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The following application has been received by the **International Commission on Zoological Nomenclature** and has been published in vol. 43, part 2, of the *Bulletin of Zoological Nomenclature* (9 July 1986). Comments or advice on it is welcomed and should be sent **c/o The British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.** Comments will be published in the *Bulletin.*

Case No. 1051 *Bubo* Dumeril, 1806 and *Surnia* Dumeril, 1806 (Aves): proposed confirmation on the Official List.

Visual Resources for Ornithology (VIREO) accession numbers for voucher photographs for Nichols et al. (Auk 103: 825–828) are V06-1-002 through V06-1-005.

EGG FORMATION IN CASSIN'S AUKLET

LEE B. ASTHEIMER[1]
Department of Avian Sciences, University of California, Davis, California 95616 USA

ABSTRACT.—Female Cassin's Auklets (*Ptychoramphus aleuticus*) were given oral doses of lipophilic and proteophilic dyes during their prelaying period. Yolk ring structure in freshly laid eggs was analyzed to determine the timing of yolk deposition using the dye-stained layer as a date marker within the yolk. Additional information from necropsies of five females killed at specific intervals during the formation of a replacement egg indicated that only a single follicle enlarges in the ovary during a reproductive event and this yolk requires about 8 days to complete rapid yolk deposition (RYD). Once RYD is completed, the egg is not laid for a period of 4.2 ± 1.0 days, an interval termed the lag period (Astheimer et al. 1979). Albumen synthesis appears to begin at, or just before, completion of the yolk and continues until approximately 1 day before oviposition. During this time, however, the yolk remains in the follicle. Replacement eggs are laid 14.5 ± 1.7 days following egg removal or natural loss. Combining the above information with egg composition data, the daily deposition of lipid and protein from the female into the egg was computed. Evidence from the size distribution of small (<5 mm) primordial follicles suggests that the auklet ovary undergoes a cycle of follicular growth and atresia before a single follicle is selected for RYD. Based on these findings, and the correlation between initiation of spring egg laying and decreased sea surface temperatures for Farallon Island auklets, I suggest that the onset of RYD is modulated by environmental conditions. *Received 26 August 1985, accepted 17 February 1986.*

THE process and timing of events leading to egg production are integral components of the reproductive cycle, but generally have been neglected in quantitative assessments of the energy costs of reproduction. Recent studies have focused on the temporal aspects of egg formation in seabirds and the consequent energetic cost to the female (Grau 1982, 1984; Grau and Astheimer 1982; Astheimer and Grau 1985; Astheimer 1985). Theoretically, the prelaying period is energetically more demanding for species that lay larger eggs relative to their body mass because females must direct a greater proportion of dietary or stored nutrients to the egg. In addition, for many colonial seabirds, intraspecific competition for nest sites or mates necessitates remaining close to the colony and may restrict foraging range and, indirectly, food availability during this period. The daily energy cost of egg production could be reduced by extending the period of egg formation; however, this must be weighed against the effects of carrying extra mass on locomotory costs.

Most avian biologists would agree that the timing of hatching relative to food availability is critical to nestling survival and thus constitutes a strong selective pressure. However, because periods of incubation and of egg formation are relatively fixed for a given species (Astheimer 1985, Astheimer and Grau 1985, Grau 1984), hatching dates are inextricably linked to the initiation of the clutch in the ovary (with the notable exception of a few Procellariiformes; Boersma and Wheelwright 1979). Although environmental factors are known to influence the timing of recrudescence, endocrine activity, and courtship behavior, it is the beginning of yolk deposition in follicles selected for growth (the follicular hierarchy) that marks the definitive initiation of the clutch and that, barring yolk resorption, will determine the hatching date. The relationship of this process of rapid yolk deposition (RYD) to environmental stimuli has not been investigated in nondomestic avian species.

In this paper I report on studies of egg formation in Cassin's Auklet (*Ptychoramphus aleuticus*) conducted on Southeast Farallon Island (SEFI), California between 1978 and 1982. Cassin's Auklets are small, nocturnal alcids that nest in burrows and rock crevices on islands

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[1] Present address: Department of Anatomy, University of Tasmania, Hobart, Tasmania 7001, Australia.

off the Pacific coast, from Buldir Island in the Aleutian Island chain, Alaska (52°N), to Guadalupe Island, Baja California, Mexico (26°N; Harrison 1983). The Farallon Islands (34°N), 43 km west of San Francisco, support an auklet breeding colony, estimated at 105,000 birds (Manuwal 1972), that is unusual in its apparent year-round residency in the waters surrounding these islands (Manuwal 1974b).

Although equipped with a pair of lateral incubation patches, Cassin's Auklets lay only a single-egg clutch (Manuwal 1974a). Double brooding commonly occurs in years when first broods are begun early in the season (Boekelheide 1980, Manuwal 1979). The auklets begin excavating burrows and engaging in preliminary courtship activity in early January, and the first eggs usually are laid in March (Manuwal 1979, pers. obs.). Laying synchrony is variable in the Farallon population; in some years laying extends over a 4-month period (Manuwal 1972, Boekelheide pers. comm.). The proximate stimuli that initiate a reproductive effort remain unclear, although there appears to be a highly significant correlation between the onset and synchrony of laying with a decrease in sea surface temperature, itself an indicator of oceanic productivity [Point Reyes Bird Observatory (PRBO) unpubl. data; see Discussion]. I attempted to relate egg laying and the timing of egg formation to sea surface temperatures for the years 1979–1982.

MATERIALS AND METHODS

Two hundred and seventy wooden nest boxes designed for auklets were installed on SEFI in the fall of 1977 (Ainley et al. 1981; nest-box design in Ainley et al. 1979). I had access to these boxes thereafter, and by 1979 most were occupied by mated pairs.

To study the time sequence of yolk deposition, I fed doses of lipophilic dye to prelaying females. This dye is incorporated into yolk lipoproteins, synthesized in the liver, and deposited on the developing follicle in a discrete layer (Gilbert 1971, Grau 1976). Because dye uptake and lipid deposition is rapid when a bird is forming a yolk, the dye effectively marks the date of dosing as a layer within the yolk structure.

In a preliminary study, 9 females were fed a nonrepeating sequence of different dye capsules (25 mg each) to ascertain whether yolk rings in auklet eggs exhibit a circadian periodicity in deposition, as they do in poultry (Riddle 1911, Grau 1976). In eggs from domestic chickens (*Gallus domesticus*) and Japanese Quail (*Coturnix c. japonica*), each pair of light- and dark-staining rings (as enhanced by treatment with potassium dichromate) is deposited over a 24-h period (Warren and Scott 1935, Opel 1966).

Combinations of the following four dyes were administered at 40-mg doses in 1979: lipophilic dyes Sudan Black B, Sudan IV (red), and Victoria Blue and proteophilic Rhodamine B (magenta). The latter binds to both yolk and albumen proteins and, although a pattern of albumen deposition is not retained in the laid egg, I anticipated that Rhodamine B would bind to albumen being synthesized in the magnum portion of the oviduct on the day the dye was administered. In 1981 only Sudan Black and Rhodamine were given; the dose of the former was doubled to 80 mg. Except for birds treated in the 1978 nonrepeating sequence experiment, no bird was treated more frequently than 5-day intervals.

Because Cassin's Auklets are monomorphic in plumage characteristics, gender recognition was difficult. Therefore, in 1978 and 1979, to ensure dosing the females, both members of pairs were given dye capsules. In 1981 and 1982 bill depth at the anterior border of the nares was measured to distinguish gender, following Nelson (1981), who determined bill-depth ranges for male and female auklets from salvaged carcasses. In 1981 only the smaller-billed member of a pair, presumed to be female, was dosed.

Dyes, contained in number 0 gelatin capsules, were administered orally. Birds were removed from their nest boxes at night, and moistened capsules were placed well down their throats, followed by sufficient water to induce swallowing. Treated individuals were marked on the breast with picric acid (1979) or banded with a number 3 U.S. Fish and Wildlife Service stainless steel band. Birds were normally returned to their nest boxes within 3–5 min of capture. Regurgitation of capsules sometimes occurred, and occasionally red- or blue-stained vegetation was found surrounding a box the day following dosing; eggs were not collected from these birds.

Transit time for passage of visible signs of dye in the excreta was 4–6 h for three birds retained overnight, with a large portion of the dose expelled in the first hour. Transit of the dye through the gut may have been accelerated in birds with empty stomachs, which may have resulted in poor dye absorption. To improve dye uptake in 1981, capsules contained a larger dose of dye and 30–40 mg of dried egg yolk.

All boxes (240 in 1979, 125 in 1981) were checked daily beginning in early March. Dosing was begun after the first egg in the colony was found, on the assumption that a large proportion of the females of pairs found in boxes at that time could be expected to lay within 2 weeks. All dosing was done at night, between 2100 and 0200. In 1979, 224 birds (100 pairs and 24 singles) were given dye, while in 1981 84 females were dosed. During 1981, females that did not lay within 2 weeks of dosing were given a second dye capsule. After dosing, boxes were checked daily for the presence of an egg and for parent identification (dyed breast or band number). When the parent was recognized as a dosed bird or its mate, the egg was removed, weighed, measured, and stored at 5°C. Seventy-two eggs were collected in 1979 and 65 in 1981.

In the laboratory eggs were placed under vacuum to remove air bubbles in the yolk and frozen at −20°C for 48 h. After fixation in 4% formalin at 65°C for 18 h, yolks were weighed and halved in the plane perpendicular to the chalazae. One half was immersed in 6% potassium dichromate at 65°C for 18 h to enhance the definition of light and dark rings. Central slices were cut from each half, ring pairs were counted on the dichromate-stained slices, and the position of the dye ring was determined. Using the dye ring as a marker for dose date, the dates of initiation and completion of RYD and the difference (number of days) between the completion of RYD and oviposition (i.e. the lag period) were determined.

During 1981, daily checks of nest boxes from which the first egg had been removed continued through July to determine the timing and frequency of replacement laying. All replacement eggs were measured, and the identity of both parents was verified. A second replacement egg (third egg) was laid by 14 females. The regularity of replacement laying permitted me to devise a schedule to kill a small number of females at selected intervals during formation of their replacement egg. Five females were killed between 11 and 15 days after their first egg had been removed to document the size and location of the yolk during the lag period. These auklets were weighed and killed quickly by cervical dislocation. Oviducts and ovaries were removed, photographed, and placed in 10% buffered formalin, with the exception of the enlarged follicles, which were treated as above and analyzed for yolk ring structure. Small ovarian follicles (0.5–4 mm), separated from the ovarian tissue, were counted and ranked according to their diameter. Pre- and postovulatory oviducal tissues were prepared for histological sections.

Egg composition was determined for 43 eggs, with albumen mass computed as the difference between fresh-egg contents and yolk mass. Fixed yolks were separated from adherent albumen with absorbent tissue and weighed to the nearest 0.01 g. Previous comparisons of frozen, fixed, and boiled domestic turkey (*Meleagris gallopavo*) egg components showed no significant differences in the yolk mass obtained by each method (Goldfarb unpubl. data). Albumen was washed from the shells with warm water, and shells, with membranes, were air dried at 60°C and weighed to 0.01 g. The caloric value of 4 auklet yolks was determined using a Parr Adiabatic Calorimeter with benzoic acid as a standard.

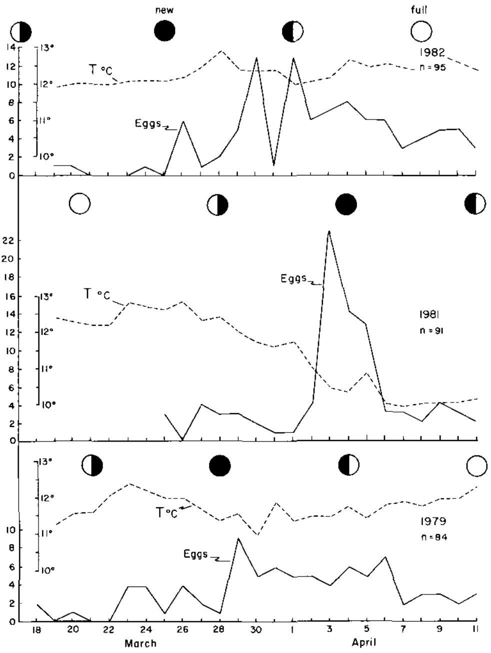

Fig. 1. The pattern of egg laying (solid line) in nest boxes on Southeast Farallon Island (SEFI) in 1979, 1981, and 1982. Inset scale, 10–13°C for sea surface temperatures (broken line) taken daily at SEFI (PRBO unpubl. data). Phases of the moon are indicated.

The daily increment in yolk mass was calculated for 9 eggs on the basis of total yolk mass and the sequential difference between increasing radii defined by the yolk rings (Astheimer and Grau 1985). This method assumes yolk deposition occurs on a spherical surface, although the yolk rings may become compressed or appear irregular following freezing, fixation, and slicing.

Statistical tests follow Zar (1974) and were performed using a statistical package (STATPAK, Northwest Analytical); sample means are reported ±1 SE.

