demonstrates that nest boxes can be an effective tool for the conservation of the Muscovy Duck and also can provide a practical research tool allowing for study of this secretive species. More research is needed to increase the sample size of Muscovy Duck nests, particularly to examine the role of dump nesting and mixed-species clutches on Muscovy Duck productivity. Effectiveness of the nest box program and status of Muscovy Duck populations also is in need of continued monitoring.

Table 1

<table>
<thead>
<tr>
<th>Nest type</th>
<th>No. nests</th>
<th>No. eggs</th>
<th>% hatch</th>
<th>Average no. ducklings/nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>7</td>
<td>86</td>
<td>73</td>
<td>9.0</td>
</tr>
<tr>
<td>Dump</td>
<td>3</td>
<td>56</td>
<td>59</td>
<td>11.0</td>
</tr>
<tr>
<td>Combined</td>
<td>10</td>
<td>142</td>
<td>68</td>
<td>9.6</td>
</tr>
</tbody>
</table>
Acknowledgments.—This project was supported by DUMAC and Auburn University. We thank E. Rangel-Woodyard for providing logistical support while in Mexico. This is publication number 15-881893P of the Alabama Agricultural Experiment Station.

LITERATURE CITED


BOLEN, E. G. 1983. 


Bald Eagle use of a communal roost.—In many areas where Bald Eagles (Haliaeetus leucocephalus) concentrate at seasonal food sources, they forage and roost at separate sites (Isaacs and Anthony 1987, Keister et al. 1987). Migrating Bald Eagles have congregated in Glacier National Park, Montana, each autumn since 1939 to feed on non-native kokanee salmon (Oncorhynchus nerka) spawning in the 4-km stretch of lower McDonald Creek. Peak censuses of Bald Eagles have ranged as high as 639 in 1981 (McClelland et al. 1982). Eagles
at the concentration come from summering areas in the Northwest Territories, Alberta, and Saskatchewan, Canada, and winter in areas as distant as southern Utah and northern California (Young 1983). Most eagles at Glacier National Park roost nocturnally 3 to 7 km from the lower McDonald Creek foraging area (Shea 1973, McClelland 1973, Young 1983). During the autumns of 1980–85, we documented total numbers and arrival and departure times of Bald Eagles at the Fish Creek communal roost (FCR). On some nights, FCR was used by more than 400 Bald Eagles, the highest number recorded in any roost in the contiguous United States. This is the first detailed report of eagle use at a major roost composed primarily of western larch (Larix occidentalis). This paper reports correlations between patterns of roost use and total area census, eagle age class, time of sunrise and sunset, and cloud cover.

Methods.—Glacier National Park, in northwestern Montana, is bordered on the north by Canada. The primary study area encompassed lower McDonald Creek (the primary eagle foraging area), the southern end of Lake McDonald, and adjacent forest stands. Four roosts are composed of old-growth western larch, Douglas fir (Pseudotsuga menziesii), ponderosa pine (Pinus ponderosa), and black cottonwood (Populus trichocarpa). Locations of roosts were verified by examining records of previous research (particularly Shea 1973), by tracking transmitter-equipped eagles to roost sites, and by observing flight paths to roosts (Crenshaw 1985). FCR is the largest roost, encompassing 42 ha. The adjacent Lakeshore Roost covers 25 ha. Both lie near the northwest shore of Lake McDonald. Two much smaller roosts located 1.3 km and 1.6 km from lower McDonald Creek were used by fewer eagles.

Eagles were counted from a location 200 m north of the creek as they flew to roost in the evenings (PM counts) and as they returned to the creek in the mornings (AM counts). Eagles flying to the Lakeshore Roost were incorporated in FCR counts because the Lakeshore Roost often is used as a staging site for eagles flying to FCR, and flight paths to both sites are similar. PM counts (1980–84) were made from 60 min before to 40 min after sunset. AM flights occurred over a shorter period and counts (1980–81, 1983–85) covered from 40 min before to 50 min after sunrise. All counts were divided into 10-min intervals in relation to sunrise and sunset times for Kalispell, Montana, 60 km to the southwest (U.S. Naval Observatory 1946). Percent cloud cover was estimated visually at the beginning of each count. Clear was considered <25% and cloudy >75% cloud cover. Eagles were classified as either adults (head and tail appeared fully white) or subadults (all other plumages).

Weekly systematic censuses of the Lake McDonald shoreline were conducted by foot and vehicle; lower McDonald Creek was censused by canoe (McClelland et al. 1982). Censuses represented an index of the number of eagles at the foraging areas and were compared with FCR counts from the prior morning or evening to calculate the percentage of eagles using FCR. On days when both AM and PM counts were conducted, the higher was used in comparing nightly fluctuations in roost use. Counts of <10 at the beginning or end of each autumn concentration were eliminated from the analyses to standardize annual cut-off dates.

Non-parametric tests were used in cases where we did not want to assume any underlying data distribution. Counts were standardized on the peak recorded for the year, paired with another year based on this peak, and tested for significant differences ($\alpha = 0.05$) in the location, dispersion, and skewness of the cumulative frequency distributions between years with a Kolmogorov-Smirnov test (SYSTAT, Inc. 1984). Pearson product-moment correlations (SYSTAT, Inc. 1984) were computed for corresponding pairs of census and roost-flight count totals to test the degree of linear association; $t$-tests were used to test the validity of the null hypothesis, i.e., the population correlation $= 0$ (Sokal and Rohlf 1981). For each 10-min interval of roost arrival and departure times, mean percentages and their variances were computed; significant differences ($\alpha = 0.05$) between eagle flight times, and age class and percent cloud cover were determined for proportions greater than 5% (proportions less
than 5% were considered too small for valid comparison) (Snedecor and Cochran 1980). Data from 1980 were omitted from these tests due to the small number of AM and PM counts.

Roost-flight counts. — During the six autumns, counts of ≥10 eagles were recorded on an average of 54 days. In 1983 the earliest count (7 October) and the lowest number of days between first and last counts (44 days) were recorded. The latest count occurred in 1985 (18 December), the same year in which the highest number of days (67) was recorded (Fig. 1).

Peak roost-flight counts ranged from 154 (1983) to 414 (1981); all occurred in early to mid-November (Table 1). The distributions of daily counts were significantly different between all years except 1981/1984 (P = 0.100), 1981/1985 (P = 0.226), and 1982/1983 (P = 0.167). Mean combined counts including highest AM or PM counts for all years averaged 112 eagles. Mean AM counts (x = 123.3) averaged 14% higher than mean PM counts (x = 103.0); however, there were some days on which PM counts were much higher than AM counts. Differences between PM and following AM counts probably resulted from: (1) atypical roost-flight paths due to high winds, (2) migrating eagles' first arrival into the roost during the day or by routes which bypassed the PM count location, (3) eagles' arrival at the roost prior to the beginning of the PM count because of human disturbance in the feeding area or an early end to a successful day of hunting, (4) migration departure after the AM count, or (5) limited observer visibility resulting from precipitation or fog.

Peak FCR counts averaged 63% of the peak censuses of the foraging area (Table 1, Fig. 2). Annual variations in peak censuses were positively correlated (r = 0.973, P ≤ 0.05, Pearson correlation) with peak kokanee salmon numbers (McClelland and McClelland 1986).
Table 1
Roost-Flight Counts (≥10 Bald Eagles) for FCR and Peak Censuses, 1980–85

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Roost-flight counts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date of peak count</td>
<td>9 Nov.</td>
<td>14 Nov.</td>
<td>2 Nov.</td>
<td>1 Nov.</td>
<td>23 Nov.</td>
<td>15 Nov.</td>
</tr>
<tr>
<td>AM mean</td>
<td>b (18)</td>
<td>143 (47)</td>
<td>c</td>
<td>67 (39)</td>
<td>160 (57)</td>
<td>124 (53)</td>
</tr>
<tr>
<td>PM mean</td>
<td>b (29)</td>
<td>118 (52)</td>
<td>75 (44)</td>
<td>65 (41)</td>
<td>126 (60)</td>
<td>c</td>
</tr>
<tr>
<td>Combined mean (highest AM or PM)</td>
<td>113 (37)</td>
<td>142 (56)</td>
<td>75 (44)</td>
<td>72 (43)</td>
<td>151 (64)</td>
<td>124 (53)</td>
</tr>
<tr>
<td>Number of days &gt;100</td>
<td>22</td>
<td>32</td>
<td>13</td>
<td>8</td>
<td>35</td>
<td>22</td>
</tr>
<tr>
<td>Area censuses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peak census</td>
<td>377</td>
<td>639</td>
<td>306</td>
<td>251</td>
<td>571</td>
<td>520</td>
</tr>
<tr>
<td>Date of peak</td>
<td>5 Nov.</td>
<td>11 Nov.</td>
<td>3 Nov.</td>
<td>26 Oct.</td>
<td>28 Nov.</td>
<td>5 Nov.</td>
</tr>
<tr>
<td>Peak count as % of peak census</td>
<td>56</td>
<td>65</td>
<td>62</td>
<td>61</td>
<td>68</td>
<td>63</td>
</tr>
</tbody>
</table>

*Values in parentheses refer to the number of counts conducted.
*Insufficient number of counts for representative mean.
*Counts not conducted.
The percentage of the weekly census represented by the FCR count averaged 48% for the six years (range: 42–55%); corresponding counts and censuses were highly correlated ($r = 0.911$, $P < 0.01$, range: 0.824–0.977). Count totals were lower than census totals primarily because eagles used the other two roosts and scattered locations along lower McDonald Creek and adjacent areas. The mean peak count of subadults at FCR was 51% of the mean peak census of subadults. The corresponding mean for adults was 63%. This suggests that a higher percentage of subadults than adults roosted along the creek close to the food source. This is similar to the pattern described for the Klamath Basin, Oregon, where the proximity of food to roosts influenced use by subadults (Keister et al. 1987).

Peak numbers of subadults in FCR counts occurred earlier than adult peaks in all years except 1984 ($t = 3.5$ days, range: 0–7 days). In censuses, subadult numbers peaked earlier in 1980 (8 days) and 1985 (7 days), but on the same date as adults from 1981–84 (overall range: 26 October–28 November). The highest percentage of subadults in FCR counts (range: 38–87%) occurred early in the autumn in all years (range: 10–26 October) and then declined. Peak censuses of subadults from 1965–80 occurred earlier than for adults in 10 of 16 years and peaked on the same date in the other 6 years (McClelland et al. 1982).

**Roost arrival and departure times.**—The timing of roost flights appeared to be influenced by cloud cover. From 1981–84, PM counts on clear evenings peaked 10 min later and were higher (20%) than on cloudy evenings (16%) (Fig. 3). Flights before sunset on clear and cloudy evenings were 53% and 71%, respectively. Within each time interval, clear and cloudy PM counts were significantly different ($P \leq 0.05$).

More eagles departed FCR before sunrise on clear (84%) than on cloudy mornings (77%). On clear mornings peak counts (28% of total) occurred 30–40 min before sunrise, 10 min earlier than peaks on cloudy mornings (26% of total). Clear and cloudy AM counts were significantly different ($P \leq 0.05$) within all time intervals except 10–20 min before sunrise.

Lish (1973) found that Bald Eagles in Oklahoma generally arrived at roosts earlier on clear days than on overcast days. Roost-flight counts of Bald Eagles along the Nooksack River, Washington, also were influenced by the presence of cloud cover (Knight 1981). However, on average, counts in Glacier National Park peaked 30 min later on clear evenings.
Fig. 3. Mean arrival times (above) and departure times (below) of Bald Eagles on clear and cloudy days.

and 40 min earlier on cloudy mornings than at the Nooksack. These variations may have resulted from differences in study area terrain or from contrasts in the areas’ relationships to standard sunrise and sunset times.

Subadults tended to fly to FCR earlier than did adults. The peak (mean percentage per 10-min interval) of subadults (17%) enroute to FCR during PM counts occurred just before sunset; the adult peak (17%) occurred 10 min later (Fig. 4). Most subadults (72%) and adults (62%) arrived in the roost before sunset. Percent subadult arrivals were significantly different ($P < 0.05$) from adult percentages within all time intervals except 50–60 min before sunset.

During AM counts, subadults peaked at 27% during the time interval 20–30 min before sunrise, 10 min earlier than for adults (27%). More subadults (82%) than adults (76%) departed the roost before sunrise. Percent departures within all but the interval 10–20 min before sunrise differed significantly ($P < 0.05$) between adults and subadults. Differences in roost arrival and departure times between adults and subadults may be related to subadults’
poorer hunting skills and to food availability. Spawned-out salmon wash onto the gravel bars along lower McDonald Creek at night and are readily available to eagles arriving first in the morning. Adults obtain prey by stooping on fish in water more often than do subadults (Bennetts 1986) and may not need to compete for the more accessible fish. Stalmaster and Gessaman (1984) and Knight (1981) recorded subadult Bald Eagles arriving at food sources earlier than adults, possibly due to subadults' greater food stress and motivation to feed. The lack of fish carcasses late in the afternoon at lower McDonald Creek and increased competition with adults may explain subadults' earlier flight to FCR.

Acknowledgments.—Funding for this study was provided by the National Park Service (Glacier National Park), the University of Montana Cooperative Wildlife Research Unit, the Montana Forest and Conservation Experiment Station, and the Glacier Natural History Association. This study would not have been possible without the excellent field assistance of H. Allen, R. Bennetts, P. McClelland, B. Williams, R. Yates, L. Young, and Glacier National Park naturalists. R. Anthony and H. Zuuring provided constructive comments on a previous draft.


The original description and author of the genus Dumetella (Mimidae).—The “Cat Bird” of Mark Catesby (1731–1743), now known as the “Gray Catbird,” served as the type of the Muscicapa carolinensis of Linnaeus (1766). When the species was first segregated in its own monotypic genus (as opposed to Mimus), it received the name Galeoscoptes Cabanis (1850), under which it was widely known until 1907 as Galeoscoptes carolinensis (see Ridgway
At that time, C. W. Richmond advised Witmer Stone that the name *Dumetella* had been applied to this species in 1837 by one “S.D.W.” in a journal called *The Analyst*, and accordingly Stone (1907:193) proposed that *Dumetella* be substituted for *Galeoscoptes*. This change was adopted in the 3rd edition of the A.O.U. Check-list of North American Birds (A.O.U. 1910), and the North American catbird has been *Dumetella carolinensis* ever since. It is not certain, however, that even Stone saw the original reference, which may not have been consulted by any ornithologist since Richmond. Furthermore, *Dumetella* has always been attributed only to “S.D.W.,” apparently with no successful attempt having been made to determine the author’s identity. This struck me as such a curious and unacceptable lacuna in ornithological knowledge, especially regarding such a familiar bird, that I undertook to solve the mystery if possible.

*The Analyst* was a short-lived “journal of science, literature, natural history, and the fine arts” published in London from 1834 to 1840, at first monthly and then quarterly after July 1835 (Bolton 1897:33). As was the custom of the times, many of its contributors signed only their initials, pseudonyms, or pseudonymous initials. The original “description” of the genus *Dumetella* actually appears in the preamble to a paper entitled “The Fishes (Pisces) of Britain, Systematically Arranged” (S.D.W. 1837). In previous issues of *The Analyst* are several discourses on ornithological nomenclature and similar lists of British birds and mammals by the same author (S.D.W. 1835a, b, 1836a, b, c), in which S.D.W. is seen as a vigorous proponent of a system of nomenclature and orthography that even in his own time must have seemed highly idiosyncratic. Among S.D.W.’s basic tenets was that the genus be reflected in the English as well as the scientific name of an organism, a proposal that had already been advanced in *The Analyst* by one Neville Wood (N. Wood 1835a). As a result of his beliefs, S.D.W. made massive arbitrary changes not only in English names but in scientific names as well. Richmond (1908) listed all the new generic names of birds proposed in *The Analyst*, attributing them only to “S.D.W.” (virtually all of these are junior synonyms). Previous to Richmond, at least one of S.D.W.’s generic names, *Densirostra*, was listed by Waterhouse (1889:64), who gives the author as “Wood,” which provides us with our first clue.

Neville Wood (fl. 1835–1839) was the fourth son of Charles Thorold Wood (1777–1852), both of whom published books on ornithology in the period 1835–1836 (Mullens and Swann 1917:661–664). In the “Ornithological Guide,” C. T. Wood (1836a) extracts practically the whole of one of S.D.W.’s treatises in *The Analyst* as answering to his own views of nomenclature. In “The Ornithologist’s Text Book,” Neville Wood (1836b:94) reviews some of the contributions of S.D.W. with the greatest approbation, and both authors are high in their praise of *The Analyst* as a journal. From the character and tone of their writing and the inference from Waterhouse, it is quite clear that S.D.W. is either Wood père or Wood fils.

Circumstantial evidence immediately favors the former, as Neville Wood signed his own name to contributions in *The Analyst* and refers to material by S.D.W. as though written by other than himself (e.g., N. Wood 1835b, 1836b). Furthermore, at one point C. T. Wood states that “I have altered the name of the hedge coahood . . . (See *The Analyst*, Nos. xi. and xiii.),” where the articles in question are signed “S.D.W.” (C. T. Wood 1836b:143). That S.D.W. is a pseudonym of Charles Thorold Wood is repeatedly corroborated in Neville Wood’s *British Song Birds* (N. Wood 1836c). Here we find the names of several birds attributed directly to C. T. Wood, and in each case the reference cited is either “Analyst 13” or “Analyst 14,” in which issues the names in question appeared only in the lists of British birds signed by S.D.W. The S.D.W. names attributed to C. T. Wood in N. Wood (1836c) are: Garden Thrush (*Turdus hortensis*), Sibilous Brakehopper (*Locustella sibilatrix*), Garden Tit (*Parus hortensis*), Alpine Annet (*Curruca collaris*), Pied Wagtail (*Motacilla sibilatrix*), and Pine Thickbill (*Densirostra enucleator*).
From this evidence, the identity of S.D.W. is certainly established, so that any further citation of the author of *Dumetella* should read: "S.D.W." = C. T. Wood.