RESULTS

Laying was initiated in nest boxes 1 week later in 1981 than in 1979 and 1982 (Fig. 1). The laying pattern of treated birds closely paralleled that of untreated birds that resided in undisturbed nest boxes and burrows checked less frequently (PRBO unpubl. data). The mean male bill depth of 10.83 ± 0.04 mm differed significantly from the female mean of 9.59 ± 0.05 mm in a paired Student's t-test of 99 breeding pairs ($t = 21.60$, $P < 0.001$). These results, from live

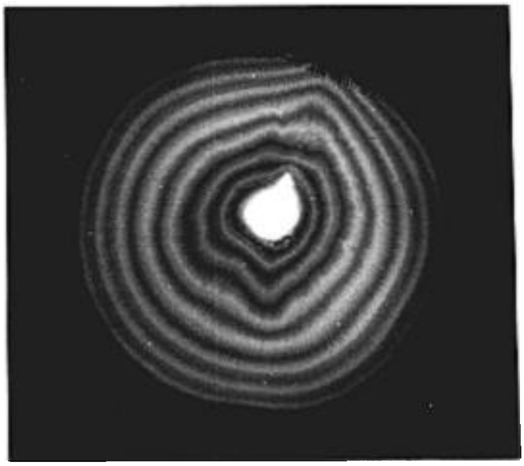

Fig. 2. A central section through the yolk of a Cassin's Auklet egg stained with potassium dichromate. Eight pairs of light- and dark-staining rings can be identified.

mating pairs, are consistent with those obtained by Nelson (1981) from salvaged carcasses.

The 1978 nonrepeating dye sequence experiment (Table 1) demonstrated that in the 4 eggs (of 9) that contained dye rings, each pair of light and dark yolk rings represented approximately 24 h of deposition in auklets, thus confirming the circadian periodicity of yolk deposition and agreeing with previous studies of domestic birds (Grau 1976) and Emus (*Dromaius novaehollandiae*; Hirsch and Grau 1981). The poor uptake of dye, resulting in faint dye rings, however, prompted an increase in dye dosage from 25 to 40 mg in 1979.

Fresh Cassin's Auklet yolks varied in color from yellow to red-orange, the latter indicative of deposition of dietary carotenoids, presumably from euphausiids, the dominant prey item during most breeding seasons (Manuwal 1972, pers. obs.). The central slices of yolk stained with potassium dichromate showed clear light- and dark-staining layers (Fig. 2). Analysis of 94 yolks revealed a mean of 8.1 pairs of yolk rings (range = 6–9; Table 2), which indicates that 7–9 days were required for the completion of RYD. The same length of time was necessary for formation of the yolks of replacement eggs (8.0 days; Table 2).

Most of the contents of dye capsules fed to auklets was excreted as a single bolus; appar-

TABLE 1. Yolk ring analysis from eggs of Cassin's Auklets fed a nonrepeating sequence of dyes.

Bird/ yolk no.	Dose sequence[a]										Yolk ring pattern[b]							
	April			May							Inner ring							Outer ring
	28	29	30	1	2	3	4	5	6	7								
1	B			R							0	0	B	0	0	R	0	0
2				R				B		B	0	0	0	0	B	0	B	0
3	B			R							0	B	0	0	R	0	0	0
4	B										B	0	0	0	0	0	0	0

[a] B = dose of 25 mg Sudan Black B, R = dose of 25 mg Sudan IV (red).

[b] B = black dye ring, R = red dye ring, 0 = no dye ring present.

ently only a small percentage of the dose was absorbed by plasma yolk lipids. Faint, but definite, dye rings were distinguished in 20 (27.8%) eggs collected in 1979 and 34 (52.0%) in 1981. This allowed determination of the lag period, which averaged 4.2 ± 0.19 days in 1981 (range = 2.5–6 days). In 1979 this period was somewhat longer and more variable (4.6 ± 0.49 days, range = 3–9 days).

The phenomenon of the lag period gives rise to questions concerning the events occurring during this period. By feeding female auklets the proteophilic dye Rhodamine B, I hoped to determine whether albumen was synthesized during a particular segment of the lag period, that is, between 1 and 5 days before the auklets laid. Of the eggs laid by birds dosed with Rhodamine during their lag period, 39% (25 of 64) had magenta-stained albumen. An additional 20.4% of the 1981 eggs laid by dosed females contained albumen stained a fluorescent chartreuse green. Assuming that the intensity of albumen pigmentation can be correlated with the amount of Rhodamine deposited in the albumen, and that Rhodamine deposition can be used as a qualitative estimate of albumen synthesis, it appears that the largest amount of albumen is synthesized in the early half of the lag period (Fig. 3). The occurrence of green albumen in eggs from birds dosed 3–9 days before laying (Fig. 3) may be due to deposition of a metabolic by-product of Rhodamine B, since samples of both wet and dry Rhodamine- and green-stained albumen fluoresce intensely under UV light (254 nm), while dried white albumen from eggs laid by untreated birds does not. The bright chartreuse pigment was unique to eggs from Rhodamine-treated birds and also occurred in similarly treated Adélie Penguin (*Pygoscelis adeliae*) eggs (Astheimer and Grau 1985).

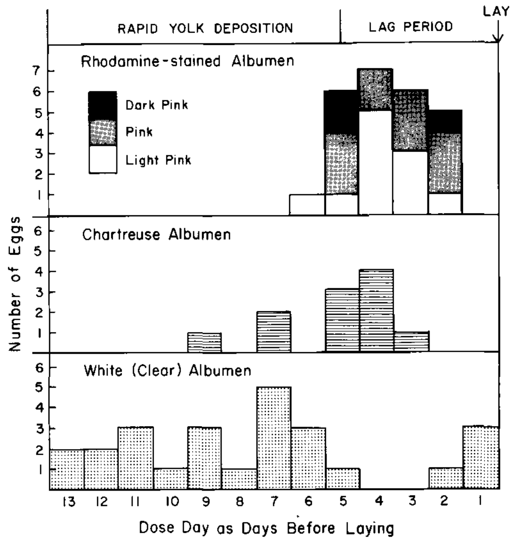

Fig. 3. The distribution of albumen color in eggs laid by birds treated with 25 mg of Rhodamine B 1–15 days before laying.

After removal of 86 eggs from banded auklets in 1981, 78 (90.7%) of these females laid a replacement egg, usually in the same or a nearby nest box with the same mate (Astheimer unpubl. data). The mean time between the removal of the first egg and laying of the replacement egg (i.e. the relaying interval) was 14.5 days (Table 3). In 6 instances, not included in the above mean, the elapsed time was 24–30 days, or approximately double the expected relaying interval; several of these cases involved nest-box switches or disturbances by researchers. The relaying interval corresponds well with the combined time required for RYD (8–9 days) and the observed lag period (4–6 days). The additional 1–4 days may be necessary for hormonal changes required to reinitiate the pro-

TABLE 2. Comparison of first and replacement eggs in Cassin's Auklets.

	First egg			Replacement egg				
	Mean	SE	*n*	Mean	SE	*n*	*t*-stat[a]	
Rapid yolk deposition (days)	8.12	0.06	94	8.01	0.26	6	0.463	NS
Relaying interval[b] (days)	14.45	0.21	70	15.77	0.31	14	2.386	*
Length (mm)	46.64	0.26	42	46.56	0.23	42	0.114	NS
Width (mm)	33.36	0.17	42	33.31	0.19	42	0.136	NS

[a] Paired *t*-tests between first and replacement egg data. * = $P < 0.05$, NS = not significant.

[b] First-egg relay interval is between 1st and 2nd eggs; replacement relay interval is between 2nd and 3rd eggs.

TABLE 3. Characteristics of egg formation in Cassin's Auklets.

	Bird identification							
	Birds killed for necropsy					Salvaged carcasses		
	A	B	C	D	E	F	G	H
Female mass (g)	209	203	196	—	245	—	—	—
Hematocrit (%)	49.3	49.0	49.4	41.7	41.4	—	—	—
Serum Ca (mg/dl)	21.4	30.0	16.8	11.0	—	—	—	—
Days between egg removal and death	11.5	12	14	15	15	—	—	—
Stage of egg formation[a]	OF	OF	OF	OF	SH	OF	POV	POV
No. of follicles in RYD	1	1	1	1	0	1	0	0
No. of yolk rings	7	7-8	8.5	8	8	—	—	—
Yolk mass (g)	6.52	7.98	8.62	7.75	10.18	—	—	—
Yolk diameter (mm)	22.8	23.5	24.0	22.8	24.5	19.0	—	—
Oviduct								
Length (mm)	—	234.9	270.5	292.0	—	182	37.6	78.0
Mass (g)	—	9.45	10.55	14.25	—	8.7	0.4	0.9
Magnum width (mm)	12.0	9.7	13.5	11.2	—	8.8	2.4	4.2
Follicular hierarchy (no. of follicles <4 mm)								
Size class								
>3 mm	0	0	0	0	1	1	1	0
3 mm	1	1	1	1	2	1	4	3
2-3 mm	10	3	7	7	1	5	5	6
1-2 mm	17	6	4	30	5	6	11	9
<1 mm	42	9	43	32	26	21	0	27

[a] OF = ovum in follicle, POV = postovulatory follicle, SH = shelled egg in uterus.

cess of egg formation (see Discussion). Surprisingly, removal of an egg at various times during the 37-42-day auklet incubation cycle does not significantly affect the relaying interval, although replacement time tends to be slightly shorter (14.8 ± 0.67 days, $n = 5$) when removal occurs in the last half of incubation than in the first half (15.8 ± 0.30 days, $n = 7$, excluding eggs removed within 1 day of laying). In 14 incidents where the replacement egg was removed, a second replacement was laid, with a somewhat longer relaying interval (Table 2). Paired measurements of length, width, and RYD periods of first and second eggs laid by the same female were compared and did not differ significantly (Table 2).

Results from necropsies of 5 females killed during the last third of their relaying interval and of 3 salvaged carcasses showed either one enlarged ovum contained in a follicle or one postovulatory follicle (Table 3). The timing of formation of the replacement egg relative to the day of removal of the first egg is presented in Fig. 4. These results indicate that the completed yolk remains in the follicle until its release, about 24 h before laying (Fig. 5). Note (Fig. 5) the completed yolk and the albumen-replete magnum of bird B (5A) and the shelled egg in the uterus and the albumen-depleted magnum of bird E (5B). Follicular retention of the ovum is substantiated by birds C and D (Table 3).

Based on the number of yolk rings present in the single enlarged ova of birds A-D, RYD was completed at the time of sacrifice, with the possible exception of bird A, whose yolk had only 7 pairs of yolk rings. The masses, however, are 0.4 g (4.5%) to 2.5 g (27%) less than the mean yolk mass of freshly laid eggs (Table 4). This discrepancy may be explained by the process of plumping, the influx of water into albumen just before shell deposition. During the passage of the egg through the oviduct, the yolk may also experience an increase in water content during plumping. Draper (1966) found that in chickens the water content of oviposited yolk was 8% greater than that of oviducal yolk ($n = 10$). It is also possible that in the smallest of these yolks (A and D) the last layer of yolk was not completed.

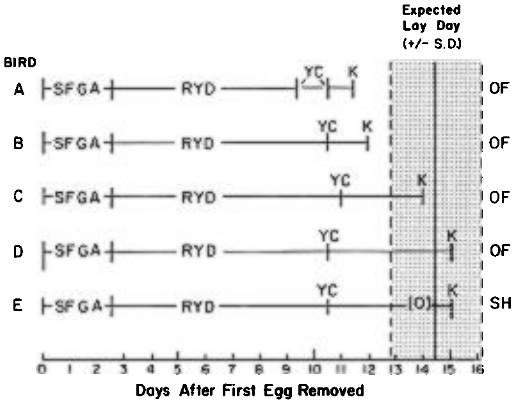

Fig. 4. The timing of egg formation for 5 auklets necropsied during the formation of a replacement egg, where the first egg was removed on day 0. SFGA = estimated period of small follicle growth and atresia cycle (length of this period estimated from that in chickens; see text), RYD = rapid yolk deposition, YC = yolk completion, K = bird killed, OF = enlarged ovum in follicle, SH = shelled egg in uterus, (O) = estimated day of ovulation. Note: 2.5 days are allowed after egg removal for the enlargement of the primordial follicles (see Discussion).

Composition of 43 eggs is presented in Table 4. The mean caloric value of auklet yolk was 7.35 ± 0.007 kcal/g dry weight ($n = 4$).

DISCUSSION

Yolk formation by Cassin's Auklets is a rapid process, particularly when compared with Procellariiformes of similar size. For example, the Fairy Prion (*Pachyptila turtur*) also lays a one-egg clutch, but requires twice as long as a Cassin's Auklet to form a yolk of comparable mass (16.7 days to produce a yolk of 9.09 g, $n = 22$; Fig. 6). When synthesis is expressed as average total yolk mass/mean total days of yolk deposition as a crude index for species comparison, however, yolk formation in Cassin's Auklets is somewhat slower than in other alcids for which data are available: Cassin's Auklet, 1.13 g/day; Common Murre (*Uria aalge*), 2.34 g/day; Tufted Puffin (*Fratercula cirrhata*), 3.13 g/day; Ancient Murrelet (*Synthliboramphus antiquus*), 1.94 g/day; and Pigeon Guillemot (*Cepphus columba*), 1.19 g/day (Grau et al. 1978, Roudybush et al. 1979, Grau and Astheimer 1982, Astheimer unpubl. data.). The latter two species, which exhibit relatively slow rates of deposition, both lay a two-egg clutch. This index ignores other important intraspecific differences such as female body mass, relative yolk mass, and the actual rate of yolk deposition.

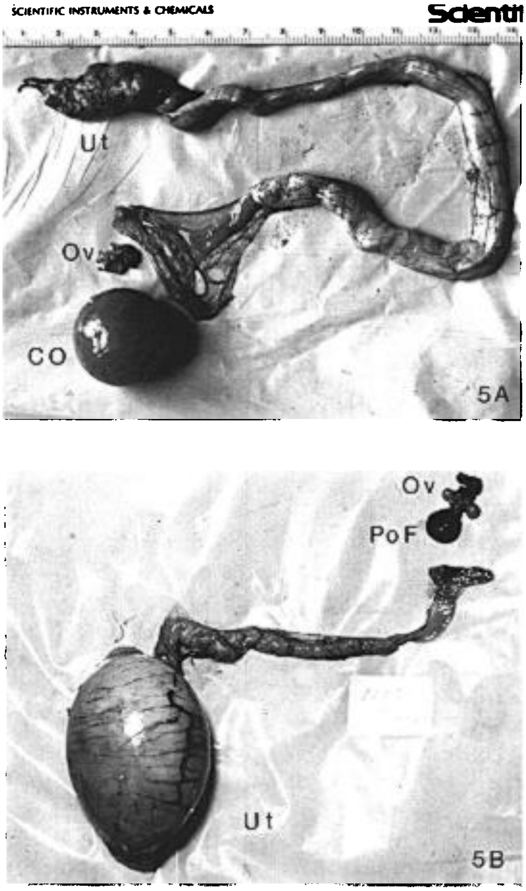

Fig. 5. Oviducts and ovaries from Cassin's Auklets killed 12 (5A) and 15 (5B) days after removal of their first egg. In 5A the single completed ovum (CO) is held in the follicle and the oviduct is enlarged. The yolk of the shelled egg in the uterus (Ut) of 5B was ovulated from the single postovulatory follicle (PoF) apparent in the ovary (Ov).

The total time required for a female Cassin's Auklet to form its single egg was estimated at 15 days (range = 12.5–17.5 days). This includes 2.5 days growth of the small follicles, 8.1 days RYD on the primary follicle, and 4.2 days lag period. The time required for small follicular growth is not known empirically and was estimated here (Gilbert et al. 1983; see below). The assumption that the presence of Rhoda-

TABLE 4. Cassin's Auklet egg composition ($n = 43$).

	Mean	SE	% FNBM[a]
Fresh mass	28.19	0.34	16.59
Shell			
Mass	1.91	0.03	
%	6.77	0.07	
Yolk			
Mass	9.04	0.12	5.32
%	32.31	0.41	
Albumen			
Mass	17.23	0.28	10.13
%	61.03	1.47	

[a] FNBM = female nonbreeding body mass = 170 g (Fry et al. unpubl. data).

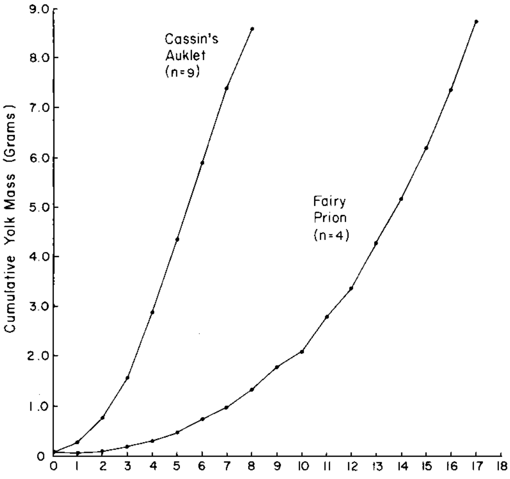

Fig. 6. Cumulative yolk growth in Cassin's Auklet and the Fairy Prion.

mine-stained albumen in a laid egg indicates the albumen was being synthesized on the dose day may not be completely justified, because this water-soluble dye is pervasive and stains all body tissues. Excretion of Rhodamine may be dependent on the strength of its binding to protein or on the rate of protein turnover. The distribution of albumen color and dye intensity in relation to the timing of egg formation, however, reveals a pattern that suggests that albumen is synthesized 2–5 days before laying, an interval that corresponds surprisingly well to the lag period (Fig. 3). The constancy in the duration of both the RYD and lag periods between years, and the predictable replacement interval, attest to the determinant nature of the process of egg formation.

From determinations of the mean daily increment in yolk mass ($n = 9$), I calculated the amount of lipid and protein (Fig. 7, top) and the corresponding energy content (Fig. 7, bottom) of material deposited on the yolk. All albumen dry matter (12% of wet mass) was considered to be protein, containing gross energy of 5.65 kcal/g (Ricklefs 1977), while the gross energy of auklet yolk was determined empirically to be 7.35 kcal/g dry yolk mass (dry mass being 48.5% of wet yolk mass). The mass of albumen synthesized daily during the lag period (days 9–12 of egg formation; Fig. 7, bottom) was assumed to be constant because, although it appears to be greatest early in the lag period (days 9 and 10; Fig. 3), no quantitative estimates of daily albumen synthesis were made. Under this assumption, the total albumen protein content was divided evenly over the lag period and was estimated to be 0.52 g/day, 1.6 times that deposited during maximal yolk deposition (about 0.33 g/day on days 4–7 in Fig. 7).

The basal metabolic rate (BMR) of an auklet-size nonpasserine (170 g nonbreeding female mass; Fry et al. unpubl. data) was estimated to be 22.7 kcal/day (allometric equation for nonpasserines, Kendeigh et al. 1977). Assuming a conversion efficiency of 77% (Brody 1945) for synthesis of egg lipids and proteins, the peak daily cost of egg production during RYD was estimated to be 7.27 kcal/day, or 32% of estimated BMR, of which only about 2.4 kcal (10.6% of estimated BMR) constitute yolk protein production. During the lag phase, when only albumen proteins are being synthesized, the average daily cost was estimated as 3.86 kcal/day, or 17% of BMR. The extent to which synthesis of particular yolk or albumen proteins may limit egg formation is unknown, but there may be an overall energetic benefit in reducing daily protein demand by extending albumen synthesis over the 4-day lag period.

The observed lag period was much longer for Cassin's Auklets than the 24–26 h observed in domestic hens (Warren and Scott 1935), Japanese Quail (Opel 1966), and usually in the domestic turkey (Wolford et al. 1964). Bacon and Cherms (1968), however, reported that turkeys have sporadic "rest" periods of 2–4 days between an expected ovulation and laying. Lag periods of predictable length occur in other species, notably a lag of 5-7 days in Adélie Penguins (Astheimer and Grau 1985), 7 days in Fiordland Crested Penguins (*Eudyptes pachyrhynchus;* Grau 1982), 4 days in White Flippered Penguins (*E. minor albosignata;* Grau 1984), and 10 days in Northern Royal Albatrosses (*Diomedea epomophora sanfordi;* Grau unpubl. data) and in Emus (Hirsch and Grau 1981).

The functional significance of the lag period is elusive. If this 4-day period allows the female auklet flexibility in the time of oviposition, greater variability in its length would be expected. Instead, egg formation appears to be of fixed duration; once rapid yolk deposition has begun, the options are limited either to continuing through to laying or to resorbing the yolk, thus abandoning that potential clutch. In Cassin's Auklet, the completed yolk is held, apparently quiescent, in the follicle during most of the lag period. Yolk resorption can occur during this time, but after ovulation resorption from the oviduct is not possible unless the yolk is extruded into the body cavity. Resorption of a completed yolk could occur during the lag period in birds that lack sufficient protein to complete albumen synthesis. Without evidence for yolk resorption in natural populations, however, the role of nutritional status as a selective pressure in the evolution or maintenance of the lag period remains speculative.

Gilbert et al. (1983) found that numerous small follicles (1-5 mm in diameter) in the ovaries of domestic hens undergo enlargement, but within 2-5 days most of these "primordial" follicles become atretic, leaving a few of the largest the potential to undergo RYD. This cycle of atresia results in a single small follicle entering the follicular hierarchy daily during the reproductive cycle of the domestic hen. Such prebreeding "priming" of the ovary may be a physiological necessity in wild birds that allows for ovarian production of estrogens early in the breeding season and a readiness to respond to appropriate environmental stimuli (proximate factors). Evidence for a similar cycle was observed in the ovaries of female auklets killed while producing an egg (birds A-E, Table 3), where a distinct reduction in the number of small follicles of increasing diameter classes was seen. Because RYD occurs on only one follicle in these auklets (i.e. the follicular hierarchy contains only one follicle), the remaining large primordial follicles may become atretic shortly after the single yolk is completed. Evidence for the latter hypothesis is implied by the well-vascularized, "non-atretic" condition (Gilbert et al. 1983) of small follicles in birds A and F (Table 3), each of which had one nearly completed yolk. In contrast, small follicles in birds B-E had either blood pools within the follicle or no follicular vascularization, both indicative of atresia; all four of these birds had either a completed yolk in the follicle or a shelled egg in the uterus.

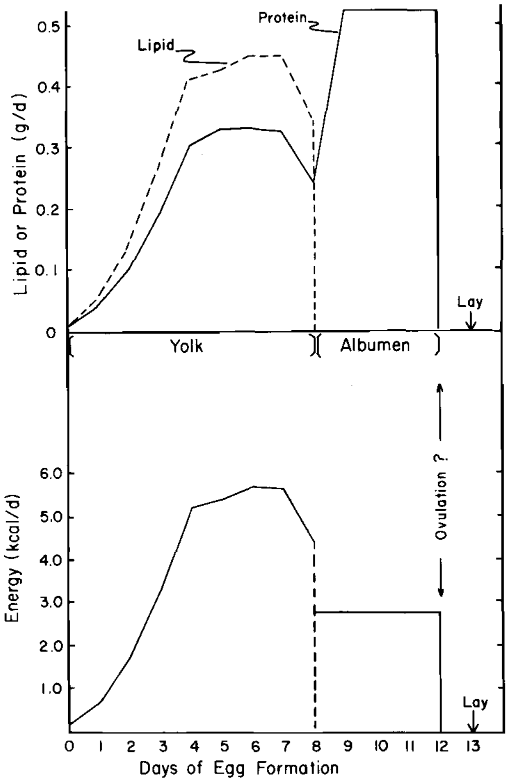

Fig. 7. Mean lipid and protein deposition in Cassin's Auklet eggs ($n = 7$; top) and corresponding energy deposited as egg components ($n = 7$; bottom).

The predictable nature of the relaying interval is of interest when considering the timing of follicular development and egg formation. The time necessary for reducing (via atresia) a cohort of 20-30 1-mm follicles to a few 5-mm follicles appears to be 2-5 days in domestic hens (Perry et al. 1983). After removal or loss of a first egg, Cassin's Auklets probably require a similar period to produce a single 4-5-mm yolk that will complete RYD and become the replacement egg. Based on the relaying interval and the time required for yolk deposition and the lag period, the period of early follicular development was estimated to be 2–3 days (Fig. 4). The capacity to relay also emphasizes the flexible nature of the reproductive effort in this species. This plasticity, alluded to by Manuwal (1979), allows the initiation of a reproductive bout within days of appropriate environmental cues. Alternatively, abandonment of eggs, as a response to actual or predicted resource limitations or to mate loss, can occur with impunity, as the birds are able to repeat the process rapidly.

The physiological or cognitive ability of birds to assess environmental stimuli early in the breeding season that may facilitate successful chick rearing later is especially important where such stimuli are temporally unpredictable. The Farallon Island population of Cassin's Auklets are resident in the waters off central California year-round and breed earlier than other seabirds nesting there. It is possible that climatic trends indicative of sea conditions during the breeding season would be evident to the birds as early as December or January. One possible stimulus for the Farallon auklets is upwelling of deep, cold, nutrient-rich water along the north and central California coast in early spring (Sverdrup et al. 1942, Ainley and Lewis 1974). The onset, extent, and duration of upwelling, however, vary annually. A decrease in sea surface temperatures is one indication of local upwelling, which auklets and other seabirds might respond to in assessing potential ocean productivity near a breeding colony. This hypothesis is supported by the correlation of early laying initiation in years where sea surface temperatures averaged below 12°C during January and February (1979 and 1982; PRBO unpubl. data). In contrast, 1981 sea surface temperatures remained relatively high (12–14°C) until mid-March, and peak auklet laying was delayed until early April. This apparent relationship, however, requires analysis of many more years of data to interpret any causal relation between sea surface temperatures and auklet laying.

When upwelling occurs early in spring, auklets may be able to predict an assured food supply for feeding their chicks, and thus lay early. In such years many auklets attempt a second brood, and those with greatest success are those pairs that fledge their first chick early in the season (Boekelheide 1980). Thus, there is a definite advantage to laying early, if an adequate food supply can be anticipated.

For auklets to respond successfully to proximate effectors, such as water temperature or phytoplankton density, such cues must predict suitable conditions at least 13 days in advance of laying to accommodate the time required for egg formation. It is interesting, but probably coincidental, that the 12–15-day period required for egg formation matches half a lunar cycle. Specifically, if egg formation began during a full moon, that egg would be laid during a new moon. Peak laying dates for Cassin's Auklets on Southeast Farallon Island vary annually, and are sometimes correlated with a new moon (1979 and 1981, Fig. 1). Auklets may use lunar cues in the absence of decreasing ocean temperatures (e.g. 1981, Fig. 1) or possibly in late spring when breeding Western Gulls (*Larus occidentalis*) are more restricted in their feeding range and a potential threat (Manuwal 1972), but lunar phase is not an important determinant in laying replacement eggs. In fact, replacement eggs seem to be produced as rapidly as physiologically possible, a response that may reflect experimental manipulation in the present context.