What of the actual "description" of the genus *Dumetella*? Because the work has probably never been seen by systematists, I shall here quote a substantial portion of the paragraph in which the name *Dumetella* first appears, from which the reader may appreciate the eccentric flavor of the work and sense the spirit in which the name was advanced. Recall that all this appeared in a treatise on British fishes. "I have several corrections myself to make, as *Surnia for Nictea* [Wood consistently substituted 'i' for 'y' in scientific names], and *Aluco for Surnia* (see errata, vol. iv., page 350); *glandarius* for the Bee-eater was, of course, an oversight. Locustell is better than Brakehopper, which will do for *Dumetella felivox,—*the Cat Thrush of Latham. The best British name for the *Silvia* is Willet, an unexceptionable appellation. The Garden Willet (*Silvia melodia*, Blyth) is a familiar example. Siskin is preferable to Goldwing (see vol. iii., page 32). Mr. Blyth has proposed Alp for Coalhood (*Pirula*). Poppin is the name of a genus in the Parrot family; so that the *Cristoptilus* may be called by the common name Yaffel." (S.D.W. 1837:206).

At this point, the combination *Dumetella felivox* is not really identifiable, as no author is given for the specific name *felivox*, which for all one knows from the original reference could have been S.D.W.'s invention as well as *Dumetella*. Thus the genus may be identified only with "the Cat Thrush of Latham." But, as noted by both Stone (1907) and Richmond (1908), there is no "Cat Thrush" in Latham (1783), who calls the bird "Cat Flycatcher." There is no doubt as to the species that S.D.W. had in mind, as Stevens (1817:272) in his continuation of George Shaw's General Zoology, a work doubtless well known to Wood, refers to the North American catbird as the "Cat Thrush" and applies the name *Turdus felivox* Vieillot, 1807, to it. But the identity of S.D.W.'s *Dumetella* can actually be determined only by inferences from sources other than in the original reference to the genus. Although a case might be made that *Dumetella* is technically based on a non-existent type species and therefore was not validly proposed, it is not at all clear which, if any, of the rules of nomenclature could be invoked, so there is no compelling reason for pursuing such action.

Oberholser (1974), followed by Phillips (1986) and Steadman (1988), revived the generic name *Lucar* (Bartram 1791) to replace *Dumetella* on grounds of priority. Although Bartram was not a binominal author, his classification was binary, so his generic names would seemingly have as much validity as those of Brisson (1760), whose genera are in wide use today in ornithology. Nevertheless, all of the editions of Bartram's *Travels* have been suppressed for nomenclatural purposes by the International Commission on Zoological Nomenclature (Melville and Smith 1987). Thus if one accepts those powers of the ICZN, the name *Lucar* would not be available as an earlier replacement for *Dumetella*.

Acknowledgments.—I thank Leslie Overstreet and other staff of the Smithsonian Institution Libraries for assistance in tracking down some very obscure references. For reading and commenting on the manuscript I am grateful to R. C. Banks, M. Ralph Browning, K. C. Parkes, and D. W. Steadman.

LITERATURE CITED


"S.D.W." [=C. T. Wood]. 1835a. Remarks on vernacular and scientific ornithological nomenclature. Analyst 2(11):305–307. [This contribution is signed “N.F.” which was later explained as a printer’s error (S.D.W. 1835b:34). In the copy examined (Library of Congress) someone has pencilled “Charles” before the “N.F.,” possibly for Charles T. Wood.]


Body size of Northern Goshawks on coastal islands of British Columbia.—The Northern Goshawk (Accipiter gentilis) is broadly distributed across the boreal parts of North America and Eurasia. Small-bodied insular populations recognized as subspecies occur in Sardinia-Corsica and Japan (Brown and Amadon 1968). Goshawks probably occur on most of the larger coastal islands of British Columbia where the species is apparently resident (Taverner 1940, Beebe 1974). There are specimen records from Vancouver, Graham, Denman, Mayne, Sydney, and Pender islands.

In his description of these insular populations as the subspecies A. g. laingi, Taverner (1940) made no reference to body size. Beebe (1974, 1976) characterized the populations of Vancouver Island (and the Olympic Peninsula of Washington) as an undescribed subspecies with a mass fully one-third smaller than the mainland form. For a male weighing 500 g (Beebe 1976), this represents a linear (cube root) reduction of 12.5%. He described goshawks inhabiting the Queen Charlotte Islands as similar in size to continental birds. There are few published data on A. g. laingi body size (Palmer 1988) and that available (e.g., Brown and Amadon 1968:454) is inadequate to evaluate these conclusions.

In this note I compare the body size of A. g. laingi populations with those of mainland British Columbia. For this study I utilized measurements of 180 specimens (132 males and 48 females) housed in collections at the Burke Museum, University of Washington (BMUW), University of Puget Sound (UPS), Royal British Columbia Museum (RBCM), Cowan Vertebrate Museum, University of British Columbia (CVM), Royal Ontario Museum (ROM), Museum of Natural Sciences, Ottawa (MNS), and Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Wing length was measured as the convex distance (arc) from the right wrist to the tip of the longest primary. Culmen length (chord) was measured as the distance from the cere to the tip of the bill. I made >85% of the measurements used in this analysis; the remainder were provided by Ross James (ROM) and Michel Gosselin (MNS).

Specimens were sexed based on tag information and body size. When the tag information was lacking or in conflict with that provided by measurement, the sex as determined by measurement was accepted as correct. Age groups were identified as hatching year (HY), second year (SY), or after second year (ASY) based on plumage characteristics. I excluded HY birds collected before September 1 because of the greater potential of misidentifying their sex based on body size. Two birds in typical SY plumage collected in July demonstrated unusually short wing lengths: RBCM 2644 (labelled female) WL = 325 mm and MVZ 42044 (labelled male) WL = 290 mm. These values are shorter than HY birds in this sample, suggesting that growth of replacement primaries was incomplete. Because of this variability and the small number of SY birds available, that age class was excluded from the analysis.

There was no significant difference in wing length between populations of Vancouver Island and the Queen Charlotte Islands (Kruskal-Wallace ANOVA test, Table 1). However,
wing length and culmen length were significantly different between insular and mainland populations in four of eight comparisons (Table 1), confirming that coastal island goshawks are 2–3% smaller than mainland birds. Because wing length values represent curvature (arc) distance, it is inappropriate to compare them with wing chord measurements (e.g., Henny et al. 1985). One may question whether the sample of mainland birds is representative of a resident population, given the periodic invasion of goshawks in the Lake States (Mueller et al. 1977). There is, however, no clear pattern of goshawk migration west of the continental divide (Beebe 1974), suggesting that the sample of mainland birds is probably representative of the breeding population there.

Dimorphism indices (ASY male wing length as a proportion of ASY female wing length) are 0.91 and 0.9 for insular and mainland populations, respectively. These values are similar to those of other North American populations (e.g., Great Lakes: 0.91, calculated from Storer 1966).

Acknowledgments.—I thank R. W. Campbell (RBCM), G. Alcorn (UPS), C. Wood (UWBM), R. Cannings (CVM), R. James (ROM), M. Gosselin (MNS), and B. Stein (MVZ), who provided access to, or measurements of, specimens in their care. R. Storer, D. Amadon, and two anonymous reviewers made several suggestions which considerably improved the manuscript.
Close nesting of a Black Vulture and a Turkey Vulture.—Close nesting by Black Vultures (*Coragyps atratus*) was reported by Hoxie (cf. Bendire 1892) who observed "perhaps a dozen or twenty pairs nesting on a 1.5 acre island near Beaufort, South Carolina." Baynard (1909, 1913) commented on large numbers of nesting Black Vultures in Florida swamps but did not indicate exact numbers or proximity of nests. However, Turcotte (1933) found two Black Vulture nests within 100 m of each other in Mississippi. Whereas Black Vultures have been noted to nest in close proximity (Bendire 1892, Turcotte 1933), Davis (1979) and Jackson (1983) reviewed the literature and found no evidence that Turkey Vultures (*Cathartes aura*) nest in close proximity. Jackson (1983) suggested that this may be a result of the more solitary and perhaps territorial nature of Turkey Vultures. Here I report the close nesting proximity between a Black Vulture and a Turkey Vulture.

On 5 March 1988, a Black Vulture nest was discovered in an abandoned one-story house in a mixed-deciduous forest about 6 km northeast of Pheba, Clay Co., Mississippi. The nest contained two eggs, and was located in a room (1.5 m × 3.5 m) with a window through which a Black Vulture exited upon being disturbed. On 8 May 1988, I observed two downy, buff-colored Black Vulture chicks in an adjacent room. A Turkey Vulture was also observed on this date peering through an opening (about 1.5 m²) in the ceiling and roof. On 21 May 1988, I observed an adult Black Vulture with two chicks in the house. The chicks were still downy, but some black feathers were emerging from the remiges and rectrices. A Turkey Vulture was flushed from the attic and exited through the roof opening. I inspected briefly the attic but did not locate eggs or chicks. On 11 June 1988, the two Black Vulture chicks were fully feathered but not fledged. I inspected the attic again and found two downy white Turkey Vultures (2–4 weeks old) in a corner of the attic. On 9 July 1988, the Black Vulture chicks were gone and presumed fledged. On this day, I observed the Turkey Vulture chicks on the main floor of the house. The rectrices and remiges were well developed, but the body
and head still were downy. I did not revisit the house to determine whether the Turkey Vulture chicks successfully fledged.

This observation may represent the first report of Black and Turkey vultures nesting in close proximity. Jackson (1983) suggested that suitable nest sites in tree cavities are becoming less available because of forestry management practices and fire control. I suggest that although Turkey Vultures are normally solitary nesters, these two species apparently tolerate each other during breeding. Perhaps limited nest sites and/or other factors influenced the close nesting proximity.

Acknowledgments. — J. Duncan discovered and reported the Black Vulture nest. Comments by J. A. Jackson, R. M. Kaminski, B. D. Leopold, and two anonymous reviewers helped improve the manuscript (Miss. Agric. For. Exp. Stn. Publ. J-7039).

LITERATURE CITED


An unsuccessful clutch of Northern Bobwhites with hatched pheasant eggs. — Ring-necked Pheasants (Phasianus colchicus) are known to lay eggs in nests of other birds (Bennett 1936). Laying by pheasants in nests of Northern Bobwhites (Colinus virginianus) has been reported (Hamerstrom 1936, Carlson 1943, Leedy and Hicks 1945, Rosene 1969); conversely, bobwhites also lay eggs in pheasant nests (Eklund 1942, Blain 1954, McHenry 1966, Holcomb 1968, Platt 1968). However, we know of no accounts of hatching in nests containing eggs from both species. This paper describes an instance of a bobwhite nest apparently parasitized by pheasant(s) whose eggs hatched at the expense of the bobwhites.

From 1970 through 1988, 281 bobwhite nests were examined during a study on Greater Prairie-Chicken (Tympanuchus cupido pinnatus)–pheasant relationships in Jasper County, Illinois. Only one bobwhite nest showed evidence of parasitic laying by pheasants.

On 20 May 1988, a bobwhite hen was found incubating in a nest that lacked the usual canopy of dead vegetative concealment. The hen did not flush then (about 08:00 h CST), when the nest was reinspected at about 09:00, on 31 May, or on 8 June. Thus, at least 19 days of incubation by the bobwhite was likely. On 13 June the hen was absent and the nest contained 15 intact quail eggs and seven pheasant eggs of which four had hatched. Shells from the four hatched pheasant eggs were on top of the quail eggs and three other pheasant
eggs. Two of the intact pheasant eggs contained dead embryos estimated to have been incubated 22 days (Labisky and Opsahl 1958); one pheasant egg showed no sign of fertility. The ages of embryos extracted from 13 of 15 quail eggs were estimated (Roseberry and Klimstra 1965) as 11 days (1), 13 (2), 14 (1), 16 (4), 19 (1), 20 (2), and 21 (2). All quail embryos were dead except one at 19 days of incubation. Two quail eggs were infertile.

The wide range of ages at death among the quail embryos suggested gradual attrition. Evidently, sufficient heat energy for full embryo development was limited to the topmost pheasant eggs, despite similar incubation periods of about 23 days for both species. Roseberry and Klimstra (1984) noted higher embryonic mortality in large bobwhite clutches (>16 eggs) than in smaller sets. These authors speculated on the physical inability of quail hens to successfully incubate larger than average clutches.

This quail nest was in a 4-ha field dominated by smooth brome (Bromus inermus) and common timothy (Phleum pratense), 10 m from a mowed lane that was adjacent to a shrubby fenceline. Brome, timothy, and tall fescue (Festuca arundinacea) dominated at the nest site. There was some indication that a nest canopy had been present when egg laying began and was later washed down by the pheasant hen(s). The nest was within 400 m of five artificial nests created to attract parasitic egg laying by pheasants on prairie-chicken sanctuaries (Westemeier 1988). The five artificial nests, each containing two plastic eggs, attracted 15 pheasant eggs—and 16 bobwhite eggs—during April and May 1988. The nearest of the five artificial nests, which was only 12 m from the bobwhite nest, attracted four pheasant eggs. The nearest pheasant nest under observation was 63 m from the bobwhite nest. We cannot be certain which species initiated the nest, but the prevailing evidence suggests parasitism of the bobwhite nest by pheasant(s). However, the incidence of nest parasitism by pheasants of bobwhites is low.

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LITERATURE CITED


Notes on the Honduran Emerald.—The Honduran Emerald (Amazilia luciae) is a little-known hummingbird endemic to Honduras. Monroe (The Birds of Honduras, AOU monograph 7:182–183, 1968) summarized what was then known about the species, and nothing has been added since. Eleven specimens have been collected at various localities from Santa Barbara in the west to Catacamas in the east, the most recent in June 1950. Monroe (1968) speculated that A. luciae was “presumably a forest inhabitant and . . . possibly common locally.” The AOU Check-list of North American Birds (1983) gives the habitat of A. luciae as “Unknown, localities generally in the humid lowlands.” However, plotting the collecting localities on a habitat map of Honduras (Monroe 1968:20) reveals that all sites where A. luciae has been taken lie in or close to “arid and mixed scrub and thorn forest.”

During two weeks in Honduras, from May to early June 1988, we found A. luciae to be a common inhabitant of arid thorn forest and scrub in the upper Rio Aguan valley, Department of Yoro. We began our search around Coyoles Central, 7 June 1988, assuming it to be the same “Coyoles” where Twomey and Hawkins collected the most recent specimens of A. luciae (hereafter also referred to as “emeralds”). Fairly large tracts of thorn forest (6 to 10 m), dominated by Mimosaceae, Cactaceae, and Euphorbiaceae, grew close to town, although the understory was grazed heavily by cattle. About 6 km west-northwest of Coyoles we located at least six emeralds in about 1 h. Few flowers were evident, and all emeralds appeared in response to imitations of Ferruginous Pygmy-Owl (Glaucidium brasilianum) calls. They seemed slow to respond and usually appeared well after a mobbing band of other birds, mainly White-bellied Wrens (Uropsila leucogastra) and White-lobed Gnatchatchers (Polioptila albiloris) had formed. Emeralds perched 1.5 to 8 m up in bare trees and bushes and sat for up to 30 sec before losing interest. When a pygmy-owl did appear one emerald stayed with it for several min and followed it closely from tree to tree. Other birds at the site included Cinnamon Hummingbird (A. rutila), Black-headed Trogon (Trogon melanoccephalus), Elegant Trogon (T. elegans), Northern Bearded Tyrannulet (Camptostoma imberbe), Brown-crested Flycatcher (Myiarchus tyrannulus), and Green Jay (Cyanocorax yncas).

Having learned a little of the habitat, we easily found emeralds in similar, but more cut-over and heavily grazed, thorn forest and scrub 4 km west of Olanchito (about 16 km east
of Coyoles). At that site we spent several hours observing emeralds the morning of 8 June 1988. At least 12 to 15 individuals were present in an area 200 × 200 m. At this second site, emeralds fed at several flowering plants, namely *Pithecellobium lentiscifolium* (Rich.) C. Wright, *Aechmea cf. bracteata* Griseb., *Pedilanthus cf. tithymalooides* (L.) Poit., and a conspicuous organpipe cactus, probably *Lemairocereus* or *Cephalocereus*; the emeralds fed at heights from 0.5 to 10 m. Several birds also made prolonged insect-catching flights (up to 60 sec or longer), particularly around the trunks of organpipe cacti. One bird, watched for about 40 min, strongly defended a territory of about 10 × 10 m against at least two other emeralds which periodically came by to feed on *Pithecellobium*.

Other birds characteristic of the Olanchito site included those listed for Coyoles (except *T. elegans* and *C. yncas*) plus Thicket Tinamou (*Crypturellus cinnamomeus*), Spot-bellied Bobwhite (*Colinus leucopogon*), Striped Cuckoo (*Tapera naevia*), Lesser Ground-Cuckoo (*Morococcyx erythropygus*), Fork-tailed Emerald (*Chlorostilbon caniveti*), and *Arremonops* sp., referred to Green-backed Sparrow (*A. chloronotus*) by Monroe (1968).

During our field work, we also visited Santa Barbara and Cofradia, two other *A. luciae* localities. At both sites we found arid conditions similar to the upper Aguan valley, but most thorn forest had been cleared for grazing and what little remained was extremely dry, with few birds of any species apparent.

From close-range observations of at least 15 emeralds, we estimate that *A. luciae* is slightly smaller than *A. rutila* and in posture and habits differs little from other Middle American *Amazilia*. The sexes appear to differ only slightly, mainly in the intensity and extent of the gorget. In life the maxilla is blackish, the mandible pinkish-red with a dark tip; the bill appears relatively long and slightly decurved. A white post-ocular spot and smaller pre-ocular spot lend the species a distinctive facial expression. The upperparts are deep emerald green and the upper tail-coverts and tail are more bronzey with a blackish subterminal band on the outer rectrices. Remiges are dark brown. Seen in the right light, the gorget flashes solidly turquoise but most of the time the underparts appear pale grayish, with dark mottling on the throat and upper chest. At rest the wings fall slightly short of the distinctly cleft tail. Feet are dark gray. One bird (apparently singing) appeared in very fresh plumage. A second, relatively duff bird (female?) had the outer two primaries and several secondaries very worn and faded in contrast to the newer and darker remiges; no rectrix molt was noted on any birds.