One interpretation of the stimuli responsible for initiating egg production in auklets may be as follows: Ovarian (and testicular?) activity begins in response to increasing day length, even as early as January when auklets begin cleaning out nest burrows and pairs occasionally are found together. If the limited cycle of follicular growth and atresia begins at this time, and if sea conditions, as a secondary modulator, are positive, formation of the single egg may begin shortly thereafter, permitting auklets to lay as early as the first week of March (Manuwal 1972). If, as in 1981, upwelling is not anticipated, follicular cycling may continue until signs of upwelling appear.

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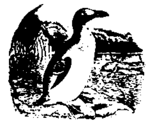
100 Years Ago in The Auk



From "On an old portrait of Audubon, painted by himself, and a word about some of his early drawings" by R. W. Shufeldt (1886, Auk 3: 417-420):

[Shufeldt had come into possession of three drawings, which he described as follows.]

"They are each and all drawn by a combination of crayon and water-colors upon a thin and *not expensive* kind of drawing-paper, now brittle and soiled by age. Audubon had evidently numbered these drawings of his, and these numbers are 44, 77, and 96, a European Magpie, a Coot, and a Green Woodpecker, respectively . . . .

"As I have said, the earliest of these drawings is the one of the Magpie—and let us look at it for a moment. It is life size, as they all three are, and the bird is represented standing on the ground, being drawn lengthwise on the paper. The execution is quite crude, though the naturalist 'sticks out' in it, for notwithstanding the somewhat awkward position the bird is in, there is life in it. The ground is simply a wash of pale green and brown, while over on one side of the paper he has 'tried his brush,' having made some rough concentric circles with paint dabs about them. Beneath this drawing we find written in lead-pencil in two lines, 'La Pie, Buffon,' 'Pye, Piot Magpye, Pianet, english,' and over to the left-hand corner, 'No. 44.'

"The second picture is that of a Coot, and is a marked improvement upon the Magpie. Far more pains have been taken with the feet, legs, bill, and eye, though little has been gained in the natural attitude of the bird. It is also represented standing up on the dry ground, which is here of a pale violet wash, unbroken by anything in the shape of stones or vegetation. Except very faintly in the wing, no attempt has been made to individualize the feathers, the entire body being of a dead black, worked in either by burnt cork or crayon. Beneath this figure has been written in lead-pencil, but gone over again by the same hand in ink, 'La foulque *ou* La Morelle—Buffon, Riviere Loire Joselle—' 'English—the Coot,—'

"As is usually the case among juvenile artists, both this bird and the Magpie are represented upon direct lateral view, and no evidence has yet appeared to hint to us of the wonderful power Audubon eventually came to possess in figuring his birds in their every attitude.

"There is a peculiar pleasure that takes possession of us as we turn to the third and last of these figures, the one representing the Green Woodpecker (*Gecinus viridis*). It is a wonderful improvement, in every particular, upon both of the others. The details of the plumage and other structures are brought out with great delicacy, and refinement of touch; while the attitude of the bird, an old male, is even better than many of those published in his famous work. The colors are soft and have been so handled, as to lend to the plumage a very flossy and natural appearance, while the old trunk, upon the side of which the bird is represented, presents several evidences of an increase of the power to paint such objects. We find written in lead pencil beneath this figure, in two lines, and in rather a Frenchy hand, 'Le Pic vert, Buffon,' 'the Green Woodpecker—British Zoology.' "

FEMALE CHOICE IN MIDDENDORFF'S GRASSHOPPER-WARBLER (*LOCUSTELLA OCHOTENSIS*)

HISASHI NAGATA

Department of Biology, Faculty of Science, Kyushu University 33, Fukuoka 812, Japan

ABSTRACT.—Morphological and territorial factors that influence female mate choice were examined in the monogamous Middendorff's Grasshopper-Warbler (*Locustella ochotensis*) on an islet near Fukuoka, Japan. I assumed that pairing date corresponded with female mate choice. Pairing date was correlated with both territory size and food abundance but was not correlated with selected morphological characteristics of males. Territorial quality was assumed to be correlated with territory size because preferable food resources and nest sites were distributed randomly. I conclude that female mate choice was influenced by territory quality rather than by the morphological characteristics of males. *Received 8 July 1985, accepted 28 January 1986.*

MORE than 90% of all songbird species are monogamous (Lack 1968), but monogamy only recently has received detailed attention by investigators. Several models of female choice exist for polygynous species (Verner 1964, Orians 1969, Weatherhead and Robertson 1979, Alatalo et al. 1981). The "male deception" hypothesis (Alatalo et al. 1981) cannot be applied to female choice in monogamous species, however, because it explains only why females select already-mated males. The "sexy son" hypothesis (Weatherhead and Robertson 1979) and the "polygyny threshold" model (Verner 1964, Orians 1969) may be potentially applicable. Mating success among males is influenced by male quality in the former model and by territory qualities in the latter. Female choice is expected to play an important role in monogamous species if there are differences in fitness among females. Monogamous females will choose the male with the best territorial or physical characteristics at the time, because delayed mating decreases reproductive success (Perrins and Birkhead 1983). Female choice is difficult to detect, however, in resident monogamous species that have high mate fidelity. Little attention has been paid to mate choice in monogamous species.

I investigated female choice in a monogamous species, Middendorff's Grasshopper-Warbler (*Locustella ochotensis*). The work was designed to assess the relative importance of territorial characteristics that might influence female choice in this species.

STUDY AREA AND METHODS

Middendorff's Grasshopper-Warbler breeds on only six islets in northern Kyushu, Japan. Four (Ohtsukue-jima, Kotsukue-jima, Hashira-jima, and Okitsu-jima) of the six islets are located at the mouth of Hakata Bay. The study was conducted on Okitsu-jima about 10 km north of Fukuoka (130°18'E, 33°41'N) in the vicinity of Shikanoshima Island. A small hill, 16 m high and 0.31 ha in area, is located at the center of the island and is covered with coastal vegetation. The coastal vegetation is divided into a coastal evergreen dwarf-forest, about 4 m in height, dominated by *Pittosporum tobira*, *Lista japonica*, and *Eurya emarginata;* a thicket consisting of *Arundo donax;* and scrub. There are also patches of *Pseudosasa japonica* shoots. The marginal vegetation is halo-xerophyte dominated by *Angelica kiusiana*, *Carex kobomugi*, and *Boehmeria* sp. (Fig. 1).

There were no predators and no competitors on the islet, and only the Pacific Reef Egret (*Egretta sacra*) and Rufous Turtle-Dove (*Streptopelia orientalis*) bred in the study area. The Great Tit (*Parus major*), Japanese Pygmy Woodpecker (*Dendrocopos kizuki*), and Blue Rockthrush (*Monticola solitarius*) occasionally visited the study area.

The study was conducted from 1981 to 1984. Birds were captured with a mist net and uniquely color-ringed. Twelve males, 9 females, 1 juvenile, and 38 nestlings were banded. The wing length, tail length, culmen length, tarsus length, and lengths of the tenth primary and the second phalange of each banded bird were measured. Nestlings were measured every 1-2 days. Sex was determined by individual behavior after release. Males were identified by their advertising on a song post. Females were identified when they mated with males or carried nest materials. Only females built nests.

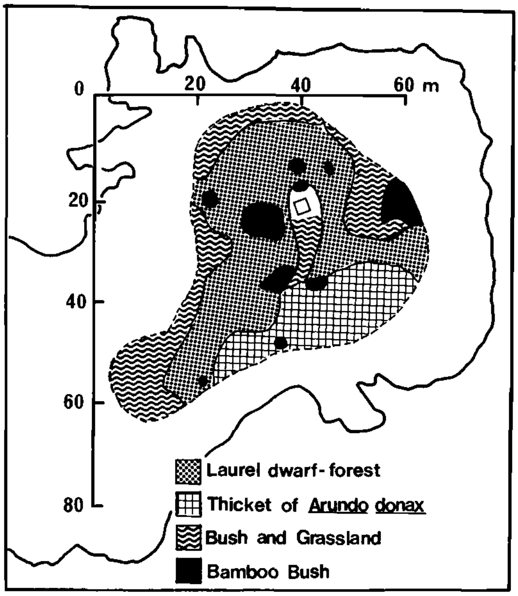


Fig. 1. Vegetation map of Okitsu-jima islet.

I assumed that early pairing leads to increased reproductive success. Therefore, I used pairing date as a measure of mate preference of females. Censuses by line transect were made every 1-2 days beginning in late April of each year. Initiation of pair formation was readily identified by the males' intense courtship and females' solicitation displays.

Territories were determined by the "time mapping method" (Nakamura 1969). Territory was defined in this study as any area defended by advertising, i.e. territory was the convex polygon connecting outer singing points of the owner. The times of observation, locations of individuals, specific behaviors, and vocalizations were recorded.

The abundance of insects and other arthropods was measured at the main study site by the sweep-net method and quadrat sampling of a 25 × 25-cm area, respectively. Twenty strokes of a sweep net in an area of about 1 m^2 comprised a single sample. All samples were taken on two consecutive days at approximately the same hour. Sampling was conducted every two weeks from May to August in each year. Sampling sites were selected to include representative amounts of each type of vegetation. All arthropod specimens were preserved in 80% ethanol and then sorted, identified to the level of order, and their body lengths measured.

Food items fed to nestlings and fledglings were observed at the sites near the nest through 8× binoculars. To evaluate the quality of territories in terms of food availability, each food item was scored on the basis of Ivlev's electivity index (*E*; Ivlev 1961):

$$E = (r_i - p_i)/(r_i + p_i),$$

where r_i = the relative content of any element in the food items and p_i = the relative value of the same element in the food complex of the environment (as a percentage of the whole sweep and quadrat samples). Positive preference was expressed by an index value from +1 to 0, absence of preference by an index value of 0, and negative preference by an index value between 0 and −1. Each food item was scored on the basis of one-half point awarded for each 0.2 interval of an index value, 0 points for no available items ($E = -1$), and 1-5 points for items with an index value between −1 and +1. The food score associated with each territory was calculated by the formula:

$$\text{food score} = \Sigma\,(\text{point } i) \times (\text{density } i) \times (\text{size of territory}),$$

where point *i* = the point value of item *i* and density *i* = the density of item *i*.

TABLE 1. Site fidelity and return ratio of returning birds, 1981-1984.

	Return ratio (%)	Distance (m) shifted between years ($\bar{x} \pm$ SD)
Adults		
Males	12/22 (59.1)	7.3 ± 1.54 (n = 12)
Females	7/13 (54.5)	22.5 ± 4.39 (n = 7)
Juveniles	5/24 (20.8)	—

RESULTS

Middendorff's Grasshopper-Warbler arrives in late spring at northern Kyushu from a wintering area in Southeast Asia. The first influx of males occurred 28 April in 1981, 4 May in 1982, 30 April in 1983, and 8 May in 1984. Females arrived at the breeding site 20 (1983) to 26 days (1984) after the males (for males n = 6 in 1983 and 3 in 1984, for females n = 6 in 1983 and 7 in 1984). Older birds continued to arrive until mid-June. Yearling males returned to the breeding site around late June. Fifty-seven percent of the adults banded were recovered at breeding sites used in the previous year. There were no differences between the sexes in rates of return (Table 1).

Males established territories shortly after arrival and generally returned to the same territory in consecutive years (Fig. 2). Females usually paired within two days of their arrival. Yearling males did not establish territories in 1982 or 1983, and they disappeared by early

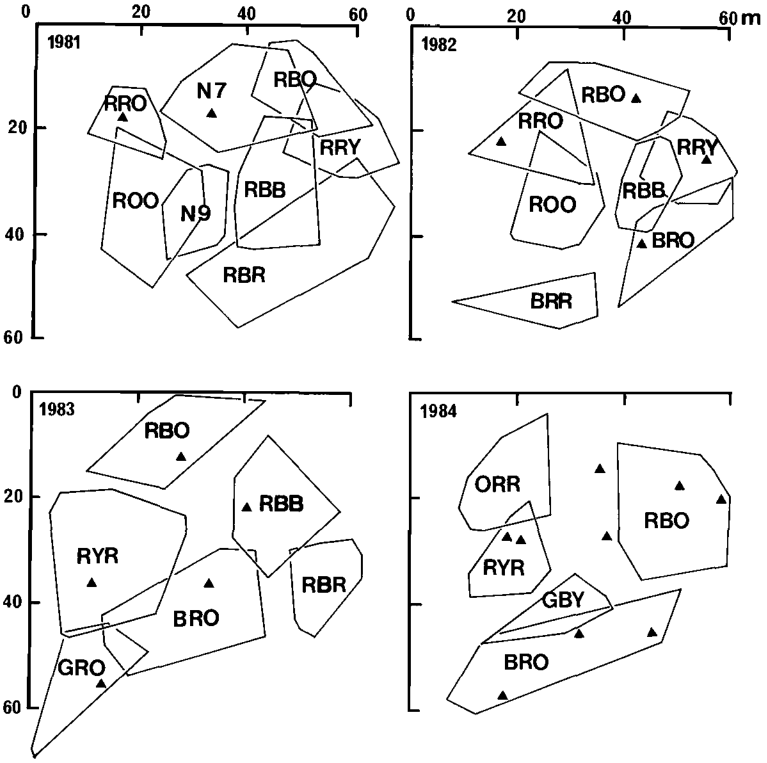


Fig. 2. Territorial arrangement of individual males, 1981-1984. Triangles indicate nest sites. Axes are the same as in Fig. 1.