The most commonly heard vocalizations were a hard, slightly metallic ticking call, often steadily repeated “chik, chik-chik, chik chik...” and a hard, slightly buzzy chattering given in flight “zzchi ---” and “chik chi zzhi ---,” reminiscent of the calls of Chestnut-collared Swift (*Cypseloides rutilus*). On returning to a perch, an emerald defending its feeding territory often uttered a dry, quiet gruff warbling, possibly the song, or at least a “whisper song.” During intra-specific chasing we heard a hard buzzy chatter “chirr-rr-rr-rr-rr” and a high sharp “siik” given in pursuit.

An association with arid interior valleys explains the restricted range of *A. luciae*. Given the pressures to convert much land to agricultural practices, *A. luciae* may be a threatened species. Photographs of the food plants and habitat and a copy of Webb’s field sketches of *A. luciae* have been deposited at the American Museum of Natural History, New York.

**Acknowledgments.**—We thank D. Daly, R. Barneby, and M. Nee of the New York Botanical Garden for their assistance in identifying the food plants of *A. luciae*, and R. W. Dickerman for his helpful reading of the manuscript. This is contribution number 410 of the Point Reyes Bird Observatory.

**Steve N. G. Howell**, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970; and **Sophie Webb**, Box 664, Wellfleet, Massachusetts 02667. Received 1 Nov. 1988, accepted 10 Mar. 1989.
Above-ground nesting by Wild Turkeys.—The Eastern Wild Turkey (*Meleagris gallopavo silvestris*) is a ground nester (Mosby and Handley 1943, Williams 1981). Nest-site selection may vary greatly within and among regional habitat types. In the Southeast, suitable nesting habitat occurs in most forest types (Healy 1981). Successful nest sites are characterized by a rich herbaceous ground layer, a moderately dense woody understory, and relatively open canopy, plus immediately adjacent vertical cover, such as dense vegetation or stumps (Healy 1981, Lazarus and Porter 1985). The combination of these features gives an incubating hen both horizontal and vertical cover, while allowing her field of view to remain partially open. Here we describe aberrant, above-ground nesting by two Wild Turkey hens in coastal North Carolina.

As part of a larger study on the influences of unnatural river flooding on Wild Turkey populations, radio transmitters were placed on 49 hens. Only 19 hens nested, two above ground. The two nest sites were on North Carolina Wildlife Resources Commission and Georgia-Pacific Corporation properties along the Roanoke River in Bertie County, North Carolina. The area is a water tupelo (*Nyssa aquatica*)/bald cypress (*Taxodium distichum*) backswamp which was flooded during alternate years of the study. Nesting chronology and site selection were documented using telemetric locations, and visual observations after 20 days of incubation. The quadrat method (Muller-Dombois and Ellenberg 1974) was used to sample overstory and understory vegetation in 0.04- and 0.004-ha circular plots.

Nest A was in an old-growth tupelo/bald cypress backswamp on a 65.5-cm tall × 79.0-cm wide × 360.0-cm long log which had decayed to form a 37.5-cm trough. The nest depression was 22.0 × 30.2 cm. Incubation of nine eggs was completed on 17 June. Nest B was in the same backswamp habitat on a 56.8-cm diameter × 1.4-m tall bald cypress stump. The nest depression was 29.6 cm in diameter. Incubation of 10 eggs was completed on 1 June. Both hens were adults (>1 year old), but it was not known whether either hen had nested in previous years. Water tupelo and bald cypress dominated the overstory at site A. The sparse understory consisted of hawthorn (*Crataegus marshallii*) and Carolina ash (*Fraxinus caroliniana*). No herbaceous vegetation was present at site A, although a rich but dissected herbaceous layer occurred within 50 m of site A. Site A was 1.8 m below the high water flood level. Standing water persisted throughout the nesting season. There was no vertical cover beside nest A. Site B had overstory and understory features similar to site A, but in contrast, had a rich herbaceous layer of false nettle (*Boehmeria cylindrica*), lizard’s tail (*Saururus cernuus*), and poison ivy (*Toxicodendron radicans*). It was approximately 30 m from the alluvial ridge, the nearest uninundated habitat. When the nest at site B was initiated, the stump was completely surrounded by water. At the completion of incubation, water surrounded only 25% of the stump. Site B was 0.1 m above the high water flood level.

Nesting on elevated objects by Wild Turkeys is unusual. The nest-site selection observed in these two instances may have been random occurrences. It is interesting to note, however, that both individuals were adults with probably at least one year’s nesting experience and flood exposure in the preceding year. With “typical” nesting habitat in close proximity to both nests, there should have been an anti-predatory advantage to nesting in an area with a rich herbaceous layer giving the maximum amount of cover at the ground layer. However, both hens had the advantage of being above the field of view of most ground predators, and of choosing a site at which nest destruction from flooding could not have occurred until flood waters reached a depth of approximately 79.0 and 130.0 cm for sites A and B, respectively.

Acknowledgments.—This work was funded by the North Carolina Wildlife Resources

LITERATURE CITED


Dead-leaf-searching by the Orange-crowned Warbler in Louisiana in winter.—Searching for arthropods in dead leaves caught in vegetation above ground is a foraging behavior used heavily by many Neotropical and some North American bird species, the latter mainly on their Neotropical wintering grounds (Remsen and Parker 1984 and references therein; Greenberg 1987; Rosenberg, in press). Such dead-leaf-searching has been reported for four species in the wood-warbler (Parulinae) genus *Vermivora* (Golden-winged Warbler, *V. chrysoptera*; Blue-winged Warbler, *V. pinus*; Bachman’s Warbler, *V. bachmani*, and Orange-crowned Warbler, *V. celata*; Ficken and Ficken 1968 and references therein; other references in Remsen and Parker 1984; Greenberg 1987). Although the degree to which these species of *Vermivora* specialize on this foraging behavior is generally unknown, Greenberg (1987) found that in winter the Blue-winged Warbler searched dead leaves in 40% of 75 foraging maneuvers, and K. V. Rosenberg (in litt.) found that in winter in Costa Rica the Golden-winged Warbler searched dead leaves in 82% of 22 foraging maneuvers. In general, the *Vermivora* warblers frequently use probing and gaping motions to investigate curled green leaves, leaf clusters, leaf buds, flowers, bark crevices, moss, and sap wells made by *Sphyrapicus* sapsuckers (Root 1967, Ficken and Ficken 1968, Ehrlich and Daily 1988); the more acute, icterid-like bill of most *Vermivora* species relative to most other wood-warblers presumably reflects adaptation for such probing and gaping movements.

Remsen’s initial observations of Orange-crowned Warblers wintering in south-central Louisiana indicated that this species searches dead leaves more frequently than any other
Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of observations (%) total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dead leaf</td>
</tr>
<tr>
<td>Orange-crowned Warbler</td>
<td>145 (37)</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>2 (3)</td>
</tr>
<tr>
<td>Ruby-crowned Kinglet</td>
<td>6 (5)</td>
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substrate. In fact, wintering Orange-crowned Warblers could be located consistently by searching areas in second-growth woodland and forest edge where dense undergrowth and vine tangles trapped many dead leaves above ground. The purpose of this study was to quantify the degree of specialization on dead-leaf-searching by Orange-crowned Warblers in winter.

**Methods.**—We studied the foraging behavior of Orange-crowned Warblers in second-growth deciduous forest and forest edge in southern Louisiana, with 95% of all data recorded from two sites: (1) Burbank Drive, 1–3 km south of the campus of Louisiana State University, Baton Rouge, East Baton Rouge Parish, and (2) Bonnet-Carré Spillway, near Norco, St. Charles Parish, Louisiana. Observations were recorded from late December to early March in 1984 and 1986–89. Individual birds were followed as long as possible. Each foraging maneuver (=bird unambiguously picked or probed substrate) was scored as to type of substrate used, i.e., dead leaf, green leaf, branch, moss, etc. Data were gathered from at least 17 individual birds. Similar data were gathered simultaneously on two other small, wintering insectivores, the Ruby-crowned Kinglet (Regulus calendula) and Yellow-rumped Warbler (Dendroica coronata), for comparison.

**Results.**—Of 200 records of substrates searched by Orange-crowned Warblers, 145 (73%) were dead leaves; this contrasts strongly with data for the Ruby-crowned Kinglets and Yellow-rumped Warblers at the same study sites, neither of which searched dead leaves in more than 5% of our foraging observations (Table 1). However, our qualitative observations of three other passerine species that are permanent residents (Carolina Wren, Thryothorus ludovicianus; Carolina Chickadee, Parus carolinensis; Tufted Titmouse, P. bicolor) indicated that these three species regularly search dead leaves; quantification of their frequency of use of dead leaves is in progress (as is arthropod availability in dead leaves in winter).

**Discussion.**—Although Orange-crowned Warblers at our study sites searched dead leaves more frequently than any other substrate, the degree of specialization on dead-leaf-searching does not approach the 90%-level shown by some species of tropical forest passerines (Remsen and Parker 1984; Rosenberg, in press).

Greenberg (1987) found that another species of parulid, the Worm-eating Warbler (Hemithloheres vermivorus), searched dead leaves in 75% of its foraging maneuvers on its tropical wintering grounds. Thus, the data for Orange-crowned and Worm-eating warblers in winter are remarkably similar. Greenberg found that during the breeding season, the Worm-eating Warbler shifted its substrate preference to green foliage, where 78% of all foraging maneuvers were directed. Unfortunately, comparable data for the Orange-crowned Warbler in the breeding season do not exist. Further, although Root (1967) studied the foraging behavior of the Orange-crowned Warbler during the breeding season, he studied a different subspecies (V. c. lutescens) from the one that winters in Louisiana (V. c. celata). Although Root found
that the California birds searched foliage almost exclusively (97% of all observations), he
did not distinguish live from dead foliage; we suspect, however, that in view of the careful
detail of Root's observations, he would have noted this specifically if the California Orange-
crowned Warblers searched dead leaves frequently. Nonetheless, a comparison of summer
and winter foraging behavior to determine whether Orange-crowned Warblers, like Worm-
eating Warblers, undergo pronounced seasonal shifts in substrate preference will require
additional data from the breeding season.

We suspect that the Orange-crowned Warbler may extensively search substrates other
than dead leaves in other habitats in winter. For example, substantial numbers winter in
acacia (Acacia smallii) thickets in coastal southwestern Louisiana, where dead leaves are
not common and where all of our foraging observations so far (N = 18) are of probing moss
or bark and of searching green foliage. Also, in suburban Baton Rouge, one individual
Orange-crowned Warbler visited a hummingbird feeder for sugar water daily from 26 Jan-
uary to 14 February 1988 (Remsen and C. L. Cummins pers. obs.); feeding at hummingbird
feeders is noted occasionally in southern Louisiana (N. L. Newfield pers. comm.) and the
lower Colorado River Valley (Rosenberg et al., in press). At the latter locality, Rosenberg
et al. (in press) also found that Orange-crowned Warblers that winter there feed frequently
in flowering trees and shrubs (40% of 336 observations). Also, P. E. Scott (pers. comm.) has
found that in San Diego County, California, the Orange-crowned Warbler feeds extensively
on the nectar of Beloperone californica by piercing the bases of its flowers. Therefore, the
species as a whole is flexible in its preference for foraging substrates, even within the same
season and geographic region. Such flexibility is, so far, unknown in the many tropical
species that heavily use the dead-leaf-searching foraging behavior, regardless of habitat,
season, or geographic region (T. A. Parker, K. V. Rosenberg, and J. V. Remsen unpubl.
data).

Year-round availability of dead leaves has been proposed as a resource that contributes
to species richness in tropical bird communities (Remsen and Parker 1984, Remsen 1985).
With the untested assumption that removal of a substrate used by a bird in over 70% of its
foraging maneuvers would also remove the bird species from the local avifauna, our data
suggest that winter availability of dead leaves adds at least one species, Orange-crowned
Warbler, to certain bird communities in the southeastern United States.

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The significance of mate loss in Florida Sandhill Cranes.—Monogamy, in which “one male and one female join to rear at least a single brood” (Wilson 1975), is the most common mating system among birds. In perennial monogamy the pairbond is persistent, even during the non-breeding season (Brown 1975) and is common in species with prolonged parent/offspring involvement. Established adult pairs of Sandhill Cranes (Grus canadensis) i.e., those with a history of fledging young, are perennially monogamous (Walkinshaw 1973, Nesbitt and Wenner 1987). Re-pairing of adults following separation or the death of a mate has been reported (Littlefield 1981; Nesbitt and Wenner 1987; Bishop 1988; Bennett and Bennett, in press) although the circumstances preceding and following these cases of mate loss were not usually known.

Florida Sandhill Cranes (G. c. pratensis) captured as part of a long-term study were individually color banded beginning in 1977 (Nesbitt 1981). Each bird was aged at banding as adult (>3 years), subadult (1–3 years), or juvenile (<1 year), based on plumage characters (Lewis 1979, Nesbitt 1987). Sex of pair members was determined, in the field, during episodes of unison calling. The territories of these pairs were in Paynes Prairie and Kanapaha Prairie (Fig. 1), areas of freshwater marsh and improved pasture in southern Alachua County in north central Florida. Twenty-one nesting pairs were monitored for a total of 122 crane-pair years between 1977 and 1988 (Table 1). Seven pairs (33%) remained together while 14 (67%) changed mates (1 four times) for a total of 17 re-pairings. Nine of 17 (53%) re-pairings followed the known death of a pair member, three (18%) resulted from “divorce” (separation of a pair that had nested previously), in five (29%) the fate of the missing pair member was unknown.

Minton (1968) observed a 14% divorce rate among breeding pairs of Mute Swans (Cygnus olor). In the Black-legged Kittiwake (Rissa tridactyla), Coulson and Thomas (1983) found a higher divorce rate among younger breeding pairs that was “correlated with the failure of the pair to rear young.” Prior to the three recorded divorces in Florida Sandhill Cranes, although the pair nested and the female laid fertile eggs, they never fledged young. Pair #113, for example, hatched two young in 1986, failed to fledge either, then separated briefly during summer 1986. In 1987, after one nesting attempt with his first mate (a 4-year-old female), the male (a 3-year-old) paired with a new (3-year-old) female and made two additional nesting attempts with her in 1987. His former mate remained within the vicinity of the territory and associated with a mixed flock of adult and subadult cranes before leaving the area.

Unproductive pairs did not necessarily always divorce. The KSE pair remained together between 1984 and 1988 without fledging young, though they nested several times and hatched young three times. It is possible they produced young prior to 1984. Pairs with a reproductive history have remained together for several years without producing young. The first YEL
Fig. 1. Study area and relative location of nesting territories for 21 pairs of Florida Sandhill Cranes.

pair fledged young at least three times prior to 1981 then remained together from 1981 until the death of the female in 1985, although they produced no young.

Retention of the territory subsequent to mate loss was related to the sex of the surviving bird. Males retained the territory eight of nine times (89%), surviving females only four of ten times (40%). In three of the four instances that females retained a former territory, the bird re-paired with a younger, inexperienced male (a first-time nester) that had no established
### Table 1

**Pairing History for Twenty Pairs of Florida Sandhill Cranes**

<table>
<thead>
<tr>
<th>Pair</th>
<th>Years of contact</th>
<th>Did pair fledge young</th>
<th>Fate</th>
</tr>
</thead>
<tbody>
<tr>
<td>126</td>
<td>1982-1988</td>
<td>Yes</td>
<td>Male b—Female d</td>
</tr>
<tr>
<td>128</td>
<td>1982-1988</td>
<td>Yes</td>
<td>Male b—Female e</td>
</tr>
<tr>
<td>106 first</td>
<td>1984-1985</td>
<td>Yes</td>
<td>Female b—Male e</td>
</tr>
<tr>
<td>106 second</td>
<td>1985-1986</td>
<td>No</td>
<td>Female b—Male e</td>
</tr>
<tr>
<td>106 third</td>
<td>1986-1987</td>
<td>No</td>
<td>Female c—Male e</td>
</tr>
<tr>
<td>106 fourth</td>
<td>1987-1988</td>
<td>Yes</td>
<td>Male b—Female d</td>
</tr>
<tr>
<td>100</td>
<td>1981-1984</td>
<td>Yes</td>
<td>a</td>
</tr>
<tr>
<td>077</td>
<td>1983-1988</td>
<td>Yes</td>
<td>a</td>
</tr>
<tr>
<td>111</td>
<td>1983-1988</td>
<td>Yes</td>
<td>Female c—Male e</td>
</tr>
<tr>
<td>134</td>
<td>1977-1988</td>
<td>Yes</td>
<td>Male b—Female e</td>
</tr>
<tr>
<td>081</td>
<td>1983-1985</td>
<td>No</td>
<td>Female d—Male e</td>
</tr>
<tr>
<td>YEL</td>
<td>1977-1985</td>
<td>Yes</td>
<td>Female b—Male e</td>
</tr>
<tr>
<td>104</td>
<td>1985-1988</td>
<td>Yes</td>
<td>Female c—Male e</td>
</tr>
<tr>
<td>098</td>
<td>1985-1988</td>
<td>Yes</td>
<td>Female c—Male e</td>
</tr>
<tr>
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<td>1984-1988</td>
<td>No</td>
<td>Male b—Female e</td>
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<tr>
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<td>No</td>
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<td>a</td>
</tr>
<tr>
<td>107</td>
<td>1983-1988</td>
<td>Yes</td>
<td>a</td>
</tr>
<tr>
<td>NEW</td>
<td>1985-1988</td>
<td>No</td>
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<td>1984-1988</td>
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<tr>
<td>182</td>
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<td>Male c—Female d</td>
</tr>
<tr>
<td>120</td>
<td>1982-1984</td>
<td>No</td>
<td>Male b—Female d</td>
</tr>
</tbody>
</table>

a—Pair remained together.  
b—Died.  
c—Fate unknown.  
d—Left territory and re-paired.  
e—Remained on territory and re-paired.

territory. In the fourth instance, following the death of #114 male in August 1986, #114 female re-paired in January 1987 with the "NEW" pair male. In 1986, the "NEW" pair (a 2-year-old male and 3-year-old female) failed in their first-ever nesting effort on a small, newly established territory adjoining the 114 territory. His former mate retained the original territory and re-paired with an inexperienced male that made a first nesting attempt with her in 1987. In four of the six instances when females lost their mates and did not retain the territory, the territory was quickly appropriated by neighboring pairs. In the other two instances, occupation of the vacant territory was not immediately apparent.

Successful reproduction was a major factor in perpetuating a newly initiated pairbond. Without a successful reproductive history, a pair would likely separate. The consequences of mate loss were more significant for females than males. Following mate loss, established males usually retained the territory, secured another mate and attempted nesting, often successfully, the following season. Surviving females usually (6 of 10 times) left the territory
following mate loss and in four instances it was 2–3 years before they re-paired and attempted to nest again. Females that retained former territories and re-paired usually paired with younger, often inexperienced, males. Males that retained their territories re-paired with females that were as old or older than themselves. It is apparently more difficult for single females to defend a territory and resist the pressure from neighboring pairs to appropriate the territory. These patterns are consistent with a male-dominated resource defense system (Greenwood 1980) in which the male has a higher investment in securing and maintaining the resource (territory) and the females' mate choice is imposed upon that mating system. The consequence of mate loss that I have observed may be reflective of a particular population density of this non-migratory subspecies. Mate loss among another subspecies, especially one that is migratory, may not have the same significance.

LITERATURE CITED


STEPHEN A. NESBITT, Florida Game and Fresh Water Fish Commission, Wildlife Research Laboratory, 4005 South Main St., Gainesville, Florida 32601. Received 18 Oct. 1988, accepted 15 Feb. 1989.
Basal metabolic rate of Pacific Golden-Plovers.—It appears that shorebirds have higher basal metabolic rates (BMR) than previously recognized (Castro 1987, Kersten and Piersma 1987). Johnston and McFarlane (1967) measured BMR in two Pacific Golden-Plovers (Pluvialis fulva) and found discordant results. They favored the lower value, which was only 79.5% of the BMR predicted by Lasiewski and Dawson’s (1967) equation for nonpasserine birds, as the more accurate figure. The purpose of the present note is to report data from a larger sample of *P. fulva* that indicate a relatively high BMR similar to other shorebirds.

**Methods.**—Twelve Pacific Golden-Plovers were captured in mist nets from a wintering population at Bellows Air Force Station located on the east shore of Oahu, Hawaiian Islands. Capture was between 04:00 to 06:30; all birds were adults (i.e., older than one year). There were seven males, four females and one of undetermined sex. They were brought to the laboratory before 10:00 (three individuals on 8 March, four on 10 March, and five on 12 March 1988) and measurements of BMR made over the next 1–7 hours, after which the birds were color banded and released at Bellows. Subsequent observations through early May disclosed that all of the plovers survived and migrated. During transfer from the study site, and while in the laboratory, the plovers were held individually in darkened containers. Since the birds had not fed prior to being netted (they were returning to the study area from overnight roosts when captured), and no food was provided in captivity, all specimens were in postabsorptive condition during experiments. Each bird was placed in a Collins Small Animal Chamber (covered by an opaque cloth) housed in a Hotpack Environmatic Chamber at 26°C. Following equilibration of at least 45 min, the individual’s total oxygen consumption was measured during a period of 30 min using closed circuit spirometry. Immediately thereafter, rectal temperature was measured with a YSI thermistor probe (No. 402) connected to a YSI Telethermometer (No. 46 TUC). Body mass was recorded at the time of capture, time of release, and before and after the bird was enclosed in the small animal chamber.

**Results.**—The mean body mass of the 12 birds over the period of oxygen consumption measurement was 127.0 g ± 9.6 (SD). Their mean oxygen consumption was 1.85 ml O₂/g·h ± 0.58, equivalent to 1.31 W per bird (Table 1). The mean rectal temperature of 11 plovers was 40.5°C ± 0.6. During the time in captivity (13.3 h ± 1.0), nine birds lost body mass at a mean rate of 0.61 g/h ± 0.13. The total average mass loss over 13.3 h was 6.3% of initial body mass.

**Discussion.**—As shown in Table 1, mean BMR for our sample ranged from 34–54% higher than predicted values. Similarly, BMR in six other species of shorebirds averaged 42% above predicted nonpasserine levels (for details and references see Kersten and Piersma 1987). Based on these six species, Kersten and Piersma proposed the following allometric equation for shorebirds: BMR in W = 5.06(body mass in kg)⁰.⁷³⁹. For a 127 g plover, the equation predicts a BMR of 1.12 W, thus our measured value of 1.31 W fits the expression reasonably well. Finding measured BMR to be higher than predicted BMR was not surprising. The Kersten and Piersma equation includes resting phase BMR from birds adapted to confinement, whereas we measured only active phase BMR in recent captives. Perhaps the difference would have been greater except for the very docile nature of captured Pacific Golden-Plovers. While in the chamber, there were no indications (fluttering, etc.) of agitation. Whether the birds were in a standing posture during the measurements is unknown. Possibly, this contributed to their high BMR values, although plovers normally spend much of their time standing. We conclude that the metabolic characteristics of *P. fulva* provide further evidence of relatively high BMR among shorebirds.
Kersten and Piersma (1987) interpret high BMR in shorebirds as a reflection of the visceral processes necessary to sustain very active skeletal muscles. Furthermore, they suggest that the daily energy expenditure “at some period of peak demand, could well lead to a higher-than-expected BMR.” Such peaks might accompany “periods of mid-winter cold spells” and “the periods of migration and premigratory fattening.” Given the tropical climate on central Pacific wintering grounds, P. fulva’s “peak demand” likely occurs in the arctic during the inclement weather of early spring.

The mean deep-body temperature of the plovers was within the range of body temperatures reported for 18 species of shorebirds (compiled by Neumann et al. 1968). Also, it was close to the estimated body temperatures of Ruddy Turnstones (Arenaria interpres) and Black-bellied Plovers (P. squatarola) as extrapolated from a regression of heat production on air temperature (Kersten and Piersma 1987). The deep-body temperatures, air temperature, and oxygen consumptions measured in the present study allowed us to calculate the total (wet) thermal conductance of P. fulva’s tissues and plumage. The value calculated (0.71 mW/g°C) was higher than predicted values of 0.31–0.51 (Herreid and Kessel 1967, Aschoff 1981). It is tempting to correlate the high BMR of the plovers with their high thermal conductance, as the latter implies a low thermal insulation. However, at an air temperature of 26°C, it is unlikely that thermal conductance of the plovers was minimal and comparisons with allometrically derived predictions may be invalid. An important factor in the overall insulation of plovers would be their long legs which facilitate heat loss. It is notable that Kersten and Piersma (1987) found shorebirds to be poorly insulated, but cautioned that their laboratory results might not be representative of natural conditions.

Acknowledgments.—This work represents a component of a larger project dealing with the long-term ecology and behavior of wintering Pacific Golden-Plovers. Financial support (to O. W. and P. M. Johnson) was provided by the National Geographic Society, Hawaii Audubon Society, and Moorhead State University through a faculty research grant program. Special thanks are extended to P. and A. Bruner for assistance in the netting of plovers. We are grateful to various officials of the Hawaii Division of Forestry and Wildlife, U.S. Fish and Wildlife Service, and U.S. Air Force for their kind cooperation in furnishing the netting and access permits essential to our studies.

### Table 1

<table>
<thead>
<tr>
<th>Comparison of Measured and Predicted BMR in the Pacific Golden-Plover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Metabolism (W)</td>
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<tr>
<td>----------------</td>
</tr>
<tr>
<td>Measured BMR</td>
</tr>
<tr>
<td>N = 12</td>
</tr>
<tr>
<td>Allometric equations</td>
</tr>
<tr>
<td>Lasiewski and Dawson (1967)</td>
</tr>
<tr>
<td>Aschoff and Pohl (1970)</td>
</tr>
<tr>
<td>Kendeigh et al. (1977)</td>
</tr>
</tbody>
</table>

* All calculations reflect a body mass of 127.0 g.
* Figures show mean ± SD, and range. BMR was less than predicted in only two individuals.
* Nonpasserines, day and night.
* Nonpasserines, active phase.
* Eq. 5.5 (nonpasserines, day and night).
LITERATURE CITED


Intraspecific nest usurpation by a Yellow-eyed Junco.—Although the nesting activities of a number of avian species have been well studied, there are few published accounts of either inter- or intraspecific nest usurpation (Whitmore, Emu 81:111–112, 1981). We report here an observation of intraspecific nest usurpation by a pair of Yellow-eyed Juncos (Junco phaeonotus). Yellow-eyed Juncos are small (19 g) passerines that are monogamous, maintain all-purpose territories and build concealed cup nests on the ground (Sullivan, Ecology 69: 118–124, 1988). We made these observations at Rustler Park (elev. 2560 m, 31°55’N, 109°17’W) in the Chiricahua Mountains (Coronado National Forest) of southeastern Arizona during the 1984 breeding season (see Balda, Ph.D. diss., Univ. Illinois, Urbana, Illinois, 1967, for a detailed description of the study site and breeding biology of the Yellow-eyed Junco).

On 29 June, J. Cole found the nest of an unbanded pair of Yellow-eyed Juncos at the base of a clump of orange sneezeweed (Helenium hoopsis). This nest contained four warm eggs. He checked the nest on 3 July and flushed the incubating female off the four eggs. The next day (4 July) a banded female (female B) from an adjacent territory was observed entering the nest while the unbanded female (female U) was incubating. Female U flew off and began foraging when female B entered the nest. Female B remained in the nest for a few minutes but did not lay an egg. Female B and her banded mate had successfully fledged three young
from a nearby nest on 11 June. This pair ceased feeding their fledglings and evicted them from the family territory on 3 July. On 5 July, J. Cole flushed female U off the nest and counted five eggs in the nest. On 7 July, the nest was checked again and found to contain seven eggs. We did not mark the original four eggs in the nest, but we were able to identify them as they were considerably longer and narrower than the other three eggs.

E. Villalobos watched the nest from 06:30 to 09:30 on 8 July. Female B spent 165 min (78.6%) of the observation period on the nest, while the unbanded female spent only 13 min on the nest (6.2% of the period). On three occasions, both females attempted to incubate the eggs, and female U spent 4 min perched on female B's back. During this observation period, female B's mate chased female U from the nest site twice and her mate three times.

Female B was incubating the double clutch and the unbanded female was foraging near the nest when the nest was checked on 9 July. By 10 July the unbanded pair had disappeared from their territory and did not return during the remainder of the breeding season. Female B continued to incubate the clutch, and on 15 July one of the original eggs in the clutch pipped (incubation usually takes 13 days in Yellow-eyed Juncos). That afternoon and evening, rain washed away the contents of the nest. The next morning we found two eggs near the nest site. One egg had pipped, and the other egg had never developed. The banded pair renested nearby, and a clutch of three eggs was completed by 25 July. Three young fledged from the nest on 18 August. The male of the usurping pair disappeared from the population during the following winter. Female B was still present in the 1988 breeding population and has been one of the most successful females (in terms of the number of offspring entering the breeding population) in the study population.

This case of nest usurpation appears to be aberrant behavior for Yellow-eyed Juncos. This is the only case of nest usurpation we have observed in monitoring 292 nesting attempts over a five year period. Under most situations, the usurping female's eggs would hatch several days later than the first female's and the young would be ill-prepared to leave the nest when the first female's clutch fledged (10–13 days after hatching, Sullivan 1988). Among Yellow-eyed Juncos, nest usurpation may be related to intraspecific brood parasitism. On two occasions females laid three eggs in their own nest and we observed them lay a fourth egg in a neighbor's nest. We suspect, based on egg shape and the timing of egg laying (clutch size increasing by two eggs in one day), intraspecific brood parasitism has occurred at additional nests.

Acknowledgments.—We thank S. Land for finding nest S5, the Southwestern Research Station of the American Museum of Natural History for providing housing and laboratory space, the Douglas ranger district office of the Coronado National Forest for their cooperation and the American Philosophical Society, Frank M. Chapman Memorial Fund, National Institute of Health (HD-06552) and the National Science Foundation (BSR-88-02577) for providing financial support.

Peach-fronted Parakeet feeding on winged termites.—Insectivorous habits in parrots are reported for the Australasian genus *Calyptorhynchus*, which seem to feed habitually on larvae of wood-boring insects in addition to seeds and fruits (Forshaw 1981). Among Neotropical psittacids insectivory is poorly known, although Forshaw (1981) believes that these birds are far more insectivorous than is generally supposed. The White-eyed Parakeet (*Aratinga leucophthalmus*) is said to take adult and larval insects (Forshaw 1981), and the crop and stomach of one specimen of the Peach-fronted Parakeet (*A. aurea*) contained crushed seeds, a geometrid larva, a beetle pupa, and many fly larvae, the latter possibly due to ingestion of infested fruit (Schubart et al. 1965). Here I report on a flock of Peach-fronted Parakeets feeding on alate termites (Isoptera) in southeastern Brazil. Termites are a protein-rich, but unpredictable and ephemeral food source, opportunistically taken by a number of birds and other vertebrates (Thiollay 1970, Dial and Vaughan 1987).

On 27 October 1973 (at the onset of the rainy season), ca 16:00 h, I observed about 10–12 Peach-fronted Parakeets in “cerrado” (savanna-like) vegetation near Vacarias, Minas Gerais, southeastern Brazil (ca 19°25'S, 43°40'W). The parakeets were on the ground pecking at something, and from time to time perched on branches nearby. The birds were picking up winged termites which were swarming on a nuptial flight. Termites were crawling abundantly on the ground near the earthmounds and also flying slowly on the wing. One bird occasionally made short, clumsy flights as if to take the insects in mid-air, but most termites were sought on the ground. The stomach and crop of a voucher specimen (ZUEC 046, Museu de História Natural, Universidade Estadual de Campinas) were full of alate termites along with masticated palm nuts.

Feeding habits of most *Aratinga* species are not known in detail, but their diet includes seeds, fruits, berries, nuts, flowers, and other vegetable matter generally procured in the treetops or amongst the outer branches of bushes (Forshaw 1981). However, the White-eyed Parakeet is known to forage both in the treetops and on the ground (Forshaw 1981), and the Peach-fronted Parakeet may also forage on the ground taking seeds from low-growing plants (Sick 1984). I suggest that feeding on termites by the Peach-fronted Parakeet might be related both to its ground-foraging and, perhaps, to its habit of nesting in termitaria.

The Peach-fronted Parakeet may excavate nest holes in arboreal termitaria (Sick 1984), a habit shared by the Orange-fronted Parakeet (*A. canicularis*), another presumably insectivorous species (Forshaw 1981). I observed a pair of Peach-fronted Parakeets digging with their bills in an occupied arboreal termite nest ca 1.2 m above the ground in the Pantanal region (Poconé, Mato Grosso, SW Brazil) on 30 April 1986, ca 09:30 h. During the excavation the parakeets surely make contact with the nest occupants, and the birds may take some termites as food on these occasions. Together with ground-foraging ability, this situation would facilitate *A. aurea* in promptly shifting to feed on swarms of winged termites, a locally abundant but unpredictable food source.

**Acknowledgments.**—I thank H. Sick and W. W. Benson for useful comments and reading the manuscript; M. Sazima and O. C. Oliveira for help in the field; the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support (grant 300992/79).

**LITERATURE CITED**


ORNITHOLOGICAL LITERATURE

Biographies for Birdwatchers. By Barbara and Richard Mearns. Foreword by Sir Peter Scott. Academic Press, London and San Diego. 1988:xx + 490 pp., bird drawings by Darren Rees; maps and portraits of biographees. $35.00.—In the interests of prompt publication of this review, I had originally intended merely to sample the 89 biographies in this book. I found, however, that I could not do that; the accounts were so fascinating that I simply had to read every word. Most of the books I have reviewed are technical or reference works; this is the first of a new series called “Books About Birds,” intended for interested laymen and published under the general editorship of Andrew Richford of Academic Press (London). Richford has every right to be proud of his first production. I hope, also, that the authors are receiving a good royalty and that many copies are sold, because the Mearnses have been working since 1983 on what is obviously a labor of love; I would like to see them get a more tangible reward for their efforts.

The subtitle of the book is more informative than the title: “The lives of those commemorated in Western Palearctic bird names.” “Names” include both English and scientific, and the species covered even include introduced species (such as five exotic pheasants) and those merely accidental or peripheral in the Western Palearctic (such as Baird’s Sandpiper [Calidris bairdii] and Verreaux’s Eagle [Aquila verreauxii]).

Biographees range from ancient (Aristotle) to living (Christian Jouanin), and most are illustrated with portraits, from busts to photographs. The authors were unable to find portraits of a few of their subjects, and in one instance, that of Chersophilus duponti, they are not certain as to which Monsieur Dupont was honored by Vieillot.

The 14 maps illustrate the overland travels or sea voyages of biographees, on some maps only one (Pallas, Steller), and on others as many as eight, on a map of Africa. My only major criticism of the book has to do with the placement of the maps. They are scattered among the pages, located adjacent to the alphabetically first biography among those whose routes are mapped. This results, when several persons’ routes are shown on one map, in time-consuming backward searches for the map appropriate to a biography appearing later in the alphabetical order. It would have been simpler had the maps been collected together in the front or back of the volume.