July. In 1984, however, two yearling males occupied territories in vacant areas between territories of older males. Territorial fidelity was measured as the distance between the center of territories in consecutive years. The annual shift in the ranges for females was significantly larger than that for males ($t_{17} = 3.91$, $P < 0.05$). Hence, females returned to different territories on the islet, suggesting less strict territorial fidelity (Table 1). Eight banded birds that returned to the same sites in consecutive years changed mates. Mate fidelity was low; only 1 of 7 pairs in which both sexes returned in consecutive years maintained the pair bond. Territory size averaged 310.6 ± 27.5 m^2 (±SE, $n = 30$) over 4 yr. Territory size increased as population size decreased ($r = -0.83$, $n = 4$, $P < 0.20$). The mean territory size in May 1984, when only three males established territories, was 710.7 ± 69.1 m^2 (±SE, $n = 3$). The mean territory size in 1984 was significantly larger than in other years (273 ± 25.3 m^2, ±SE, $n = 25$; $t_{26} = 5.78$, $P < 0.001$).

Fledging occurred between late June and early August. Lepidopterans and chilopods (e.g. millipedes and centipedes) were preferred food items in the breeding season (Table 2). These taxa, with homopterans and orthopterans, comprised about 80% of total food items (Table 2). The numbers of lepidopterans collected by sweep sampling were lower than homopterans but were stable throughout the seasons (Fig. 3). The density of soil arthropods (spiders, millipedes, and centipedes) estimated by quadrat sampling fluctuated, but soil arthropods were abundant (Fig. 3). Orthopteran nymphs (grasshoppers, mantids, and cockroaches) appeared in late July, but they were less abundant than lepidopterans and homopterans (Fig. 3). The patterns of changes in food abundance were similar among the three vegetation types (Fig. 3). The preferred dietary items (lepidopterans, orthopterans, and chilopods) were distributed randomly in late May 1984 (Table 2).

The food score for each territory in 1983 increased gradually until late June and decreased

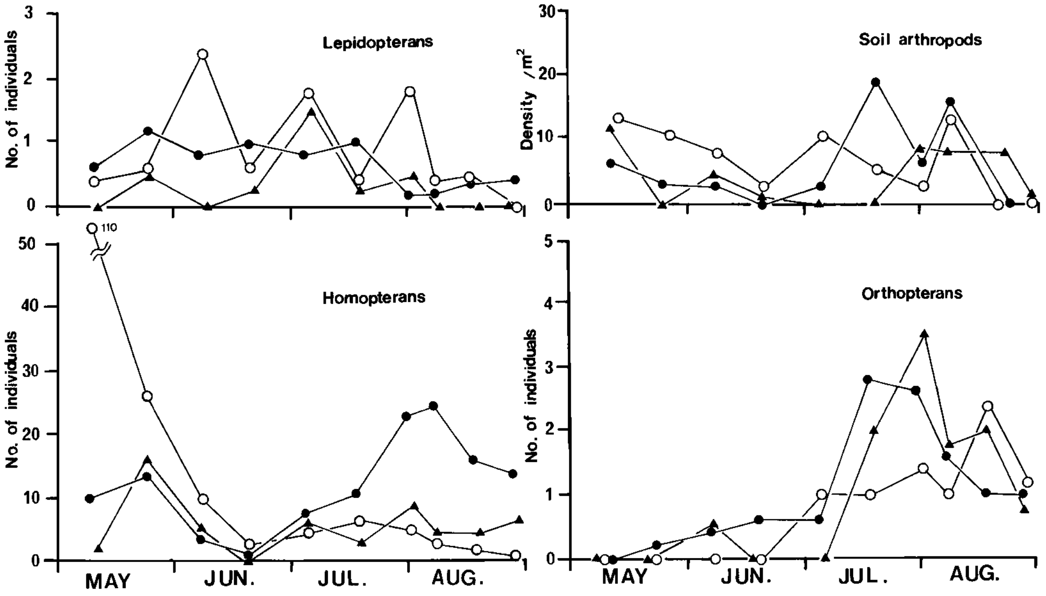


Fig. 3. Seasonal changes in arthropod abundance in 1984. Open circles represent the laurel dwarf-forest, closed circles represent the bush and grassland, and closed triangles represent the *Arundo donax* thicket.

thereafter (Fig. 4). The seasonal change in this derived measure was bimodal in 1984, with peaks in late May and early July. The first peak appeared to be the consequence of large territories because almost the entire area was occupied by only three males. Each possessed a large territory during May 1984. The nestling period started when food abundance became high.

Morphological variation among mates was tested with respect to several characters, but no significant correlations were found (wing length: $r = 0.47$, $n = 12$; tail length: $r = 0.29$, $n = 12$; culmen length: $r = -0.25$, $n = 12$; tarsus length: $r = 0.05$, $n = 12$; body mass: $r = 0.29$, $n = 7$). I conclude that there was no assortative mating in this species. There was no correlation between the pairing date and wing length (Kendall's rank correlation coefficient, $\tau = -0.44$, $n = 9$, NS), tail length ($\tau = -0.33$, $n = 9$, NS), culmen length ($\tau = 0.06$, $n = 9$, NS), tarsus length ($\tau = 0.17$, $n = 9$, NS), and body mass ($\tau = 0.22$, $n = 9$, NS). There was no significant correlation between the pairing date and time spent by males feeding fledglings ($\tau = -0.38$, $n = 8$, NS). Thus, females did not employ these physical characters as relevant cues in mate choice and did not always select dili-

TABLE 2. Diet of *Locustella ochotensis* and its food preference. Asterisks indicate significant clump patterns ($P < 0.05$).

Food item	Percentage of dietary items ($n = 73$)	Percentage of sweep sample ($n = 4{,}771$)	Preference (Ivlev's index, E_i)	Food point	Index of dispersion in late May ($\sigma^2/\bar{x}$)
Lepidopterans	32.9	1.8	0.90	5.0	0.82
Homopterans	15.1	30.3	−0.34	2.0	37.87*
Orthopterans	9.6	2.1	0.64	4.5	1.00
Dipterans	6.8	20.1	−0.49	1.5	2.96*
Ephemeropterans	2.7	0.3	0.78	4.5	—
Chilopods	21.9	0.7	0.94	5.0	0.71
Wood lice	5.5	14.7	−0.46	1.5	9.55*
Spiders	5.5	6.1	−0.06	2.5	4.46*

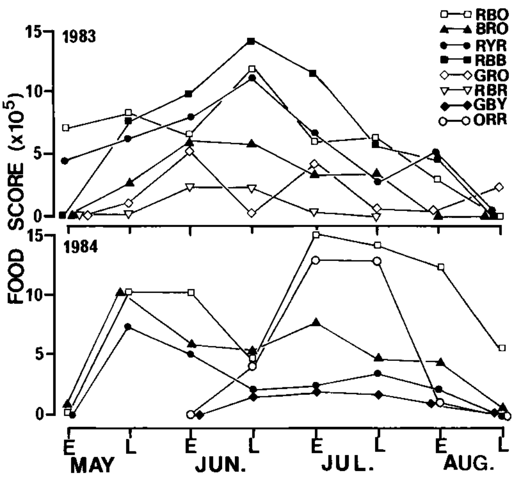


Fig. 4. Seasonal changes in food abundance at each territory in 1983 and 1984. See text for details.

gent males. There was also no correlation between pairing date and the age of males ($\tau = -0.11$, $n = 9$, NS). Yearling males, however, were excluded from breeding because they arrived after all the females had mated.

Correlations were tested among pairing date, fledging date, territory size, food score, arrival date, and the area of bamboo bush that constituted the main nesting site. To combine data from different years, arrival and pairing dates were standardized by using the median dates. There was a weak correlation between the arrival date of males and pairing date ($\tau = 0.56$, $n = 9$, $P < 0.05$) (Table 3). There was no correlation between arrival date and departure date in the previous season ($\tau = -0.13$, $n = 14$, NS).

Pairing date was associated significantly with territory size ($\tau = -0.78$, $n = 9$, $P < 0.01$) and food score ($\tau = -0.69$, $n = 9$, $P < 0.05$). Food scores in late May were associated with those in mid-July ($\tau = 0.67$, $n = 9$, $P < 0.05$). Hence, relative territory rank did not change throughout the breeding season, because the feeding areas were not different between the periods. The area of bamboo bush was not correlated with pairing date ($\tau = -0.47$, $n = 9$, NS). When food score was held constant, territory size showed a weak correlation with pairing date (Kendall's partial rank correlation coefficient, $\phi = -0.55$). When the area of bamboo bush was held constant, territory size showed a stronger correlation with pairing date ($\phi = -0.71$). When territory size was held constant, however, pairing date showed weaker correlations with food score ($\phi = -0.28$) and the area of bamboo bush ($\phi = 0.15$). These partial correlations suggest that pairing date was correlated primarily with territory size. In accordance with a step-wise multiple regression, variations in territory size accounted for 77% of the variance in pairing dates, variations in male arrival date accounted for 8%, and variations in food score accounted for only 2% of the residual variance (Table 4).

Pairing date was highly correlated with the fledging date of the first brood ($\tau = 0.78$, $n = 9$, $P < 0.01$). Female departure date was correlated closely with fledging dates ($\tau = 0.56$, $n = 9$, $P \le 0.05$). Thus, early breeding and early departure followed early pairing. Young that fledged before August received care for longer periods than those that fledged in August [early fledglings: 20.3 ± 5.1 days ($\bar{x}$ ± SE), $n = 10$; late fledglings: 12.0 ± 2.8 days, $n = 5$; Mann-Whitney U-test, $P < 0.01$].

DISCUSSION

Generally, it is assumed that males with good territories or good physical attributes acquire a mate early in the breeding season. Early mating enhances reproductive success for two rea-

TABLE 3. Correlation between six variables potentially affecting breeding. Kendall's rank correlation coefficients (τ) are below the diagonal and correlation coefficients (r) are above the diagonal.[a]

	Pairing date	Arrival date	Fledging date	Territory size	Food score	Area of bamboo bush
Pairing	—	0.73*	0.89**	−0.88**	−0.86**	−0.44
Arrival	0.56*	—	0.79**	−0.58	−0.67*	−0.26
Fledging	0.78**	0.51	—	−0.84**	−0.78**	−0.34
Territory	−0.78**	−0.38	−0.64*	—	0.83**	0.57
Food score	−0.69*	−0.38	−0.56*	0.73**	—	0.46
Bamboo bush	−0.47	−0.07	−0.33	0.69*	0.51	—

[a] * = $P \le 0.05$, ** = $P < 0.01$ ($n = 9$).

TABLE 4. Step-wise multiple regression using pairing date as a dependent variable ($n = 10$).

Step no.	Independent variable	r	r^2	Increase in r^2
1	Territory size	0.88	0.77	0.77
2	Male arrival date	0.92	0.85	0.08
3	Food score	0.93	0.87	0.02
4	Area of bamboo bush	0.93	0.87	0.00

sons. First, early pair formation leads to early fledging. If young fledge in June, then females may rear additional clutches. Indeed, pairs with successful nestings in late June in 1984 started a second clutch, although Middendorff's Grasshopper-Warbler rears only one brood in most years. Second, early fledglings were cared for longer. This results in larger and better-developed fledglings and reduced offspring mortality. The duration of parental care depended on the onset of breeding, and all males fed nestlings and fledglings. Therefore, the duration of parental care did not correlate with the starting date of pair formation.

If the difference in mating success among males is large, females will choose "sexy" males (Weatherhead and Robertson 1979). This is not the case in *L. ochotensis* because most territorial males acquired females.

Mating success was correlated with body size in Cetti's Warblers (*Cettia cetti;* Bibby 1982), but I found no correlation between body size and pairing date in Middendorff's Grasshopper-Warbler. Hence, female mate choice was not influenced by physical attributes of male quality.

Based on the strong partial correlation between territory size and pairing date, I conclude that females preferentially choose males with larger territories. Females apparently use territory quality, not age, as a cue for mate choice. Older males acquire more females in Pied Flycatchers (*Ficedula hypoleuca;* Alatalo et al. 1984) and Red-winged Blackbirds (*Agelaius pheoniceus;* Yasukawa et al. 1980). Female Middendorff's Grasshopper-Warblers did not choose older males, however, as indicated by the lack of correlation between pairing date and the age of adult male.

A large territory contains many potential nest sites and abundant food resources. Vegetation structure affects nest sites, especially light penetration to ground level, and may be an important factor (Pleszczynska 1978) in female choice. It was not in *L. ochotensis,* however, as there was only a weak correlation between the area of bamboo bush and pairing date (Table 4). Nest sites were not constrained on Okitsujima islet, because Middendorff's Grasshopper-Warbler inhabited a laurel forest and built cup-shaped nests on the twigs. Moreover, nests were free from predation in the absence of predators on this islet. The abundance of food resources correlated highly with territory sizes in Middendorff's Grasshopper-Warbler, because the spatial distribution of preferable dietary items was relatively random (Table 2). Female choice was influenced more by food resources than by nest sites. Apparently, it is a better strategy for female warblers to mate with males on large territories soon after arrival and to breed early. Females thereby maximize their reproductive success in one season.