Darren Rees, an award-winning British wildlife artist, has provided attractive scratchboard drawings of each of the bird species named for one of the biographees, in some instances two or three species per chapter (Tristram’s Warbler [Sylvia deserticolor], “Grackle” [Onychognathus tristramii = Starling], and Serin [Serinus serinus]). The poses chosen for the birds are highly varied, sometimes daring (a very dead Denham’s Bustard [Neotis denhami] lying sprawled on the sand), and sometimes anything but diagnostic; the Berthelot’s Pipits (Anthus bertheloti) are two tiny silhouettes that could be almost any slender-billed passerine, placed in a bleak Canarian landscape, and the Grey-necked Bunting (Emberiza buchanani) could be any short-billed passerine with white outer rectrices. But all of the drawings add immeasurably to the attractiveness of the book. The only color reproduction is a brightly painted Montagu’s Harrier (Circus pygargus), with an inset portrait of George Montagu (1753–1813), on the dust jacket. Dust jackets being notoriously ephemeral, it is a pity that this colorful painting was not also reproduced as a frontispiece.

The biographies are chock-full of facts of the “gee whiz, I never knew that” variety, and it is a temptation to cite more of these than the editor of The Wilson Bulletin would permit. A few examples must suffice.

All good Amherstians know, from their rousing drinking song if not otherwise, that “Lord
Jeffrey Amherst was a soldier of the King." He was also the uncle and adoptive parent of the second husband of Lady Amherst, née The Hon. Sarah Archer (1762–1838), in whose private aviary Benjamin Leadbeater saw the first specimens of the superb pheasant that he named for their owner.

One might assume that because, in addition to Barrow’s Goldeneye (Bucephala clangula), John Barrow’s name has been commemorated in Point Barrow, Barrow Sound, Barrow Straits, the town of Barrow in the Arctic, and Cape Barrow in the Antarctic, that he was an explorer in polar regions. In fact Barrow (1764–1848) was a naval bureaucrat who held a desk job in London for half his life, with his only foreign travel having been in China and southern Africa. However he was vitally interested in the Arctic, especially in the elusive Northwest Passage, and was directly responsible for expediting the travels of such explorers as Ross, Sabine, Franklin, and Richardson (all of whom are also commemorated in bird names), and the various localities named for Barrow were so designated out of gratitude for his support.

The family name of Georg Wilhelm Steller (1709–1746), of eider, jay, sea-eagle, sea-lion and sea-cow fame, was originally Stöhler. When the 25-year-old naturalist moved to St. Petersburg, he found that his Russian colleagues were incapable of pronouncing Stöhler correctly, so he changed it to Steller for their benefit.

Although the brother of Gilbert White (1720–1793) of Selborne and of White’s Thrush (Zoothera dauma) lived in Gibraltar and wrote to Gilbert about the flocks of swallows passing through southern Spain each autumn, White himself was never certain as to whether swallows really migrated or passed the winter buried in mud or hidden in chimneys.

No book like this has ever appeared on the names of North American birds. The brief biographies included (along with other bird name derivations) in Gruson’s “Words for Birds” (1973) and Choate’s “Dictionary of American Bird Names” (revised ed. 1985) cannot compare with those compiled by the Mearns team; for Charles Lucien Jules Laurent Bonaparte, for example, Choate gives one paragraph, Gruson gives four (½ page) while Mearns and Mearns give 6½ pages plus a full page portrait.

Using the list of North American birds in the sense of the 5th edition of the A.O.U. Check-list as emended in the 34th Supplement (1982. Auk 99, no. 3, supplement), I find that there are 79 persons’ names attached to bird species, other than the names among the 89 principal biographees in the Mearns book. Furthermore, four of these are included in an appendix of shorter biographies in the back of the Mearns book, “naturalists commemorated by species of uncertain status within the Western Palearctic, together with some naturalists who have had well-known races of birds named after them.” An additional 11 of the North American names appear in a second appendix of short paragraphs on “naturalists mentioned in the main text.”

It is apparent that a book of comparable size could be compiled on those persons commemorated in the names of North American birds. I wonder if, in North America, there is an author or authors interested and willing enough to do such a superbly thorough job of it as has been accomplished by Mr. and Mrs. Mearns. I recommend their book most enthusiastically. —KENNETH C. PARKES.

BIRD COMMUNITIES AT SEA OFF CALIFORNIA: 1975 TO 1983. By Kenneth T. Briggs, Wm. Breck Tyler, David B. Lewis, and David R. Carlson. Studies in Avian Biology, No. 11, Cooper Ornithological Society, 1987:74 pp., 29 figs., 5 tables. $7.00.—This latest offering in the “Studies in Avian Biology” series maintains the tradition of excellence and timeliness of topic that has become a distinguishing mark of the series since its inception in 1978. It
is also the first to deal exclusively with the pelagic ecology of seabird populations occupying a specific coastal region for a number of years in a comprehensive manner. Although the treatment is highly academic in form and aimed for use by professional marine ornithologists, a wider audience will find much of interest, particularly in assessing the approach that has been taken to ask questions about habitat characteristics and regulation of seabird communities and the modern and integrative nature of the ensuing analysis. The study of birds at sea (through space and time) has “exploded” in its sophistication and usage of technological advancements since the late 1950s/early 1960s when the oceanic study of seabirds was identified as an important branch of ornithology, one where there was a serious dearth of knowledge (see Bourne 1963: Proc. Intern. Ornith. Congr. 13:831–854). The present study vividly shows how large an expansion in information and study techniques there has been and the high degree of maturity attained over a short period of time.

The volume is structured in five parts. A brief introduction establishes the rationale behind this study of bird communities at sea off California. It reviews the recent evolution of the study of marine birds at sea, and by doing so, presents a succinct overview of the kinds of questions that have been asked in the past and those that need attention today. The object of the present work is defined as an attempt to quantify the occurrence of seabirds in waters off California and relate patterns of distribution, species composition, and abundance to oceanographic characteristics over time.

The second part details with the methods used. Details of the sampling plan used and coverage at sea and along shorelines are given: southern California from 1975 to early 1978 by ship and aerial surveys (ca 50% each), and central and northern California from 1980 to early 1983 almost entirely by airplane, supplemented by coastal surveys on land in all three regions. This is followed by a description of environmental data recorded during bird observations and the statistical analyses used to determine bird density, species diversity and associations, and water habitat relationships. Part three describes the oceanography of the California Current System comprising the study area with emphasis on those factors most likely to be influencing the distributions of birds, both directly and indirectly, through the annual cycle.

Part four, the results section, makes up the bulk of the volume, comprising more than 70% of the text. It is here where there is a wealth of information to be gleaned on the pelagic ecology of seabirds. A total of 74 marine bird species were recorded during the study (excluding all waders and shorebirds except phalaropes [Phalaropus spp.], all anseriforms except Brant [Branta bernicla] and scoters [Melanitta spp.], of which 30 were dominant based on biomass and density. These reached maximal abundance in the coastal upwelling zone in the fall and winter (reaching totals of 4–6 million individuals) and accounted for most of the energy cycling through the California seabird community. Accounts of 62 species are presented as an annotated list providing information on population size and status of each species, and comparing, where data are sufficient, monthly mean densities by species and year for the three regions (northern, central, and southern) and overall habitat affinities.

But the community analysis that follows the individual species accounts provides the real excitement. The approach is comprehensive and divided into sections comparing seabird density and biomass, diversity and species composition, species’ associations, features of aggregations, bird habitats, and determinants of bird distributions. Analyses of diversity and interspecific associations in several latitudinal/water depth regions are made, followed by an examination of habitat use for a number of important species using a multivariate ordination approach. The findings and highlights are many. They include such things as: marked biomass differences between weak and intense “El Niño” episodes (1976 versus 1982–83, respectively); concordant associations between species—several shearwaters (Puffinus spp.) and Northern Fulmars (Fulmarus glacialis), between several Larus gulls, and
several members of an inner-shelf/nearshore avifauna including loons (Gavia spp.), cormorants (Phalacrocorax spp.), Brown Pelicans (Pelecanus occidentalis), and scoters, with Leach’s Storm-Petrel (Oceanodroma leucorhoa) standing out as an exception by its very distinct regional occurrence and unique set of habitat characteristics disassociated from any other species; and overall patterns of distribution and abundance of species that suggest different scale-dependent physical processes affect patches of seabirds and their prey in different habitats. Numerous other informative and stimulating aspects of the ecology of the seabird communities are also uncovered. All of this is then elucidated in the final part, a discussion section that is effective in placing the great majority of the new information into a clear and useful perspective. Altogether, an outstanding accomplishment.

There is little in the volume to take serious issue with. It has been well edited and contains few typographical errors. The layout and composition of figures and tables are excellent, as is the quality of printing. The color photograph on the cover adds a nice touch, though it is the “meat” between the covers that forms the lasting treasure for the reader.

This monograph is a must for any student of seabirds. It is exemplary in showing where the study of marine birds at sea is at the present time. The questions asked, and the approaches taken to answer them, combined with a “state of the art” treatment of analysis and the overall high quality of conclusions that have been derived from the data gathered, go a long way in pointing the direction to be taken in the future. The authors are to be congratulated on producing such a milestone, one that is likely to stand as a principal source of reference for marine ornithologists for a long time to come.—DAVID N. NETTLESHIP.

THE KOOKABURRAS’ SONG: EXPLORING ANIMAL BEHAVIOR IN AUSTRALIA. By John Alcock, illus. by Marilyn Hoff Stewart. Univ. of Arizona Press, Tucson, 1988:x + 218 pp., 28 black-and-white drawings, 27 range maps. $19.95.—This delightful little book is an outgrowth of the author’s sabbatical work in Australia. It consists of 28 chapters, each focusing on a single animal which illustrates a particular evolutionary problem. The chapters are very personal reflections, really musings of the author, who is a confirmed adaptationist. Typically the chapters start with a description of a particular locality and its denizens, then focus in on some evolutionary aspect of one species of bird, insect, or mammal, posing evolutionary questions, and suggesting possible evolutionary scenarios as answers. The introductory chapter, “The Kookaburras’ Song,” sets the tone and format for the chapters that follow. It starts with background information on the aboriginal folklore surrounding the Kookaburra (Dacelo gigas), then moves to a description of a trip, a shakedown cruise with the family in a campervan, to Little Desert National Park in Victoria. The narrative weaves in some fascinating history of early Australian exploration. Alcock ties these themes together and tells us what the book is really about: “This book is a travel book, too. The scale of exploration, however, will not be transcontinental but biological. . . . The aborigines were on to something: the kookaburras’ song deserves a myth, and search for a modern equivalent of the aboriginal account has led me on a journey small in scale but large in pleasure.” Finally returning to the kookaburras, Alcock poses some evolutionary questions that the dawn calling of the birds raises, and uses this as a springboard for probing the significance of Charles Darwin.

The 28 chapters are divided into six sections: “On Adaptation,” “Nuptial Puzzles,” “Machismo and the Competitive Male,” “Primitive or Degenerate?,” “Life with Others,” and “Adaptive Altruism.” Each contains a cluster of chapters illustrating the evolutionary questions posed in these subject areas. In 14 chapters birds are the focal animal, in seven insects, and in six mammals (one mammal shares the focus with a plant). Each focal species
is accompanied by a range map which, along with the pen-and-ink drawings, are interesting, informative, and attractive complements to the text. Alcock uses an adaptationist perspective throughout, including taking mild exception to criticism of this approach, and creates evolutionary scenarios for a broad spectrum of structures and behaviors. For example, he suggests that the duet calling of Northern Logrunners (*Orthonyx spaldingii*) may have evolved primarily as a result of sexual conflict and competition, speculates on the adaptive significance of the red tail-panels in Red-tailed Black Cockatoos (*Calyptorhynchus magnificus*), and the mound building behavior of the Malleefowl (*Leipoa ocellata*). He touches upon evolutionary convergence in possums and gliders, reviews the arguments about whether cassowaries have flying or flightless ancestors, and the reasons why muttonbirds flock. He describes the farming of edible lerp-(protective sugary coverings) producing psyllid bugs by Bell Miner (*Manorina melanophrys*) birds (which eat the lerps but don’t “... eat the goose that lays the golden lerp”). These stories are a virtual “evolutionary primer,” with the major points illustrated by the behaviors of Australian birds, insects, and mammals.

The text is very entertaining as well as informative. Alcock weaves his evolutionary scenarios skillfully through a text describing previous published work on each species, historical anecdotes, and personal observations. He often uses metaphors attractively, as in “... beaches set parenthetically between boulder-strewn points, huge overlapping petals of water ...,” or with dramatic effect as in “It takes practice to regard a leech calmly, particularly when the creature hangs like a limp miniature sausage, fed to repletion, fat and blood-soaked, attached to an ankle, toe, or leg.” In short, the book is a pleasure to read. For those of us fortunate enough to have worked with or witnessed Australian flora and fauna, the book elicits a flood of fond memories. For those not yet so fortunate, it whets the appetite for future encounters. Clearly, Alcock thinks that science should be fun, and this book demonstrates that it can be.

I have little to criticize in the book. I found only one apparent editorial error, the word “placental” being left out of the second sentence on page 109. Some readers may take exception to certain of the author’s suggestions about the evolution of particular behaviors. Nevertheless, I highly recommend this delightful book to anyone interested in birds or natural history in general. It will be especially interesting to those concerned with evolution. This is one of the few well written books on Australian natural history, and I hope that it will stimulate the production of more.—**William E. Davis, Jr.**

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**A Guide to Bird Finding in Kansas and Western Missouri.** By John L. Zimmerman and Sebastian T. Patti, illus. by Robert M. Mengel. Univ. Kansas Press, Lawrence, Kansas. 1988:244 pp., 19 line drawings, 26 maps, 1 numbered text fig., 1 checklist. $22.50 ($9.95 paper).—Located near the center of the United States, Kansas and western Missouri lie in an ecologically diverse region that is transitional between east and west. It is thus not surprising that over 400 species of birds have been found in this region, and this timely guide to locating the many interesting birds of the area is welcome.

Kansas and western Missouri sit on the northwestern corner of the Ozark Plateau, and extend from the tall-grass prairies of the eastern Great Plains westward to xeric short-grass prairies of the west. The birds found in wooded regions of Missouri and eastern Kansas are those characteristic of the northeast, but in central or western Kansas many of the eastern species are replaced by western ones. Most North American grassland birds can be seen (at one time of the year or another) in Kansas and western Missouri, and northern-breeding birds pass through the region during migration. With this book, Zimmerman and Patti provide us with a valuable guide to finding these ornithological riches.
"A Guide to Bird Finding in Kansas and Western Missouri" is organized around 75 "birding tours," each starting from a city or town. For each tour, clear instructions are given to guide the naturalist to the more interesting local areas, and there are 26 excellent maps that provide extra information for some of the tours. In addition to comments about what species of birds to expect, many of the tours are enlivened by interesting comments on the history, geology, or ecology of the region—making this more than merely a guide to bird finding. The line drawings by Robert M. Mengel are of the fine quality that characterizes his work and greatly enhance the attractiveness of the book.

In addition to the 75 tours, there is a checklist to the birds of the region, a figure illustrating the seasonal occurrence and relative abundances of regional birds, and an annotated list of the "speciality species" of the region. Some of the specialties will surely attract birders: Kansas is one of the best places to see all four species of longspurs (Calcarius). The Cimarron National Grassland in southwestern Kansas may be the best place in the world to see Lesser Prairie-Chickens (Tympanuchus pallidicinctus), and Greater Prairie-Chickens (T. cupido) and Upland Sandpipers (Bartramia longicauda) are common in the Flint Hills of central Kansas. Mississippi Kites (Ictinia mississippiensis) and Scissor-tailed Flycatchers (Tyrrannus forficatus) are locally common in south-central and southwestern Kansas, and Painted Buntings (Passerina ciris) breed in forest edge across the southern part of the region. In the short-grass of western Kansas, Cassin’s Sparrows (Aimophila cassinii) can be seen giving their aerial song; in winter, Harris’ Sparrows (Zonotrichia querula) are found throughout this region and are especially abundant in south-central Kansas. Henslow’s Sparrows (Ammodramus henslowii) breed locally in unburned tall-grass prairie in eastern Kansas and western Missouri, and the Stafford County (Kansas) saltmarshes are perhaps the best place in the interior to see Snowy Plovers (Charadrius alexandrinus), Least Terns (Sterna antillarum) and (if you are lucky) Black Rails (Laterallus jamaicensis).

I wholeheartedly recommend this book to all ornithologists and bird watchers who live in or plan to visit, Missouri or Kansas. It has been well produced, and although at 9" × 6" is perhaps a bit too large for most pockets, it can easily be carried in the field. The writing is clear and lively throughout, the illustrations first rate, and the text so full of information that even non-birders will find much of interest.—J. D. RISING.

BIRDS OF THE MIDDLE EAST AND NORTH AFRICA: A COMPANION GUIDE. By P. A. D. Holom, R. F. Porter, S. Christensen, and Ian Willis, illus. by Ian Willis. Buteo Books, Vermillion, South Dakota. 1988:280 pp., 40 color plates, 498 range maps, numerous line drawings. $32.50—While most field guides cover an easily definable area, like North America, Japan, or Australia, books on birds of the Western Palearctic and adjacent areas suffer from an overlap problem. The original (1954) and still classic guide to European birds by Peterson, Mountfort, and Holom (“PMH”) used the Mediterranean and longitude 30°E as its boundaries. Successive “European” guides encroached farther into Russia and invaded North Africa and the Middle East, e.g., “The Birds of Britain and Europe with North Africa and the Middle East,” by H. Heinzel, R. S. R. Fitter, and J. Parslow; others were devoted entirely to extra-European regions. R. D. Etchecopar and F. Hue produced one book (1964) on North Africa and a second (1970) on the “Near and Middle East,” which they defined as Turkey and Jordan to Iran and Afghanistan, but not the Arabian Peninsula. Other books have covered more limited geographic areas: Cyprus, Lebanon, Iran, the Arabian Peninsula, Saudi Arabia, the Arabian Gulf and Oman. The monumental “Birds of the Western Paleartic,” edited by S. Cramp, covers most of the above but omits Iran and much of the Arabian Peninsula. The present volume covers North Africa and its own definition of the
Middle East, Turkey and Cyprus to Iran and all of the Arabian Peninsula, thus overlapping about 12 other books. So what is its raison d’être?

As indicated by its subtitle, it is designed to be used in conjunction with PMH; the senior author is also the “H” in PMH. Exclusion of Europe was deliberate, and complementary geographic area is mirrored by complementary, non-overlapping text and illustrations. Species covered in PMH are not described again here; the reader is simply given the length of the bird and told to “see PMH”; their species accounts give only range, status, and habitat within the region. By contrast, birds not covered in PMH are treated to a lengthy ID section, typically 10–15 lines, up to 25 for more difficult species, followed by a couple of lines on voice. Only birds breeding in the area have range maps; these show breeding but not winter range (why not?). The maps are a reasonable size for a field guide, 6 cm × 2.5 cm, the range in red on a white background, and are fine-tuned, showing many small, disjunct areas, instead of blanketing the range with the “broad brush” approach.

The close interlock with PMH means you must carry both books. This will annoy those who want to have everything within the covers of a single volume for easy comparison, but the inconvenience is worth it. Abbreviating European species leaves room for much fuller treatment of local birds, and by sparing us yet another picture of a Dunlin (Calidris alpina) or Common Tern (Sterna hirundo), the artist has given himself space for less well known species. While European birds shown in PMH are not illustrated here, an exception is made where local races look very different; thus we find the race savignii of Hirundo rustica, with bright red underparts, the race samamiscus of the Redstart (Phoenicurus phoenicurus), with white wing flash, and the race phoenicuroideos of the Black Redstart (P. ochrurus), with orange belly.

While the choice of illustrations has been thoughtful, their execution is less than satisfactory. Ian Willis’s line drawings are first class, such as the page of crows and the larks on p. 158, but the color plates compare unfavorably with Peterson’s in PMH. Feather definition is wanting for many birds, which instead are painted in blocks of an almost uniform color; this has the effect of giving them a stiff, un-lifelike appearance. Illustrations sometimes do not agree with the text and are not coordinated with PMH. The anemic-looking Long-billed Pipit (Anthus similis) on Plate 25 is said to be more upright than the Tawny Pipit (A. campestris) but drawn less upright; lower underparts correctly stated to be deep buff or buff-orange but painted white; legs said to be flesh red to flesh orange, shown as very pale brown. The bill is too short (said to be longer than Tawny but appears same size as the Tawny in PMH), and lacks the drooping tip typical of the species and mentioned in the text. The picture does score one point over the text: the upper mandible is all dark, the lower pale with a dark tip. This is correct for most specimens; few have the upper mandible also pale with dark tip, as stated in the text. Some of the plates appear too washed-out, doubtless the fault of the printer, not the artist; the desert-haunting larks on Plate 23 are pale but not that pale, and even the heavily marked Thick-billed Lark (Ramphocoris clotbey) looks rather bland and understated.

The text seems generally free from errors, but one can always find a few. Eversmann’s Redstart (P. erythronotus) is said to be a “rare scatter from central Iraq”—? Is this some kind of scatological reference? And the writer of the introduction fell into an ancient trap when he talked of “seed-eating finches such as Manakins” (p. 8). Manakins, of course are not seed-eating finches but the New World family Pipridae; he meant Mannikins, which are small, seed-eating estrildines.

In spite of some drawbacks, this book and PMH together form the most efficient combination for field identification of birds in North Africa and the Middle East. Definitely recommended.—STUART KEITH.
STATUS OF UNCOMMON AND PREVIOUSLY UNREPORTED BIRDS OF EL SALVADOR. By Walter A. Thurber, J. Francisco Serrano, Alfonso Sermeño, and Manuel Benitez. Proceedings of the Western Foundation of Vertebrate Zoology, Los Angeles, California. 1987:Vol. 3, No. 3, pp. 109–293, 54 photos, 6 color plates. $12.00.—This well-researched volume will be of value in much of Central America, and even beyond. Some of the problems—especially conservation—concern us all. Not infrequently the discussions point out problems of breeding distribution, dispersal, and/or migration in much of Central America (notably in herons, Ardeidae). Nor is it entirely restricted to uncommon birds.

Many habitat photos help envision the situation. A map and supplementary gazetteer round out Dickey and van Rossem’s classic “Birds of El Salvador” (1938, Field Museum of Natural History, Zoological Series Volume 23). While van Rossem’s collecting and careful observations remain an unequaled model for northern Latin America, Thurber et al. add greatly to it, including unpublished data from outside of El Salvador. Usually they treat only status, but rarely (Cracidae) they present and summarize life history data. New techniques (netting, banding) add to van Rossem’s findings; some “new” species are properly noted as “probably present” then. Species of changed status are summarized (not quite completely), pp. 276–284. In view of all the diverse data, a subject index would have been helpful.

Occasional lower-level taxonomic problems are also set forth, like the urgent one of the diminishing Aratinga parakeets. But most are slighted. Modern writers normally assume that all birds are known (or if subspecies, not worth knowing); all are in various check-lists, and often field guides.

But in general the Pacific lowlands, like El Salvador’s, are quite distinct faunally from both the Caribbean slope and the oak-pine mountains. Only collecting can tell us whether the big woodcreeper at El Imposible is, as presumed, Xipholaptes promeropirhynchus, and the white hawks Leucopternis albicollis. The details of structure and size cannot be told from photos, as of the Hawk in Fig. 19. One hates to have to add a scientific mite to the slaughter (as in a Kansas town where officials still believe the only good hawk is a dead hawk); but a population which cannot sustain individual losses is already doomed, and something should be preserved for posterity. And no perils prevent collecting a few of the “highly territorial” Empidonax (p. 241); such cases are indeed “worthy of detailed study.” And once collected, specimens (as Vireolanius) should be compared as soon as recalcitrant governments permit.

One must remember that in Dickey and van Rossem’s time all birds were treated separately. Of the Red-tailed Hawk (Buteo jamaicensis) we now read that they “considered the species as ‘by no means common’”; actually they so considered the resident subspecies, and did not treat the rest for lack of (racingly identifiable) specimens. Camptostoma imberbe is also confused: they reported Southern Beardless Flycatchers as not at all common except in one “thinly foliaged, low, deciduous forest,” particularly in “sparse scrub along the lagoon”—about the opposite of Thurber et al.’s “Northern Beardless Tyrannulet”: “humid forests...favor these birds.”

Generally, however, the literature is well covered. Few pertinent references are omitted (such as Browning, Amer. Birds 28:867, 1974, on winter Swainson’s Hawks [Buteo swainsoni] from U.S.). Coverage of El Salvador is less complete, as they note (cf. Sierra del Balsamo). The various typographical errors are not confusing.

More hazardous is their “Blue-throated Hummingbird, Hylocharis eliciae.” Dickey and van Rossem discussed eliciae as Elica’s Golden-tailed Hummingbird, well knowing that “Blue-throated Hummingbirds” were (and are) the more northern Lampornis clemenciae. This confusing nomenclature is due to Eisenmann’s wholesale name-changing, but has roots
in the varying generic views of Ridgway, Cory, and van Rossem. Eisenmann (1955, Trans. Linnaean Soc. N.Y. 7:47-48) followed van Rossem in uniting all in *Hyllocharis*, but followed Cory, in part, on English names, claiming (p. 2) to respect “well-settled usage.” He also claimed his new inventions for “truly neotropical birds” were appropriate to the entire species and useful to the amateur (p. 2). This reasonable introduction preceded an irresponsible assault on established patronymics and, often, geographic names, producing such absurdities and upsetting changes as “Bay-winged Hawk,” “Dark-breasted” and “Dusky-backed” swifts, “Pale-throated Flycatcher,” “Slender-billed Wren,” “Black-headed Oriole,” etc., etc. (Various other well-known names of U.S. birds fare no better, parts of U.S. being evidently “neotropical.”)

In *Hyllocharis*, Eisenmann proposed “Blue-throated Goldentail” for *eliciae*, but called the other three species hummingbird (2) and Sapphire. Thurber et al. recognize the absurdity of three entirely different names for the species of one tiny genus, but fail to revert to van Rossem’s name. Compromises between A.O.U. (Eisenmann) English names and logic can be more disastrous than simply rejecting A.O.U. names. Thurber et al. thus show, unintentionally, the importance of scientific names.

Scientific data were understood to be verifiable formerly, but not now. The many banding recoveries must be viewed with caution, as Thurber et al. say (p. 125). Even if the recovery data are correct, no specimens validate the identity of strays (such as a supposed Chipping Sparrow, *Spizella passerina*, from Alberta). Still less likely are some of the many sight reports. What is the “probability” of a brief tour’s really seeing four accipitrids seldom to never seen by resident ornithologists, an otherwise unreported vulture, *Cathartes* (which Thurber et al. properly class as hypothetical), a Sabine’s Gull (*Xema sabini*) (in February), etc.? Note, too, B. Monroe, Jr.’s, simultaneous males of Blue- and Golden-winged warbler, “*Vermivora* _pinus_ and _chrysoptera_,” both unknown in or near El Salvador on the Pacific slope, and Fish and Wildlife biologists’ innumerable Green-winged Teal (*Anas crecca*) seen from a plane (“some 40,000” in South America).

The authors themselves have no such flights of fancy, but do report a White-throated Spadebill (*Platyrinchus mystaceus*) “high in a tree” where unknown otherwise, plus two White-throated Flycatchers (*Empidonax albigularis*) netted but not preserved in the lowlands in August—exactly when van Rossem found the very similar *E. traillii brewsteri* “extremely common.”

Yet Thurber et al. question van Rossem’s identifications of the far easier _Dendroica_ warblers. Though van Rossem’s “vivid” is exaggerated, a “yellow breast and dark cheek patch” do indeed distinguish _D. townsendi_ from _virens_, the Black-throated Green Warbler, and are “very noticeable in life.” He was not “obviously describing adult male Townsend’s Warblers,” whose cheeks are black; 11 specimens of _virens_ (and 7 _townsendi_) support his statements. Were Thurber et al. in the wrong places, did they overlook _virens_ in the trees, or has its status indeed changed? (Were there earlier “southward displacements” in the 1920s?)

Still, this fine book is important in and beyond northern Central America. Strengthening its weaknesses, it could serve as a model to bring other regional avifaunas up to date. It clearly shows some of the obstacles to preservation of our planet, e.g., the mangroves (p. 164) and the area willed for safe-keeping to the government, which immediately ruined it (p. 119; Fig. 33); see also p. 122.

Expect no help from governments. These intervene primarily for “development”—in plain English destruction, desolation, and of course quick dollars and fat bribes behind the scenes. (For a recent example see International Wildlife Magazine 18, #6, Nov.-Dec. 1988, on Brazil.)

Americans should point no finger. U.S. governments are as bad or worse. They pretend
to ban the ruinous biocides that play such stalwart roles in the war on the planet’s ecosystems. But in fact they foster their manufacture and export to all possible buyers. Business is business and supports politicians (of both U.S. “parties”) and their campaign funds. Are we not responsible for our sad series of recalcitrant (and worse) governments? Maybe the finger should be pointed at US! — ALLAN R. PHILLIPS.

Hawks and Owls of the World: A Distribution and Taxonomic List. By Dean Amadon and John Bull, with the genus Otus by Joe T. Marshall and Ben F. King. Proceedings of the Western Foundation of Vertebrate Zoology, Los Angeles, California. 1988:Vol. 3, No. 4, pp. 295–357, 2 color plates. $10.00.—In this volume Amadon and Bull compile a list of all 292 species of living or recently extinct falconiforms and 162 species of Strigiforms. For each species they provide a suggested common name, scientific name, a brief description of the geographic range and typical habitat in which it is found, and any unusual or supplementary information regarding its taxonomic classification.

The taxonomic treatment of these raptor species and genera closely follows that presented by Streseman and Amadon (1979, Checklist of Birds of the World, 2nd ed. Vol. I:271–425). In the Falconiformes, the four suborders presented are the Cathartae, Sagittarii, Accipitres, and Falcons. The Strigiformes are organized into two subfamilies, the Tytoninae and Striginae.

This volume does not attempt to list subspecies, even though many species, such as the Peregrine Falcon (Falco peregrinus), are distributed widely and numerous subspecies are recognized. The authors do indicate, however, which taxa they recognize as species that formerly were considered subspecies and vice versa. In addition, they designate which closely related, allopatric species might be considered superspecies.

The range of geographical distribution for each species is indicated in descriptive, broad terms (e.g., North America, tropical America, Africa south of the Sahara). When ranges are restricted to parts of these areas, specific country or island names are given to describe species ranges. The habitat in which each species is found also is described in very broad, general terms (e.g., savannah, grasslands, seasonal forest).

One of the most important contributions of this compilation is its list of common names for all species of falconiforms and strigiforms. While disagreements will occur over some of the suggested name changes, the authors’ effort to make the vernacular names of these raptorial birds consistent and logical is much needed.

The authors also provide specific comments on various genera and the taxonomic relationships among the species contained within them. Alternative points of view are included and the literature discussing these points are cited. There is no attempt to ignore differences in taxonomic organization. To the contrary, the authors have tried to identify the issues that need more investigation.

Marshall and King contributed the section of the publication related to the genus Otus. Their taxonomic groupings are based on the literature and their experience with the species in the field, particularly tape recordings of their vocalizations. One major change is the grouping of several formerly monotypic genera recognized by many ornithologists (i.e., Gymnasio, Macabra, Ptilopsis, and Pyrrhoglaux) into the genus Otus. Those more familiar with the relationships among the Striginae will no doubt debate the merits of this suggested revision.

This compilation will not replace the specific works dealing with the biology and ecology of raptors in different parts of the world; however, it will help those struggling with the nomenclature and taxonomic relationships of these species.— MICHAEL W. COLLOPY.
Peregrine Falcon Populations: Their Management and Recovery. Tom J. Cade, James H. Enderson, Carl G. Thelander, and Clayton M. White (eds.). The Peregrine Fund, Flying Hawk Lane, Boise, Idaho. 1988:949 pp., color frontispiece, 68 photos, numerous maps, tables, graphs. $65.00.—The range of the Peregrine Falcon (Falco peregrinus) extends from the Arctic to Cape Horn and Tasmania—the greatest of any land bird. To be sure, its preference for tall cliffs excludes it from many areas. Yet locally it is adaptable, nesting in bogs in Finland, in hollow trees in Australia, and in old stick nests in trees in the Baltic countries.

In the late 1940s the populations of the peregrine and of various other avian predators crashed; at its worst in eastern North America, not a single pair of nesting peregrines remained south of the Arctic. In 1965 Joseph J. Hickey organized a conference on the peregrine; the results were published four years later. By that time Hickey and Derek Ratcliffe in England had proved that the disaster was the result of worldwide use of DDT, and to a lesser extent, other chemicals. Use of such poisons was eventually curtailed, but they are persistent and the recovery of the peregrine promised to be extremely slow.

At this juncture Tom Cade and a few others in America and Europe proposed to rear captive peregrines and eventually other species such as the Aplomado Falcon (F. femoralis) for restocking purposes. This was a daunting task but persistence and broad public support, through the Peregrine Fund, brought success. Several hundred young peregrines have been “hacked out,” and a fair percentage of them survive to nest in the wild. It was time for another international meeting to assess results and draw up plans for the future. This duly took place in Sacramento in 1985 and the considerably expanded proceedings, well-organized and ably edited, were published. The principal sections, with the number of papers (chapters) in each (in parentheses) are as follows: Keynote Addresses (3); Status of the Peregrine in North America (14); Status of Peregrine Populations since 1965—Europe (10); Status of the Peregrine in Other Parts of the World (8); DDT and Other Chemical Problems (12); Migration and Banding Studies (6); Captive Propagation, Reintroduction, and Management (12); Dynamics and Ecology of Peregrine Populations (13); Geographic Variation in Peregrine Populations (3); Humanity and the Peregrine (5); Summary and Conclusions.

Some peregrines nest on city skyscrapers and feed on the Rock Doves (Columba livia) and European Starlings (Sturnus vulgaris), which infest the streets below. Paradoxically, farther from civilization, habitat degradation may affect peregrines adversely. For example, on an island off Tunisia, peregrines are food-stressed, probably by a decline in European migrant songbirds. Not far away, in the Tunisian hinterland, Lanner Falcons (F. bimarcus), which have a wider prey base that includes lizards and mammals, are replacing peregrines.

As should be evident from the above list of contents, the present volume, in addition to the sections on propagation and management, contains much basic biology. This will be of interest to students of predation and to many others as well. The carefully captioned photographs contribute importantly. The peregrine, the world’s most spectacular avian predator, whether in the wild or in the hands of a falconer, has also become an important species in ornithological research.—D. Amadon.

Ecology and Conservation of Grassland Birds. Edited by Paul D. Goriup. International Council for Bird Preservation, 32 Cambridge Road, Girton, Cambridge CB3 0PJ, U.K. 1988:252 pp. £17.00.—This is the seventh in a series of technical publications by the ICBP which provide current treatments of major bird conservation issues. Grasslands are defined to include steppe, savanna, rangeland, prairie, and in some locales, desert scrub. At one time these communities covered over half the earth’s surface, but the climate that permits this biome to develop is also the climate that permits mankind to feed itself. Thus
grasslands have been eliminated or at least, have deteriorated under the impact of draining, cropping (cereal grains and tree plantations), mismanaged burning, grazing, and urbanization. Few grasslands remain close to the primeval state. The book, however, is mistitled. There is little on the ecology of grassland birds, and hardly anything but hopes regarding strategies for their conservation. Rather it is a status report on the extinction, extirpation, and decline of grassland birds across most of the world except eastern Europe and the U.S.S.R., as reported in 20 papers that were written in conjunction with the XIX World Conference of the ICBP. But the emphasis of this book is still nevertheless important. I suppose it should not be surprising that so little is known about the status of grassland birds; ornithologists like to work in more diverse communities. But determining population status is the initial step in conservation. Furthermore, to quote Beintema from his article on the Netherlands, "... degradation of the natural grasslands of the world, especially those in temperate regions, has taken place largely unnoticed." This book provides notice.