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(*continued on p. 808*)

LOW GENIC VARIATION BETWEEN BLACK DUCKS AND MALLARDS

C. DAVISON ANKNEY,[1] DARRELL G. DENNIS,[2] LISA N. WISHARD,[3]
AND JAMES E. SEEB[4]
[1]*Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada,*
[2]*Canadian Wildlife Service, 152 Newbold Court, London, Ontario N6E 1Z7, Canada,*
[3]*Department of Biological Sciences, University of Idaho, Moscow, Idaho 83843 USA, and*
[4]*Department of Zoology, Washington State University, Pullman, Washington 99164-4220 USA*

ABSTRACT.—We used allozyme electrophoresis to estimate the degree of genetic differentiation among allopatric and sympatric populations of American Black Ducks (*Anas rubripes*) and Mallards (*A. platyrhynchos*). Mallards were collected in California, Saskatchewan, Manitoba, and Ontario, and Black Ducks were collected in Newfoundland, Nova Scotia, and Ontario. The mean genetic distances, $\bar{D}$, between Black Duck populations (0.0007), between Mallard populations (0.0010), and between Mallard and Black Duck populations (0.0006) were virtually identical; there was as much genetic differentiation within the two species as there was between them. Such small genetic distances are characteristic of local populations of avian species in other orders, and are consistent with what is known about the lack of reproductive isolation between Black Ducks and Mallards. Although the two taxa are still somewhat split on an east-west basis, our genetic data do not support even subspecific status for the Black Duck. *Received 12 August 1985, accepted 20 February 1986.*

MALLARDS (*Anas platyrhynchos*) and American Black Ducks (*A. rubripes*) hybridize wherever they come in contact (Goodwin 1956, Johnsgard 1967, Heusmann 1974). This contact, primarily in eastern North America, has occurred with increasing frequency since about 1900 (Johnsgard 1961, Johnsgard and Di Silvestro 1976). Concomitant with this increased interaction has been a very large increase in the number of Mallards in eastern North America and a decline in the number of Black Ducks (e.g. Bellrose 1976).

The frequent hybridization of these taxa has prompted speculation about whether the Black Duck is a valid biological species. Johnsgard (1961) concluded that "the most satisfactory status for *rubripes* is to consider it a subspecies of *Anas platyrhynchos* . . ." and "Neither a subspecific nor a specific relegation can be entirely satisfactory at present." The major problem with a subspecific designation, as pointed out by Delacour (1956), is the large area of sympatry of these two groups. Because subspecies are simply named geographic races (Mayr 1970), two populations that are largely sympatric cannot be subspecies. The area of sympatry between Mallards and Black Ducks has increased considerably since Delacour's comment was made. Therefore, the only taxonomic choices are to continue to consider them as separate species or to conclude that the Black Duck is a color morph of the Mallard.

We used allozyme electrophoresis to quantify the degree of genetic differentiation among allopatric and sympatric populations of Mallards and Black Ducks and related those data to information on genetic differences at various taxonomic levels in other birds.

METHODS AND MATERIALS

We examined 131 Black Ducks and 181 Mallards, all of which were either adult females or juveniles. They were collected in several localities during or immediately after the breeding season (Table 1); adult males were excluded because, unlike females, they commonly breed far from the area where they were raised.

Liver and breast muscle tissue were removed from each bird in the field, within 2 h of death, labeled and placed in plastic bags, and frozen on dry ice (Johnson et al. 1984). Tissues were stored at −70°C until they were processed.

Electrophoresis followed procedures outlined in May et al. (1979). Three buffer systems were used: (1) MF, a tris-boric acid-EDTA gel and tray buffer (pH 8.5) (Markert and Faulhaber 1965); (2) RW, a tris-citric acid gel buffer (pH 8.5), lithium hydroxide-boric acid tray buffer (pH 8.5) (Ridgway et al. 1970); and (3) AC, an amine citrate gel and tray buffer (pH 6.5) (Clayton and Tretiak 1972).

TABLE 1. Locations, sample sizes, and collection dates. Abbreviations in parentheses correspond to those used in other tables and in the figures to denote location.

Taxon	Sample size	Locality and date
Mallard (SASK)	49	Saskatchewan: 60 km NW of Saskatoon, September 1983
Mallard (ONT)	42	Ontario: E of a line joining Peterborough in S to Cochrane in N, May 1984
Mallard (MAN)	69	Manitoba: Delta Marsh at S end of Lake Manitoba, August-September 1984
Mallard (CAL)	21	California: Suisun Marsh 50 km NE of Oakland, April 1984
Black Duck (NFLD)	50	Newfoundland: 8 collected S and E of Goose Bay, Labrador, August 1983; 42 collected near Codroy, Newfoundland, September 1983
Black Duck (ONT)	41	Ontario: location as for Mallards; 4 collected May 1984, 37 collected August 1984
Black Duck (NSC)	40	Nova Scotia: Wallace Bay, September 1984

We used a system of nomenclature for loci and alleles first outlined by Allendorf and Utter (1979) and modified by Allendorf et al. (1983). For each electrophoretically detectable locus, the mobility (distance traveled) of the most common allelic product found in Mallards was used as a standard and designated 100. Other alleles were designated by the migration ratio of their protein products to that of allele 100. Multiple loci encoding the same enzymatic activity were numbered sequentially beginning with the form migrating closest to the origin.

Staining for enzyme activity followed methods outlined in Harris and Hopkinson (1976) and Allendorf et al. (1977). We examined 24 structural proteins and enzymes, encoded by 29 presumptive loci, in all individuals (EC stands for Enzyme Commission): Aco (aconitate hydratase, EC 4.2.1.3), Ada (adenosine deaminase, EC 3.5.4.4), Ak (adenylate kinase, EC 2.7.4.3), albumen, Aat (aspartate aminotransferase, 2.6.1.2), Ck (creatine kinase, EC 2.7.3.2), Est1,2 (esterase, EC 3.1.1.1, resolved using 4-methylumbelleferyl butyrate), Gda (guanine deaminase, EC 3.5.4.3), Gpi (glucose phosphate isomerase, EC 5.3.1.9), Gr (glutathione reductase, 1.6.4.2), G3pd (glycerol-3-phosphate dehydrogenase, EC 1.1.1.8), Idh1,2 (isocitrate dehydrogenase, EC 1.1.1.42), Ldh1,2 (lactate dehydrogenase, EC 1.1.1.27), Mdh1,2 (malate dehydrogenase, EC 1.1.1.37), Me1,2 (malic enzyme, EC 1.1.1.40), Mpi (mannose phosphate isomerase, EC 5.3.1.8), Np (nucleoside phosphorylase, EC 2.4.2.1), PepC2 (peptidase, EC 3.4.11, resolved using DL-leucyl-L-alanine), PepD (peptidase, EC 3.4.11, resolved using L-phenylalanyl-L-proline), Pgd (phosphogluconate dehydrogenase, EC 1.1.1.44), Pgm (phosphoglucomutase, EC 2.7.5.1), Pgk (phosphoglycerate kinase, EC 2.7.2.3), Sod (superoxide dismutase, EC 1.15.1.1), and Tpi (triosephosphate isomerase, EC 5.3.3.1).

Statistical analyses were performed using BIOSYS-1 (Swofford and Selander 1981). Heterozygosity (*H*), was defined as the number of heterozygous genotypes recorded in a sample divided by the product of the number of loci and the number of individuals assayed (after Gutiérrez et al. 1983). The percentage of polymorphism was calculated as the number of loci at which the frequency of the most common allele did not exceed 0.99 divided by the total number of loci examined.

We used Nei's (1978) unbiased *D* and Wright's (1978) modified Rogers' *D* to estimate genetic distances. Cluster analysis, summarizing the matrix of Nei's *D*-values, was performed with the unweighted pair-group method (UPGMA) using arithmetic means. A distance Wagner tree based on modified Rogers' *D*-values was constructed according to the methods of Farris (1972). The cophenetic correlation coefficients, r_{cc}, were used to evaluate how well the resultant branching diagrams represented the original distance matrices.

To evaluate our cluster analysis of the Mallard-Black Duck *D*-values, we did UPGMA analysis that included two confamilial taxa with data (Seeb and Wishard unpubl. ms.) from American Wigeon (*A. americana*) and Canada Geese (*Branta canadensis*). For that analysis, we excluded data for Est1, Pgd, and Aco, because they were not examined for wigeon and Canada Geese.

RESULTS

Allelic frequencies for 11 polymorphic loci are given in Table 2; all other loci were monomorphic.

The average percentage of polymorphic loci for the 7 populations was 24.1% and ranged from 17.2% to 31.0% (Table 3); the average percentage was 26.4% for Black Ducks and 22.4%

TABLE 2. Allelic frequencies for 11 presumptive loci in 3 populations of Black Ducks and 4 populations of Mallards. Abbreviations of locations are defined in Table 1.

	Black Ducks			Mallards			
Locus	NFLD	NSC	ONT	CAL	SASK	MAN	ONT
Ada							
100	0.870	0.850	0.854	0.881	0.776	0.754	0.786
107	0.100	0.150	0.098	0.095	0.163	0.203	0.036
95	0.010		0.012	0.024	0.041	0.014	0.036
110	0.010		0.037			0.007	0.131
113	0.010				0.010	0.007	
85						0.007	
103						0.007	
79					0.010		
120							0.012
Mpi							
100	0.704	0.737	0.829	0.738	0.837	0.855	0.821
120	0.235	0.063	0.049	0.024	0.010	0.022	0.167
133	0.061	0.175	0.110	0.190	0.143	0.101	0.012
55		0.012	0.012	0.024	0.010	0.007	
142		0.012		0.024		0.007	
85						0.007	
PepC2							
100	0.880	0.875	0.850	0.810	0.816	0.913	0.905
82	0.120	0.050	0.050		0.143	0.036	0.095
107		0.012	0.063	0.167	0.041	0.043	
95		0.063	0.037	0.024		0.007	
Np							
100	0.700	0.750	0.646	0.725	0.771	0.688	0.762
79	0.260	0.200	0.305	0.200	0.219	0.275	0.202
113	0.030	0.025	0.012			0.014	
73		0.025	0.037	0.075	0.010	0.022	
93	0.010						0.024
55							0.012
Est1							
100	0.920	0.912	0.915	0.857	0.908	0.870	0.905
125	0.080	0.087	0.085	0.143	0.092	0.130	0.095
Pgd							
−100	0.990	0.987	0.988	0.976	1.000	1.000	1.000
−50	0.010	0.012	0.012				
−200				0.024			
Idh1							
−100	1.000	1.000	1.000	1.000	1.000	0.993	1.000
−70						0.007	
Idh2							
−100	1.000	1.000	0.963	1.000	1.000	0.986	0.976
10			0.037			0.014	0.024
Aco							
−100	1.000	1.000	0.939	1.000	1.000	0.993	1.000
−70			0.061			0.007	
Sod							
−100	1.000	0.975	0.988	0.929	1.000	0.993	1.000
−33		0.025	0.012	0.071		0.007	
G3pd2							
−100	1.000	0.987	1.000	0.952	1.000	0.964	1.000
−50				0.048		0.029	
−120		0.013				0.007	

TABLE 3. Genetic variability at 29 loci in Black Ducks and Mallards. Abbreviations of locations are defined in Table 1.

Species (location)	H_{obs} ± SE	Percentage of polymorphic loci[a]	Mean no. of alleles[b]
Black Duck (NFLD)	4.7 ± 2.1	20.7	3.0
Black Duck (NSC)	5.3 ± 2.2	27.6	2.9
Black Duck (ONT)	5.9 ± 2.3	31.0	2.9
Mallard (CAL)	7.6 ± 2.9	27.6	2.8
Mallard (SASK)	5.4 ± 2.4	17.2	2.8
Mallard (MAN)	5.9 ± 2.4	24.1	3.4
Mallard (ONT)	4.7 ± 2.0	20.7	3.0
Mean[c]	5.6	24.1	3.0

[a] Frequency of most common allele ≤0.99.
[b] Per polymorphic locus.
[c] Unweighted by sample sizes.

for Mallards. $\bar{H}$ for Mallards and Black Ducks combined was 5.6% and ranged from 4.7% to 7.6% (Table 3); $\bar{H}$ was 5.3% for Black Ducks and 5.9% for Mallards.

A matrix of genetic distances among the 7 populations is shown in Table 4. The mean genetic distances, $\bar{D}$, between Black Duck populations, between Mallard populations, and between Mallard and Black Duck populations were nearly identical (Table 5). There was as much genetic differentiation within the two species as there was between them. Furthermore, the $\bar{D}$ between Mallards and Black Ducks (0.0006) was only 1% of that between those groups and American Wigeon (0.075).

The UPGMA (Fig. 1) and distance Wagner (Fig. 2) procedures produced similar branching diagrams that had similar r_{cc}'s. The former diagram produced two distinct groups, both of which contained Mallard and Black Duck populations; the latter diagram also failed to separate populations of the two species into distinct groups. A further phenetic analysis (Fig. 3), which included data for American Wigeon and Canada Geese, emphasized the similarity of Mallards and Black Ducks relative to a congener and a noncongeneric member of their subfamily.