There is ecology in this book. Most of the papers describe the flora and illustrate the biogeography of grassland communities. The paper by Bock and Bock on the grassland birds of southeastern Arizona is an analysis of original data on the effects of fire, grazing, and exotic grasses on bird populations. Petretti's consideration of steppe habitats in Italy offers quantitative data on bird populations in Sardinia and Apulia. Most of the papers, however, are qualitative assessments of the populations of grassland birds and the impacts that affect them. Goriup's treatment of Western Europe, North Africa, and the Middle East provides an excellent synthesis of the various impacts of agriculture that modify grassland communities. The lack of any quantitative data, however, makes conclusions such as Wilson's in the paper on the sahel of central Mali that "impoverishment of the savannah environment ... does not yet appear to have resulted in a major direct negative effect on bird populations" suspect, and probably dangerous.

Little discussion concerns conservation except to stress better land management and the development of preserves of sufficient size to maintain entire grassland ecosystems. Most authors, however, provide no specific suggestions as to how these goals might be accomplished. In fact, no author even suggests that such goals are unrealistic in light of the demographic crisis in the world today. Willis and Oniki (Sao Paulo State, Brazil) do suggest two economic strategies that could lead to habitat preservation but acknowledge the political difficulty in their implementation. While many authors, but surprisingly not all, relate the loss of grassland habitat to the increase in human population, not one suggests that the long-term conservation of grassland birds is utterly and completely dependent upon control of human population growth. What this book sorely needed was a chapter by a Garrett Hardin or a Paul Ehrlich to emphasize that the bottom line for grassland bird conservation is cessation of the exponential growth of the human population.—JOHN L. ZIMMERMAN.

The present book describes the study area, the morphology of the thirty species studied, the niche dimensions of these birds, and aspects of community (peuplement in French) organization, spatial use, visual and acoustic communication systems, and breeding biology. The data were gathered by Erard during eight lengthy field trips to Gabon, yearly between 1972 and 1977, and again in 1981 and 1985, for a total of over 5000 hours of observation, covering (collectively) the entire annual cycle. No less impressive than the long-term nature of the research is the depth of analysis, since the behavior of the flycatchers in the two study areas was mapped on a grid system. Many birds were caught, marked, and individually followed for long periods of time. The raison d'etre of this extraordinarily detailed study is to examine critically several postulates of modern eco-evolutionary theory, including especially the possibility that interspecific competition imposes pressures and places constraints on the characteristics of species sharing similar resources (guilds), such that their morphology, behavior, and niche structure permits greater packing of species in tropical than in temperate regions. "Clearly, the flycatcher community constitutes an original array of species that are sufficiently numerous and diversified, so that its study should permit one a better understanding of the mechanisms of interspecific coexistence, if indeed these species exhibit interactions among themselves. Do species really partition environmental resources, and if so, how? What variables can help one to explain the remarkable diversity of food searching behaviors? What kinds of relationships tie together resemblances in food foraging behavior with habitat variables or morphological characters? How can the niche of each species be described? Can the community be considered to be really structured, with species arranged according to limits imposed by competition, or are we dealing simply with an assemblage of species that overlap because their niche is as Grinnell envisioned it?" (p. 18).

Erard does answer all these questions but, as one would have expected after such a painstaking field study and an equally exhaustive analysis of several factors, no single or simple answer emerges. Whereas clear-cut correlations exist, exceptions are frequent, and the reader reaches the inescapable conclusion that the eventual (tangible) result of "natural selection" is a compromise between opposite selection forces. I urge all ecologists and evolutionists interested in continental adaptive radiations, especially in wet tropical lowland areas, to read this book. Even though Erard's writing is very clear, the book is slow-reading, in part because it contains so much information, and in spite of the fact that the author is able to present his results in such a way that the reader can form his or her own conclusions, yet never forget what Erard himself believes. I look forward to volume two of this important monograph. Erard should be congratulated for a superb job, and he should be urged to write, perhaps after the publication of volume two, an English-language monograph that would be accessible to the broadest possible audience. I hope also that Erard will undertake a comparative analysis of the "flycatcher guild" in the Old and New Worlds, now that he has spent some time in lowland South American forests.—FRANÇOIS VUILLEUMIER.

A NATURALIST AMID TROPICAL SPLENDOR. By Alexander F. Skutch, illus. by Dana Gardner. Univ. Iowa Press, Iowa City. 1987:232 + viii pp., numerous half-tone drawings. $22.50.—This is actually two books within one cover. The even-numbered chapters are on the natural history of the tropics, primarily in Costa Rica. Whether discussing the breeding biology of the Gray Silky-Flycatcher (Ptilogonus cinereus) (Chapter 16) or the inflorescences of the hairy birthwort (Chapter 8), Skutch demonstrates in these chapters the meticulous attention to detail for which his earlier books are so well known, and which few other authors match. He describes in wonderful detail the courtship, building of the nest, timing of egg laying, and nestling care for about a dozen bird species (and lesser detail for about a dozen Euphonias
in Chapter 26). Anyone who has enjoyed Skutch's other books on natural history will also enjoy the even-numbered chapters of this book. They have the same comfortable, readable style and the same wealth of information that make his works a source of information for the educated layman as well as the experienced ornithologist.

The odd-numbered chapters are an exposition on Skutch's personal philosophy. Skutch's earlier works have often included references to emotions and attitudes, particularly those deemed most noble in humans and in birds. In this book, he has given free reign to his speculations about avian feelings, as well as his apparent belief that the world has been following some divine plan. For example, one recurring philosophical theme is that beauty and aesthetic sense are "... what the cosmos needed for its fulfillment ..." (p. 20). He suggests that beauty cannot exist without someone to appreciate it, yet appreciation requires an object on which to focus. This means that there must be a sort of coevolution of the two.

Another recurring theme is the principle of universal harmlessness. Chapter 11 is a discussion of the principle and its history in human culture. He points out the wastefulness of living high on the food chain and applies this to other aspects of life, such as choice of clothing and building materials which minimize man's impact on the planet. The theme is also found in Chapter 13, an attack on those who harm animals to learn about them, instead of the more difficult but (he maintains) equally rewarding patient observation of nature in situ, and in Chapter 7, a discussion on the importance of preserving pieces of nature (excluding predators, which are not in "peaceful coexistence with their neighbors") in order for us to learn to be closer to it.

Most of the plants and animals discussed by Skutch are illustrated in full-page paintings. Readers familiar with Dana Gardner's illustrations from other Skutch books such as "Life of the Woodpecker" will recognize the same sensitivity and beauty in "A Naturalist Amid Tropical Splendor," although the pictures are half-tone instead of full color.

It is somewhat of a shame that Skutch did not put the two sets of chapters into two separate books. There will be many who would wish to read one of these without the other. Those who wish to read the metaphysical musings of a naturalist are buying a book on biology as well, and those who wish to read about the lives of plants and animals of the tropics are buying also a book on philosophy. This reviewer appreciates the fact that the two subjects were at least segregated to separate chapters. One can choose, then, to read natural history or philosophy, depending on mood, without the possibly unpleasant intrusion of the other. —Robin K. Panza.

Birds on the Move. A Guide to New England's Avian Invaders. By Neal Clark, illustrated by Lucia deLeiris. North Country Press, Unity, Maine. 1988:196 pp., 27 black-and-white illus., 27 range maps. $8.95.—A clear case of a little knowledge being a dangerous thing, "Birds on the Move" is an "anecdotal guide to 27 species of birds that have increased their numbers and/or expanded their ranges in New England." Each account has an introduction, field guidelines, population and range, and journal notes—all served up in a potpourri of fact and anecdote. The writing is folksy, but one pitfall of the genre is that it often doesn't stand up to close scrutiny for accuracy. Examples abound but consider for example: Glossy Ibis, p. 42—"The ibis is a bird of fresh and saltwater marshes, swamps, flooded fields, and tranquil coastal bays. There it hunts crayfish, fiddler crabs, insects, and snakes—usually the poisonous water moccasin which takes scores of ibis eggs. The moccasin, or cottonmouth, ranges north to Virginia only; it's no wonder that ibises have fared so well in New England." Ornithologists will find it easy to restrain themselves, but country gardeners will love it.—James Baird.
BRIEFLY NOTED

The Great Cypress Swamps. By John V. Dennis. Photographs by Steve Maslowski. Louisiana State Univ. Press, Baton Rouge, Louisiana. 1988:xiv + 142 pp., 100 colored photos and many black-and-white maps. $29.95.—As defined in this work, the cypress swamps extend along the Atlantic and Gulf coasts from Pocomoke Swamp, Maryland, to the Big Thicket, Texas, with an extension up the Mississippi Valley to Reelfoot Lake. John Dennis, who was raised in this region, has given us an informative “coffee table” book on the biology of these areas. He writes with an obvious love and deep understanding of the area. The first seven chapters introduce us to the cypress forest and describe the plant and animal life. There follows a chapter on each of the individual swamp areas. A chapter on Vanishing Species outlines the stories of the Carolina Parakeet (Conuropsis carolinensis), Bachman’s Warbler (Vermivora bachmanii), and the Ivory-billed Woodpecker (Campephilus principalis). Dennis describes his long personal search for the latter.

The photographs taken by Steve Maslowski are fabulous, both from the photographic standpoint and on the basis of their reproduction. Steve has shown himself to be a worthy “chip off the old block.”—G.A.H.

Tracks and Signs of the Birds of Britain and Europe. By Roy Brown, John Ferguson, Michael Lawrence, and David Lees. Christopher Helm, London (available from International Specialized Book Services, 602 N.E. Hassalo St., Portland, Oregon 97213-3640). 1988:232 pp., 45 colored plates, many black-and-white sketches. $32.95.—This attractive publication will be of minimal use to North Americans, but approximately 100 species occurring in North America are included. Well-illustrated chapters illustrate Tracks and Trails, Nests and Roosts, Feeding and Behavioral Signs, Pellets, Droppings, Feathers, and Skulls. Of these by far the most useful and complete is the chapter on feathers which features good illustrations, a chart indicating the molt period, and measurements for all remiges and rectrices. The usefulness of the other chapters varies. Directions are given for preserving specimens or making casts of tracks.—G.A.H.

Obsolete English Names of North American Birds and Their Modern Equivalent. By Richard C. Banks. U.S. Fish and Wildlife Service, Resource Publication 174, Washington, D.C. 1988:37 pp. Gratis (from Publications Unit, U.S.F.W.S., Room 148, Matonic Building, Washington, D.C. 20240).—In recent years the English names of birds have been as unsettled as are the scientific names. Over 40 years ago Ludlow Griscom remarked that eventually we would need a synonymy for English names, and now we have one. Dr. Banks has gathered together names from the North American literature dating back to the times of Wilson and Audubon. Of particular interest are the English names for subspecies abandoned in the 5th edition of the A.O.U. Check-list (1957) but are prevalent particularly in the literature on birds of western North America. This will be a useful reference for beginning students as they start their careers.—G.A.H.

Status of the Marbled Murrelet in North America, with Special Emphasis on Populations in California, Oregon, and Washington. By David B. Marshall. U.S. Fish and Wildlife Service Biological Report 88(30). 1988:v + 19 pp. Gratis (from Publications Unit, U.S.F.W.S., Room 148, Matonic Building, Washington, D.C. 20240).—The Marbled Murrelet (Brachyramphus marmoratus) is considered by the I.C.B.P. to be a “near-threatened” species because of the destruction of its nesting habitat, the old growth coastal forest of the Pacific Coast. Large numbers are also killed in salmon-fishing nets. By summarizing the life history information currently available this report does much to lift the veil of mystery that surrounded the species until the 1970s when the tree-nesting habit was con-
firmed. While populations are still good, although declining, in Alaska and British Columbia, the nesting population in Washington is estimated to be between 1900 and 3500 pairs, in Oregon 2400 pairs, and California less than 1000 pairs. Suggestions for further research and management are given.—G.A.H.
PROCEEDINGS OF THE SEVENTIETH ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Seventieth Annual Meeting of the Wilson Ornithological Society was held Thursday, 25 May to Sunday, 28 May 1989, at Saint Mary’s College, Notre Dame, Indiana. The local committee chaired by Dr. Doris Watt was composed of Joan Apt, Joseph Bellina, Clarence Dineen, Julie Drey, Jeff Grams, Susan Kosek, Brett McLaughlin, Amy Moore, Marge Riemenschneider, Vic Riemenschneider, Arlene Snyder, David Snyder, Marti Wilson, and Jean Woods. The meeting was sponsored by Saint Mary’s College and co-hosted by the Department of Biology, Saint Mary’s College and the South Bend Audubon Society.

The Council met from 13:00 to 18:15 on Thursday, while registration for the 104 guests and members began in Le Mans Hall. On Thursday evening a delightful reception, provided by Saint Mary’s College, was held in conjunction with a wildlife art display in Haggard Center on the campus. The opening session on Friday was convened in the Science Hall where the Society was welcomed by Dr. William Hickey, President of the College. Dr. Mary H. Clench, President, responded for the Wilson Ornithological Society. The scientific papers sessions, which included contributed papers and a series of round-table discussions, were held on Friday and Saturday in the Science Hall.

Early morning field trips on the campus in the bottoms of the historic St. Joseph River and an evening trip for Upland Sandpipers were conducted by members of the South Bend Audubon Society. On Friday, an afternoon trip to the Fernwood Nature Center near Niles, Michigan and an evening walking tour of the Saint Mary’s campus provided additional opportunities to become acquainted with the area. On Sunday, there was an extended field trip to the dunes along Lake Michigan, bogs, Warren Woods, and other places of ornithological note in northwestern Indiana and southwestern Michigan.

The annual banquet was held in the dining hall on the campus Saturday evening, after which the following awards were presented:

EDWARDS PRIZE (for the best major article in volume 100 of The Wilson Bulletin)


LOUIS AGASSIZ FUERTES AWARD

Kevin J. Cash, “The adaptive significance of brood reduction in the Swainson’s Hawk.”

PAUL A. STEWART AWARDS

Toni L. DeSanto, “Physiological and ecological factors influencing prey selection in the White Ibis.”
Robin J. Densmore, “Comparison of aspects of reproductive success between beach and roof nesting Least Terns along the Mississippi Gulf Coast.”
Andrea Dinep, “Creching and the development of social behavior in White Ibis chicks.”
Stephen P. Flemming, “Do Red-winged Blackbird colonies and roosts function as information centers?”
Lawrence D. Igl, "Dickcissel site tenacity and mate fidelity in response to habitat alteration."

Andrew J. Neill, "The effect of territorial behavior on population density and distribution of the House Wren."

David R. C. Prescott, "Differential migration in the Evening Grosbeak: a test of hypotheses."

Lori A. Willimont, "Sexual dimorphism and foraging ecology of the Great Red-bellied Woodpecker, an island species, and the Red-bellied Woodpecker, a continental species, and reproductive ecology of Melanerpes superciliosus."

Hsiao-Wei Yuan, "Demography, dispersal, and population structure of Common Terns on Oneida Lake, New York."

ALEXANDER WILSON PRIZE (for best student paper)

Geoffrey E. Hill, Museum of Zoology, University of Michigan, Ann Arbor, MI, "Female mate preference for colorful males in the House Finch (Carpodacus mexicanus)."

Selection committees for these awards: Edwards Prize—Charles Blem, Clait Braun, Peter Hicklin, and Anne Wenner; Fuertes and Stewart Awards—Michael Armbuster, Jon Barlow, and Richard Stiehl; Wilson Prize—Jon Barlow, Charles Blem, and Nancy Mueller.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Clench at 08:50, Friday, 26 May, in the Science Hall. Secretary Zimmerman summarized the highlights of Thursday's Council meeting. Following the meeting next year with the Association of Field Ornithologists at Wheaton College, Norton, MA, 31 May–3 June 1990, the Society will meet with the Cooper Ornithological Society at the University of Oklahoma, Norman, OK, from 15–19 May 1991. Gary Schnell will be the local chairperson. The treasurer has reported that the Society is in excellent shape with income exceeding expenses by $1358. The proposed budget for next year totals $94,000. The present membership is 2280 and reflects no net change from the previous year. Charles Blem has been re-elected as editor. New business of note is the plan to develop travel awards for students giving papers at future meetings. Additionally, it was decided that all students giving papers eligible for the Wilson Prize competition will be the guests of the Society at the annual banquet. The Council also voted to budget $500 to the new book fund of the Van Tyne Library. Lastly, Zimmerman asked the membership to stand in honor of members who had died since the last annual meeting—Elting Arnold (Chevy Chase, MD), Oliver L. Austin, Jr. (Gainesville, FL), Lillian R. Birkenstein (Allende, GTO, Mexico), James Bond (Philadelphia, PA), Donald J. Borror (Columbus, OH), Elizabeth B. Clarkson (Charlotte, NC), Edward J. Danforth (Orono, ME), Alfred E. Eynon (Verona, NJ), William R. Fish (Boise, ID), Francois Havenschmidt (Ommen, Netherlands), George N. Kent (Rumney, NH), Dorothy A. Mendinhal (Easton, MD), Osborne S. Mitchell (Victoria, BC, Canada), Ruth E. Uhland (San Marcos, CA), and Yoshimaro Yamashina (Konoyama, Abiko, Japan).

Secretary Zimmerman read the report of the nominating committee chaired by James D. Rising (with Abbot S. Gaunt and Scott K. Robinson); Jon C. Barlow, president; Richard C. Banks, first vice-president; Richard N. Conner, second vice-president; Robert D. Burns, treasure; John L. Zimmerman, secretary; Judy McIntyre and Doris Watt, three-year terms as councilors; Edward J. Burtt, two-year term as councilor; and Scott Lanyon, one-year term as councilor.