DISCUSSION

Protein variation.—The percentage (24.1%) of polymorphic loci that we found in Mallards and Black Ducks is higher than that reported for some other groups of birds (Avise et al. 1980, Zink 1982, Gutiérrez et al. 1983), but is similar to that (20%) reported for Mallards by Parker et al. (1981). Patton and Avise (1985) assayed 19 loci in tissues from 10 Mallards and 4 Black Ducks and found that 10.5% and 5.3%, respectively, were polymorphic. In 6 of the 11 polymorphic loci that we found, however, the frequency of the most common allele exceeded 0.90; samples of 10 or less, such as used by Pat-

TABLE 4. Matrix of genetic distances between 7 populations of Black Ducks and Mallards. Wright's (1978) modified Rogers' distance is above the diagonal and Nei's (1978) distance is below the diagonal. Abbreviations of locations are defined in Table 1.

	Population						
Population	1	2	3	4	5	6	7
1 Black (NFLD)	—	0.033	0.038	0.032	0.044	0.042	0.050
2 Black (NSC)	0.001	—	0.030	0.040	0.031	0.027	0.031
3 Black (ONT)	0.001	0.000	—	0.039	0.028	0.033	0.037
4 Mallard (ONT)	0.000	0.001	0.001	—	0.041	0.039	0.054
5 Mallard (MAN)	0.002	0.000	0.000	0.001	—	0.027	0.041
6 Mallard (SASK)	0.001	0.000	0.000	0.001	0.000	—	0.040
7 Mallard (CAL)	0.002	0.000	0.000	0.002	0.001	0.001	—

TABLE 5. Mean genetic distances (Nei 1978), within and among Mallard and Black Duck populations, and between Mallards and Black Ducks combined and American Wigeon and Canada Geese.

Comparison	No. of comparisons	$\bar{D}$
Black Duck populations	3	0.0007
Mallard populations	6	0.0010
Mallards vs. Black Ducks	12	0.0006
Mallards and Black Ducks vs. American Wigeon	7	0.075
Mallards and Black Ducks vs. Canada Geese	7	0.322

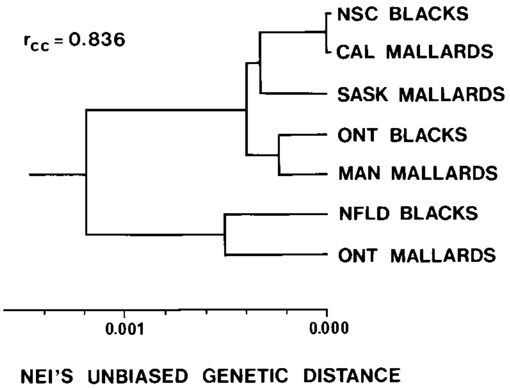

Fig. 1. Phenogram (UPGMA) of 7 populations of Mallards and Black Ducks using Nei's (1978) D-values from Table 4. Abbreviations are defined in Table 1.

ton and Avise, would be insufficient to detect many rare alleles. Clearly, the measure of polymorphic loci is dependent on both the sample size and the capability of the electrophoretic conditions used to detect allelic variation.

The $\bar{H}$s that we determined for Black Ducks (5.3%) and Mallards (5.9%) are within the range (2.0–14.6%) reported by Barrowclough et al. (1985) for 24 avian species, but higher than those reported by Patton and Avise (1985) for Mallards (3.7%) and Black Ducks (2.8%), and by Parker et al. (1981) for Mallards (2.7%).

Genetic distance.—The $\bar{D}$ (0.0006) that we found between Mallards and Black Ducks is the same as the $\bar{D}$ (0.001) that Patton and Avise (1985) found for a smaller sample of Mallards and Black Ducks. Such slight genetic distances are characteristic of local populations of avian species in other orders (Table 6). As pointed out by Patton and Avise (1985) in their study of 10 *Anas* species, the Anseriformes do not show unusually low levels of protein differentiation when compared with other birds (cf. Table 6). Note that the genetic distance between Mallards and Black Ducks is the lowest among members of the genus *Anas* (Table 6).

Cluster analyses (Figs. 1 and 2) produced groupings that neither separated Mallards from Black Ducks, nor showed any geographical pattern in the amount of genetic differentiation. The latter suggests considerable gene flow, particularly as our sampling areas spanned a distance of over 6,000 km. In eastern Ontario, where we obtained both Mallards and Black Ducks, hybrid Mallard × Black Ducks are common; Canadian Wildlife Service samples of wings from hunter-killed birds in that area contain 5–10% hybrids (Ankney and Dennis unpubl. data). Thus, a priori, we predicted that samples of Mallards and Black Ducks from eastern Ontario would show levels of genetic distance substantially lower than comparisons of samples from more geographically separate areas. This was not the case. We suggest that the amount of gene flow between groups is large enough to preclude differentiation.

For several reasons, the potential for gene flow among Mallard populations, and among Black Duck populations, is very great. First, pair formation in both species normally occurs during fall migration and on the wintering grounds (see Bellrose 1976: 236, 254–255), so that a female can easily become paired with a male raised in a different geographical area (see Bellrose 1976: 234 for a map of migration pathways and wintering areas). Second, the birds raised in a particular area do not all winter in the same area. Gollop (1965), for example, reported *direct* recoveries of three Mallard brood mates, banded in Saskatchewan, from Alberta, Oklahoma, and Oregon, and of two brood mates from another Saskatchewan brood that were recovered in Arkansas and California. Third, females normally return, with their mates, to nest in the area where they were raised (e.g. Gollop 1965). Fourth, because Mallards and Black Ducks are only seasonally monogamous, a male, during his life, may father broods in several geographic areas.

Mallard populations and Black Duck populations, throughout their North American ranges, are essentially panmictic. For example,

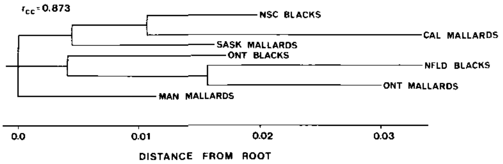

Fig. 2. Wagner Tree based on Wright's (1978) modified Rogers' D-values from Table 4. The tree is "rooted" at the midpoint of the longest path. Abbreviations are defined in Table 1.

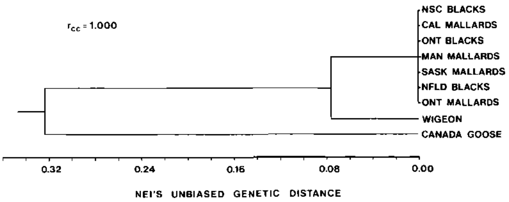

Fig. 3. Phenogram (UPGMA) derived from Nei's (1978) D-values in Tables 4 and 5. Abbreviations are defined in Table 1.

consider two female Mallards nesting on the Delta Marsh in Manitoba. Although both probably were raised there, one may have had a father raised in Ontario and the other a father from California. That presumably explains why we found no evidence of genetic differentiation on a geographical basis, even though we attempted to minimize the effects of gene flow by not sampling adult males.

For the foregoing reasons, and because Mallards and Black Ducks frequently hybridize (e.g. Heusmann 1974), gene flow between these taxa probably is very great. We show that a new allele, arising in a Newfoundland Black Duck, could appear in California Mallards within 5 years (Fig. 4).

Taxonomic implications.—We agree with the arguments of Barrowclough (1980), Gutiérrez et al. (1983), and Johnson and Zink (1983) that the genetic distance between two taxa does not, per se, indicate their taxonomic status. Johnson and Zink (1983) argued against subspecific status for Red-naped and Red-breasted sapsuckers (*Sphyrapicus nuchalis* and *S. ruber*), despite their low genetic distance ($D = 0.004$), because "these forms have 'proved' their biological species status" by mating assortatively in sympatry. Similarly, Gutiérrez et al. (1983) argued against subspecific status for Gambel's and California quail (*Callipepla gambelii* and *C. californica*) because only F_1 hybrids, and not a hybrid swarm, have been found. Clearly, decisions about taxonomic status require information about mating preferences and behavior, hybrid fitness, and historical data about stability of hybrid zones. Fortunately, there are data about those aspects of Mallard and Black Duck biology, and we thus are able to make a conclusion about their taxonomic status.

Black Ducks apparently arose from an ancestral Mallard population during the Pleistocene

TABLE 6. Genetic distances vs. taxonomic levels in three avian groups.

	Comparison		
Taxonomic group	Local population	Subspecies	Congeneric species
Anas[a]			
n			45
$\bar{D}$			0.092
Range			0.001[d]–0.186
Galliformes[b]			
n	6		3
$\bar{D}$	0.0007		0.0067
Range	−0.0015 to 0.0033		0.0051–0.0078
Passeriformes[c]			
n	113	86	71
$\bar{D}$	0.0024	0.0048	0.0440
Range	−0.0014 to 0.0125	−0.0014 to 0.0214	0.0078–0.1267

[a] From Patton and Avise (1985).
[b] From Gutiérrez et al. (1983).
[c] From Barrowclough (1980).
[d] Mallards vs. Black Ducks.

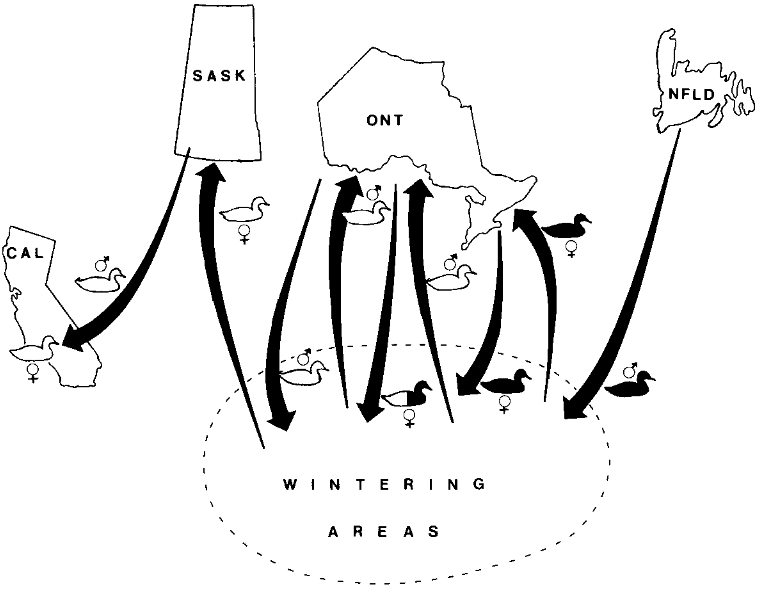

Fig. 4. Schematic demonstration of potential gene flow between Black Duck and Mallard populations. Closed symbols represent Black Ducks, open symbols represent Mallards, and the half-open, half-closed symbol represents an F_1 hybrid. A new allele, present in a male Black Duck in Newfoundland, is transferred to Ontario Black Ducks when the male pairs with an Ontario female; their daughter pairs with an Ontario Mallard . . . a male Mallard, raised in Saskatchewan, winters in California and pairs with a local female. Note: Many offspring of an F_1 × Mallard backcross are phenotypically Mallards (Phillips 1915).

(see Heusmann 1974) and were probably never very different genetically from Mallards, despite differences in plumage and habitat use. Before about 1900 there was relatively little contact between Mallards and Black Ducks (Heusmann 1974). Since then, however, due to the release of game farm Mallards in the eastern United States (Heusmann 1974) and a natural eastward range expansion of the Mallard (Johnsgard 1961), Mallards have become increasingly common in eastern North America. Coincidentally, Black Ducks have virtually disappeared from much of the western part of their range (e.g. southwestern Ontario; Dennis et al. 1985). During the past 50 years, hybrid Mallard × Black Ducks have been reported from virtually all parts of the Black Duck's range (Goodwin 1956, Johnsgard 1967, Heusmann 1974). Thus, it is inappropriate to try to delineate a hybrid zone, although some areas, e.g. eastern Ontario-western Quebec (Ankney and Dennis unpubl. data) and Massachusetts (Heusmann 1974), have a higher incidence of hybrids than do others. We predict that, based on what has happened in southern Ontario (Goodwin 1956, Dennis et al. 1985), this is not a stable situation. Rather, as the number of Mallards and hybrids increase, the number of Black Ducks will consequently decline, and eventually the number of hybrids will also decline as fewer and fewer Black Ducks will be available for mixed pairing.

The courtship displays of Mallards and Black Ducks are virtually identical (Johnsgard 1960). The factors that are important for mate selection in these groups have not been determined experimentally, but a recent field study (Brodsky and Weatherhead 1984) suggested that female Black Ducks, when courted by drakes of both groups, choose drake Mallards. That is not surprising because the bright plumages of male ducks in the genus *Anas* presumably have evolved through sexual selection (see Heusmann (1974) for an explanation of the dark, nonsexually dimorphic plumage of Black Ducks). We would be surprised if female Mallards chose drake Black Ducks over drake Mallards. Regardless, the high incidence of hybrids where both forms are common (Heusmann 1974, Ankney and Dennis unpubl.

data) suggests little if any behavioral, premating isolation. Estimates of the incidence of hybrids in an area are very conservative because many of the offspring of $F_1 \times F_1$ crosses and $F_1 \times$ Pure Type backcrosses look like one or the other parental type (Phillips 1915). This is particularly true for females. Therefore, it is highly unlikely that a classical hybrid swarm could be detected. The lack of philopatry by males (see above) reinforces the unlikelihood that a hybrid swarm could form. There is little evidence about selection for or against hybrids, but hybrid backcrosses are apparently as fertile as the parental types (Phillips 1915).