Robert D. Burns gave the treasurer's report.
REPORT OF THE TREASURER
1 January 1988 to 31 December 1988

GENERAL FUNDS

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The Wilson Bulletin

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Note: *Newsletter about $3,000.00

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<tr>
<td>1988 Earnings</td>
<td>$ 720.00</td>
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<tr>
<td>1987 Balance</td>
<td>$ 80.00</td>
</tr>
<tr>
<td>Award Funds Available</td>
<td>$ 800.00</td>
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<tr>
<td>Funds Disbursed for Awards</td>
<td>$ 600.00</td>
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<tr>
<td>1988 Cash Balance</td>
<td>$ 200.00</td>
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</table>

Alexander Wilson Prize

<table>
<thead>
<tr>
<th>Endowment Principal</th>
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<tbody>
<tr>
<td>Fund Available</td>
<td>$ 386.89</td>
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<tr>
<td>Funds Disbursed for Awards</td>
<td>$ 600.00</td>
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<td>1988 Cash Balance</td>
<td>(168.65)</td>
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Paul A. Stewart Awards

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>1988 Earnings</td>
<td>$ 1,655.22</td>
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<tr>
<td>Funds Disbursed for Awards</td>
<td>$ 1,800.00</td>
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<tr>
<td>1988 Balance</td>
<td>(144.38)</td>
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George Sutton Color Plate Fund

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<tbody>
<tr>
<td>Funds Available</td>
<td>$ 3,600.00</td>
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<tr>
<td>1988 Funds Available</td>
<td>$ 4,945.86</td>
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<tr>
<td>Funds Disbursed for Color Plates</td>
<td>$ 4,012.70</td>
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<tr>
<td>1988 Cash Balance</td>
<td>$ 945.86</td>
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Ernest P. Edwards Prize

<table>
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<th>Endowment Principal</th>
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<tr>
<td>Funds Available</td>
<td>$ 700.00</td>
</tr>
<tr>
<td>Funds Disbursed for Awards</td>
<td>$ 700.00</td>
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</table>
General Endowment Funds

Endowment Principal 1987 ........................................ $151,805.95
1988 Balance of General Endowment Principal .................. $151,786.00

TOTAL ENDOWMENT FUNDS

1987 Amount Invested (Carrying Value) ......................... $247,739.99
Market Value ................................................. $306,963.00
1988 Deposited to Endowment ................................ $2,402.50
Sale and Purchase of Securities .............................. $(2,382.51)
Endowment Principal as of 12-31-88 ....................... $247,720.00
Market Value as of 12-31-88 .............................. $320,236.00

Annual Meeting Reserve Funds

1987 Cash Balance .............................................. $ 9,000.36
1988 Meeting Expenses ....................................... $4,661.59
1988 Balance of Centennial Meeting Funds ................. $ 4,338.77

The Editor's report was presented by Charles R. Blem.

EDITOR'S REPORT—1988

In 1988, 172 manuscripts (60 major papers, 112 short communications) were submitted to The Wilson Bulletin office. This is a 2% decrease over the number of manuscripts submitted in 1987. Of these, 49% have been accepted, 46% have been rejected, 4% have been returned to authors for revision, and 1% remain under review. This amounts to an acceptance rate of approximately 60% for manuscripts submitted as major papers and 43% for manuscripts submitted as short communications. These figures are not precise because some papers submitted as major papers were accepted only after being shortened to short communication length. Manuscripts accepted for publication are usually published within 3–8 months of acceptance. Frontispiece articles may require a bit longer because there is only one such paper per issue. On the average, papers received in 1988 were returned to the author within about 68 days of receipt. Only three papers required more than 100 days for return and were all delayed by lack of referee response.

I am indebted to the Staff of Allen Press for their continued fine service. I am extremely grateful to Assistant Editors Leann Blem, Albert E. Conway, and Anne Wenner; the Editorial Board including Kathy G. Beal, R. N. Conner, C. H. Stinson, and J. R. Walters; Review Editor George A. Hall; Color Plate Editor William A. Lun; Index Editor Kathy G. Beal; numerous members of the WOS, particularly R. Banks, R. Burns, C. Braun, M. Clench, S. Gaunt, J. Barlow, J. Jackson, and the more than 280 volunteer referees who so kindly reviewed manuscripts over the past year. I am also indebted to J. E. Jeffrey, Chairman of the Department of Biology, Virginia Commonwealth University and Dean Elske Smith for support of my efforts and the editorial office. Karen Blem deserves special acknowledgment for keeping all of the paperwork in order and for running the editorial office.

We remain committed to improving the quality of the journal, to attracting a wider

1 This amount was not credited to the Mellon Bank Endowment Funds until January, 1989.
2 This amount reflects $20.00 in costs and the amount of endowment not yet credited. During the first Quarter of 1989 the $2,402.50 plus $707.52 from sales and maturities was credited. The value of the endowment funds as of March 31, 1989, was $250,496.00.
readership, and to continuing to retain the qualities that make The Wilson Bulletin a distinctive scientific publication. It is our intention to treat every author fairly, handle each manuscript promptly and carefully, and to do everything we can do to encourage submission of manuscripts. Any suggestions for improving the process would be sincerely considered.

President Clench then called for a motion to accept the change in the By-laws as previously published (1988. Wilson Bull. 100:711). It was so moved by Peter Stettenheim and seconded by D. Scott Wood. The amendment to the By-laws was passed by the membership.

Jerome Jackson moved and Helmut Mueller seconded that the meeting be adjourned.

SECOND BUSINESS MEETING

President Clench opened the second business meeting at 13:15, Saturday, 27 May in the Science Hall. The report of the Auditing Committee was received.

We, the undersigned, met on 26 May 1989 to review the financial records presented by the treasurer for the period 1 January 1988 to 31 December 1988. Upon checking these records, consisting of bank statements, cancelled checks, OSNA payments, etc., we are satisfied that they accurately reflect the financial operations of the Society. We believe the balances shown for the General, Designated, and Endowment Funds are accurately stated.

The Auditing Committee commends Dr. Burns for his continuing diligent performance in fulfilling the duties of treasurer for 1988.

Hubert P. Zernickow, Chairperson
Nancy R. Klamm
William A. Klamm

It was moved by Peter Stettenheim and seconded by Clait Braun to accept this report, and the motion passed.

President Clench recalled the report of the nominating committee to the floor of the assembly, and Richard Stiehl moved that the report be accepted. This was seconded by John Kricher, and the motion passed. Additional nominations from the floor were requested, but none being offered, George Hall moved and Hubert Zernickow seconded that the nominations be closed. This motion also passed. John Kricher then moved with a second from Zernickow that a unanimous ballot be cast. The motion passed, and a unanimous ballot was duly recorded by the secretary.

Richard Conner, chair (with William Eddleman, Peter Hicklin, and Keith Bildstein) presented the report of the resolutions committee.

REPORT OF THE RESOLUTIONS COMMITTEE

WHEREAS, historical emphasis on wildlife management has been placed on game species, and

WHEREAS, national funding for management of game species is already established through Pitman-Robertson Tax funds, and

WHEREAS, most species of wildlife are not game species, yet need research and favorable management because of habitat alteration by humans,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society strongly encourages the Congress of the United States to provide appropriate funds to finance the Nongame Wildlife Act.

Motion to accept this resolution was made by Robert Burns, seconded by E. H. Burtt, and passed by the Society.

WHEREAS, the recent crude oil spill in the Prince William Sound has devastated the
marine, littoral, and benthic environment of that area to include numerous seabirds and mammals, and

WHEREAS, EXXON and Alyeska Corporation apparently did not have an appropriate emergency clean-up action plan developed prior to this major oil spill, and

WHEREAS, a timely and appropriate response to this oil spill was not accomplished.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society deplores the lethargic clean-up efforts and condemns EXXON and Alyeska Corporation for their lack of an environmental conscience.

A motion to accept this resolution was made by John Kricher, seconded by Richard Banks, and subsequently passed.

WHEREAS, the President of the United States, George Bush, has stated a policy of "No Net Loss of Wetlands," and

WHEREAS, wetlands are a major and valuable habitat for numerous species of wildlife, to include waterfowl, shorebirds, and wading birds,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society strongly encourages President Bush to translate his stated policy into the form of an Executive Order that is binding on all Federal agencies.

A motion to accept this resolution was made by Richard Stiehl and seconded by Tom Bancroft. The motion passed.

WHEREAS, most of approximately 80 species of shorebirds are international migrants that travel some of the length of the western hemisphere, and

WHEREAS, these shorebirds depend upon suitable habitat that is adequately spaced along a chain of breeding, stopover, and wintering sites, and

WHEREAS, many of these needed habitats are wetlands and grasslands often exploited for economic benefit, and

WHEREAS, recent studies have indicated alarming declines in shorebird populations, and

WHEREAS, actions necessary to preserve critical habitat needed by migrating shorebirds are of international scope.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society applauds and supports the major international conservation initiative for shorebirds of the Western Hemisphere Shorebird Reserve Network.

Edward H. Burtt moved to accept this resolution, it was seconded by Herbert T. Hendrickson, and passed by the Society.

WHEREAS, recent information indicates that most populations of Red-cockaded Woodpeckers (Picoides borealis) are declining, and

WHEREAS, this woodpecker has been federally listed as an endangered species for more than 18 years, and

WHEREAS, current laws and management have not been effective in either stabilizing or recovering this species.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society strongly urges the U.S. Fish and Wildlife Service to reestablish a recovery team for the Red-cockaded Woodpecker to oversee and evaluate the effectiveness of existing management of this species' habitat on federal, state and private lands.

A motion to accept this resolution was made by Richard Banks, seconded by George Hall, and passed by the Society.

WHEREAS, Richard C. Banks has worked diligently to assure the timely publication of the Ornithological Newsletter, and

WHEREAS, this publication is an excellent and increasingly indispensable newsletter within the ornithological community,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commends
Dick Banks and extends its deepest appreciation and thanks to him for this dedicated contribution to ornithology.

In response to a motion to accept by George Hall, which was seconded by D. Scott Wood, the membership passed said motion with loud acclaim.

WHEREAS, Dr. William G. George served the Wilson Ornithological Society for many years as the Society's official representative in its state of incorporation, Illinois, and
WHEREAS, ill health has now required him to resign from this responsibility, and
WHEREAS, his friends and colleagues in the Society have missed his stimulating companionship at recent annual meetings.

THEREFORE BE IT RESOLVED that the members of the Wilson Ornithological Society, gathered together at Saint Mary's College in Notre Dame, Indiana, send their warm greetings to Bill, with hopes for a successful recovery and appreciation for years of friendship and important contributions to ornithology.

Peter Stettenheim moved. Richard Brewer seconded, to accept this resolution, and it was passed by the Society.

WHEREAS, the annual meeting for 1989 was graciously sponsored by Saint Mary's College, and co-hosted by the Department of Biology, Saint Mary's College, and the South Bend Audubon Society, and
WHEREAS, the excellent facilities and beautiful campus of Saint Mary's College enhanced the friendly atmosphere of the meeting, and
WHEREAS, the chair of the Scientific Program Committee arranged a series of interesting and informative papers, and a stimulating program of roundtable discussions, and
WHEREAS, the superb organization and enjoyable social events provided by the Committee on Local Arrangements contributed greatly to the smooth operation and congeniality of the meeting,

BE IT RESOLVED that the members of the Wilson Ornithological Society express their appreciation to the Committees on Local Arrangements and on Scientific Program, to the sponsor and co-hosts of the meeting, and especially to Doris Watt and Dick Banks, who all contributed greatly to a most enjoyable meeting.

A motion to accept with sincere acclamation was made by Peter Stettenheim, seconded by Richard Stiehl, and indeed acclaimed with loud applause for a job well done.

John Kricher officially invited the Society to the seventy-first meeting at Norton, MA, 31 May to 3 June 1990, in joint session with the Association of Field Ornithologists.

Helmut Mueller moved and Richard Banks seconded to adjourn the meeting, and it was.

The only written report from standing committees was provided by the library committee, which is as follows:

REPORT OF JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE—1988

The library's operations have gone forward about as usual during the year, with perhaps a slump in certain of the figures. Janet Hinshaw has been as busy as ever, keeping our affairs running, while already overworked with her regular Bird Division duties.

To continue an upward trend requires constant support of the membership at large: more donations, more use of the facilities, and more indirect help through purchase of our surplus items.

During 1988, 39 members and institutions borrowed 281 books, xerox copies, and journal issues, in a total of 77 separate transactions. This is very close to last year's level of use.

Thirty members donated a total of 852 items to the library: 33 books, 192 journal issues, 49 monographs and reports, 576 reprints, and 2 dissertations. More of these figures are low than high, as compared with last year. The donors were R. Bayer, A. J. Berger, J. Cross, W.

Twenty new books and tapes, and a dissertation were purchased from the New Book Fund for $420.44. Since only $103.70 was realized from sale (4 books and 8 journals) the fund is becoming depleted. We are asking for some more Society subsidy, at least temporarily.

Received by various means were 215 current serial publications and reprints, from a total of 161 institutions, organizations, and members: 160 were through exchange, 45 as gifts, and 10 by subscription.

Our thanks go out, once more, for all the support we keep getting. We have no choice, however, but to keep encouraging more. Our holdings become more and more valuable with each passing year.

William A. Lunk, Chair

The Committee on Scientific Program, chaired by Richard Banks, was assisted by the following session moderators: Richard N. Conner, Charles R. Smith, Kerry N. Rabenold, Robert B. Payne, and Reed Bowman.

PAPERS SESSIONS


M. H. Clench, Dept. Internal Medicine, Univ. Texas Med. Branch, Galveston, TX, “Body pterylosis of the Old World oscines.”


J. S. Castrale, Indiana Div. Fish and Wildlife, Mitchell, IN, “Summer distribution and population trends of Tyrannids in Indiana.”


G. E. Hill, Mus. Zoology, Univ. Michigan, Ann Arbor, MI, “Female mate preference for colorful males in the House Finch (Carpodacus mexicanus).”

M. S. Woodrey, Dept. Zoology, Ohio State Univ., Columbus, OH, “Economics of caching versus immediate consumption in White-breasted Nuthatches: the effects of handling time.”


J. G. Granlund, Whitefish Point Bird Observatory, Kalamazoo, MI, “Spring migration of Common Loons (Gavia immer) at Whitefish Point Bird Observatory.”


P. P. Rabenold and K. N. Rabenold, Dept. Biol. Sci., Purdue Univ., W. Lafayette, IN, “Response to predators by cooperatively breeding wrens (Campylorhynchus nuchalis) is determined by group size.”


Round-table discussions:


Non-traditional uses of museum collections, D. S. Wood.

ATTENDANCE

CALIFORNIA: Riverside, Joe Galusha.
CONNECTICUT: Storrs, Alan Brush.
FLORIDA: Tavernier, Thomas G. Bancroft, Reed Bowman.
ILLINOIS: Brookfield, Dennis and Leslie DeCourcey; Chicago, Peter Lowther, Douglas Stotz, David Willard; Monmouth, Kenneth Petersen.
INDIANA: Bloomington, Daniel Cristol; Hanover, Mr. and Mrs. Dan Webster; Lakeville, Amy Moore; Mishawaka, Rebecca Parker; Mitchell, John Castrate; Notre Dame, Joseph J. Bellina, David Snyder, Doris Watt; South Bend, Mr. and Mrs. Victor Riemenschneider, Marti Wilson; West Lafayette, Walter Piper, Kerry N. and Patricia Parker Rabenold.
KANSAS: Manhattan, John L. Zimmerman.
KENTUCKY: Richmond, Gary Ritchison.
MARYLAND: Laurel, Deanna Dawson, John Sauer.
MASSACHUSETTS: Foxboro, William (Ted) Davis; Norton, John Kricher.
MICHIGAN: Ann Arbor, Robert Blair, Robert Cullbert, Geoff Hill, Janet Hinshaw, Bob and Laura Payne, Louise and Robert Storer, Jean Woods; East Lansing, Donald Beaver, Elizabeth Rogers; Grand Rapids, Steve Kitler; Kalamazoo, Raymond J. Adams, Jr., Richard Brewer, James Granlund, John Yunger; Pleasant Lake, Hubert Zernickow; Pontiac, Mr. and Mrs. Dan McGeen.
MISSISSIPPI: Mississippi State, Jerome A. Jackson.
NEW HAMPSHIRE: Lebanon, Peter Stettenheim.
NEW JERSEY: New Brunswick, Donald F. Caccamise, Maciek Luniak.
NEW YORK: Ithaca, Karen Allaben-Confer, Dan Coker, John Confer, Charles Smith.
NORTH CAROLINA: Chapel Hill, Helmut Mueller; Durham, Nancy Mueller; Greensboro, Herb Hendrickson; Raleigh, John Gerwin.
OHIO: Bowling Green, Thomas Carpenter; Cincinnati, Duncan S. Evered, Lyla R. Messik; Columbus, David Cimprich, Mark Woodrey; Delaware, Edward Burtt; Gambier, Robert Burns; Kent, Ralph W. Dexter; Lakewood, Nancy and William Klamm; Sandusky, Richard A. Dolbeer; Toledo, Chris Manzey, Mr. and Mrs. Harold Mayfield, Elliot Tramer.
OREGON: Ashland, John McCormick.
PENNSYLVANIA: Pittsburgh, D. Scott Wood; Scranton, Michael Carey; University Park, Richard Yahner.
TENNESSEE: Martin, David Pitts; Maryville, Ralph Zaenglein.
SOUTH CAROLINA: Rock Hill, Keith Bildstein.
TEXAS: Galveston, Mary Clench; Nacogdoches, Richard Conner.
VIRGINIA: Manasses, Roxie Laybourne; Richmond, Charles and Leann Blem; Williamsburg, Mitchell Byrd, Anne Wheelely.
WEST VIRGINIA: Morgantown, George Hall.
WISCONSIN: Fond du Lac, Ron Barrett; Menasha, Mike Mnoch.
ALBERTA: Edmonton, Rogier Gruys, Esther Schaeppi, Barbara Zwefel.
NEW BRUNSWICK: Sackville, Peter Hicklin.
ONTARIO: Guelph, Alex Middleton; Toronto, Jon Barlow, Jim Dick.
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BY KATHLEEN G. BEAL

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