Thus, our data showing a very low level of genetic distance between Mallards and Black Ducks are consistent with the species' incomplete reproductive isolation. Until recently these taxa could have been best termed well-differentiated subspecies, analogous to, for example, Audubon's Warbler (*Dendroica coronata auduboni*) and the Myrtle Warbler (*D. c. coronata*). Although the two taxa are still somewhat split on an east-west basis—Black Ducks are virtually absent west of the Mississippi and Mallards are rare (although increasing) in northeastern Canada—our genetic data do not support even subspecific status for the Black Duck. We conclude that the Black Duck should be regarded as a melanistic morph of the Mallard. Furthermore, we suggest that continued interbreeding between the two forms will result in a continued decline of Black Ducks, a possibility that has been raised previously (e.g. Goodwin 1956; Johnsgard 1961, 1967; Heusmann 1974; Greig 1980; Dennis et al. 1985).

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THE DIET OF AMERICAN ROBINS: AN ANALYSIS OF U.S. BIOLOGICAL SURVEY RECORDS

NATHANIEL T. WHEELWRIGHT[1]

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853 USA

ABSTRACT.—I present a quantitative description of the diet of American Robins (*Turdus migratorius*) and consider how food habits (particularly the proportion of fruit eaten and the diversity of individual meals) are influenced by season, habitat, sex, and time of day. The study is based on an analysis of records of stomach contents compiled by the U.S. Biological Survey and the U.S. Fish and Wildlife Service. Across their entire range, robins ate fruits representing over 50 genera and invertebrates representing over 100 families. Diets were diverse even within local regions, and there was no obvious single feeding niche. The major food classes, consumed in every combination, were soft-bodied invertebrates, hard-bodied invertebrates, and fruits. The same taxa (especially fruits of the family Rosaceae and invertebrates of the orders Coleoptera and Lepidoptera) predominated in robins' diets, irrespective of habitat or geographical location, which presumably reflects both selective foraging and the availability of these widespread taxa.

The proportion of fruit (by volume) in the diet was much higher in the fall and winter (median values >90%) than in the spring (<10%); summer values were intermediate. The transition from a diet dominated by invertebrates to a diet dominated by fruits occurred over a 1-2-month period. The number of distinct food items in stomachs, a measure of the species diversity of individual meals, was positively correlated with the fraction of invertebrates in the diet. Thus, at the time of year when robins were dependent on fruits for food, the diversity of their meals was also lowest. The degree of fullness of the stomach showed few consistent trends with season or habitat.

Despite different sex roles and nutritional requirements, male and female robins did not differ in the proportion of fruit in the diet in any month or in any region. Nor did their stomachs contain different numbers of distinct food items, different amounts of food, or a different range or distribution of prey taxa. Habitat was an important variable explaining dietary differences.

The Biological Survey records have unavoidable shortcomings, most notably problems of sampling biases and the inability to correct for differential digestion of food items. Nonetheless, they are a valuable and underused data base for testing hypotheses, generating new questions of ecological interest, and describing in detail the diets of North American bird species. *Received 30 September 1985, accepted 5 March 1986.*

UNDER simple conditions, foraging models have successfully predicted birds' instantaneous food preferences on the basis of the energetic value, handling time, or other characteristics of potential prey (Krebs et al. 1983). Predicting total diets is much more difficult. The food that birds eat over their lifetimes or even a single day is a complex result of numerous foraging decisions. The foraging behavior of individuals may change diurnally (Holmes et al. 1978), seasonally (Baker and Baker 1973, Hutto 1981), or annually (Fogden 1972). Diet may depend on age (Greenberg 1983) or morphology (Herrera 1978), and it may differ in different parts of a species' range due to intrinsic preferences (Emlen and DeJong 1981) or geographical variation in prey availability (Fox and Morrow 1981). Such variation is also found in birds that eat both fruits and invertebrates (Colling 1941, Leck 1972, Crome 1975, Herrera 1978), two food types that differ strikingly in accessibility, edibility, and nutrients (Snow 1971, Morton 1973). Fruits and animal prey present different challenges for the digestive system (Walsberg 1975, Foster 1978, Milton 1981) and satisfy birds' nutritional needs to different degrees (Robbins 1983). When fruits and insects are similarly colored, their appearance may signal quite different palatability (Herrera 1985, Wheelwright and Janson 1985). Variation in the diet of fruit-eating birds has direct consequences for interactions between

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[1] Present address: Department of Biology, Bowdoin College, Brunswick, Maine 04011 USA.

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birds and the plants whose seeds they disperse (Howe and Smallwood 1982, Wheelwright and Orians 1982).

I examined in detail the diet of one species of fruit-eating bird, the American Robin (*Turdus migratorius*), to evaluate the effects of time (hour of day, season, age, year) and space (habitat, geographical region) on consumption of different food types. Knowledge of the diet of American Robins may yield insights applicable to many other passerine species besides fruit-eaters; robins belong to a diverse genus (including over 60 species) and one of the largest avian families (Muscicapidae). An analysis of stomach-content records for over 1,900 individual robins collected by the U.S. Biological Survey formed the basis of the study.

The stomach samples compiled by the Biological Survey possibly represent the most detailed data base on avian food habits in the world. Over 250,000 records exist for more than 400 native North American bird species (Martin et al. 1951). In the case of robins, birds were collected over most of their North American range, in all months of the year, at all hours of the day, and in a variety of habitats. Large samples of males, females, juveniles, and nestlings are represented. United States Department of Agriculture entomologists and botanists used extensive reference collections to identify food items to species or genus in most cases. To assemble such a data base today would be exceedingly difficult, prohibitively expensive, and ethically unjustifiable. Given the present interest in foraging behavior (Pyke et al. 1977, Krebs et al. 1983), seed dispersal by birds (Howe and Smallwood 1982, Wheelwright and Orians 1982), and plant-animal interactions (Thompson 1982), the Biological Survey stomach samples ought to be widely exploited by ecologists. Yet the data base has scarcely been used except for the general survey of Martin et al. (1951). One of my goals is to draw attention to its value in addressing ecological questions and suggesting new hypotheses to test.

METHODS

The study is based on records of food items in the stomachs of American Robins collected from 1885 to 1950. Half of the samples date from before 1908, and three-quarters had been collected (although not fully analyzed) by the time Beal (1915a, b) presented a general summary of the data in his evaluation of the economic impact of thrushes on agriculture. The original records of the U.S. Biological Survey and the U.S. Fish and Wildlife Service are currently filed on index cards at the Patuxent Wildlife Research Center in Laurel, Maryland. Each card corresponds to an individual bird and contains information on the sex of the bird, location, habitat, time of day, date, relative amount (by volume) of vegetable and animal matter in the stomach, fullness of the stomach (volume of stomach contents), and a list of food items. The relative amount (by volume) of each item in the stomach also is recorded.

This study focuses on three variables: (1) relative amount of fruit in the stomach, (2) number of distinct food types (taxa) in the stomach, and (3) volume of stomach contents. The original records summarize the proportion of fruit in the stomach under "vegetable matter." In robins, which only rarely eat leaves or seeds, the relative amount of fruit is virtually equivalent to vegetable matter, so I used the latter to estimate the degree of fruit eating. When I excluded individual robins whose stomachs contained vegetable matter other than fruits, the results of the analyses were the same. The relative amount of fruit ranged from 0 to 100% by volume; the number of food types ranged from 0 to 14; and the volume of stomach contents was scored as 0% ("empty"), 25% ("nearly empty," "quarter-filled"), 50%, 75%, or 100% ("well-filled"). I use the terms "food type" and "taxon" interchangeably to designate distinct classes of stomach contents, regardless of their taxonomic level. Thus, a record listing "2 *Rhus typhina* seeds, elytra of unidentified Scarabaeidae, 4 spiders" was considered to contain 3 food types. This information was entered into the computer at Cornell University for analysis. The untransformed data were analyzed using nonparametric statistical tests and analyses of variance (ANOVAs) for unbalanced data sets (General Linear Models, SAS 1985).

Because robins were collected from a wide geographical area (46 states, 5 Canadian provinces) and because an ANOVA of the entire data set indicated regional differences in diet, I divided the sample into three broad regions: eastern (Atlantic Coast states and provinces westward to Ontario, Minnesota, Iowa, Missouri, Arkansas, and Louisiana); central (states and provinces between the eastern and western regions); and western (Pacific Coast states and provinces eastward to Idaho, Nevada, and Arizona). These regions correspond, respectively, to the northeastern coniferous and eastern deciduous forests and southeastern coastal plain; the central prairies and eastern Rocky Mountain foothills; and the west coast and mountains. Each of these large geographical regions, which contain large sample sizes necessary for multivariate statistical tests, inevitably combines quite dissimilar habitats. Nonetheless, the regions were chosen because they roughly delimit distinct robin migratory routes and subspecies' ranges (eastern: *T. m. migratorius, T. m. nigrideus, T. m. achrustus;* central: *T. m. migratorius, T. m. propinquus;* western: *T. m. caurinus, T. m. propinquus;* Bent 1949). Even if the regions were totally arbitrary groupings of states, however, they allow a division of the sample into independent subsamples that can be compared to determine the generality of patterns in robin diet and to provide a check for sampling biases within any one region. Further subdivision into northeastern deciduous forest, mountain regions, southwestern arid areas, etc. did not qualitatively change the results presented here. I chose a smaller, more homogeneous region, the northeastern United States [New York and the states that border it (plus the ecologically similar state of Maine, included because it increased the sample size to improve statistical tests; its inclusion did not otherwise affect the analyses)] to examine robin diets in more detail and to look for interactions between factors that influence diet. Although males outnumber females in the sample (709 males vs. 460 females) and in each region, sex ratios do not differ between months or habitats in any of the different regions (Chi-square test, $P > 0.17$).

The data base has several major shortcomings. The original goal of the Biological Survey was to assess the economic impact of American wildlife on agricultural crops (McAtee 1933). As a result, many robins were shot in cultivated fruit trees (19.8%), grain fields (14.7%), and suburban areas (3.8%) at hours or on days convenient to collectors (or angry orchardists). Hence, the data base is not a random sample, which limits its usefulness for making inferences about diet in the population as a whole. Second, stomach contents may not reflect the relative importance of food types because of different rates of digestion of different foods. For example, earthworms are conspicuous elements of robins' diets (Bent 1949, Gochfeld and Burger 1984), yet they contribute to only 1.5% of all recorded invertebrate prey items in the sample ($n = 6{,}378$), presumably because of the difficulty of detecting earthworms soon after they are ingested. Beetle elytra, in contrast, remain undigested in the gut for relatively long periods (Wroot 1985; see Hamilton 1940, 1943; Johnson 1969). Third, the data base does not lend itself to answering questions about selectivity in feeding because no data were gathered on food availability in the habitats where birds were collected. Finally, because birds were killed, the records give only point samples of birds' diets, from which long-term patterns in diet can only be inferred. Despite these shortcomings, these records point to trends in feeding behavior that can be explored with a more appropriate experimental design.

American Robins occur throughout continental North America, where they are the largest species of thrush (Muscicapidae, Turdinae). In New York State during the nonbreeding season, male mass averages 86.2 ± 6.1 g ($n = 26$), and female mass averages 83.6 ± 6.4 g ($n = 18$). During the breeding season, masses average somewhat less (77.4 g for males and 80.6 g for females, $n = 21$ and 6, respectively). Although observed most commonly on suburban lawns (Eiserer 1980), robins frequent most North American habitats, from grasslands to coniferous forests (Bent 1949). Foraging mode is nearly as varied as geographical distribution and habitat use (Paszkowski 1982).

Robins begin breeding in April or May (depending on latitude and elevation), soon after returning from migration. Initial breeding dates are delayed about 3 days for each additional degree of latitude in the east, and nesting occurs later in the west (James and Shugart 1974). As in most passerines, females are responsible for nest construction and incubation; males assist in feeding nestlings. Pairs typically produce two clutches over a 2-month period (Howell 1942). Occasionally, a third clutch may be raised (Howell 1942). A complete molt occurs in July and August, at which time the fall migration begins.

RESULTS

Frequencies of different food types.—American Robins eat fruits of at least 51 genera and 28 families across their entire range (Appendix 1). For the entire sample, the most important taxa of fruiting plants were Rosaceae (34% of all fruit records), particularly the genera *Prunus* (20%; an undetermined but probably substantial proportion of these represent commercial cherries) and *Rubus* (5%, some of which may have been cultivated); Anacardiaceae (10%), particularly *Rhus* (5%) and *Schinus* (4%); Vitaceae (6%); and Cornaceae (5%) ($n = 1{,}308$ fruit records).

Robins also eat invertebrates representing at least 107 families and 14 insect orders (Appendix 1). Coleoptera comprised about 40% of robins' invertebrate diets (by frequency in stomachs) in the sample as a whole ($n = 6{,}378$ invertebrate records) as well as in most regions and habitats. These results should be interpreted cautiously because different digestive rates may introduce sampling biases and because prey frequencies are not weighted by prey mass or energetic content. Three beetle families were especially important: Carabidae (10%, particularly the genus *Amara*), Curculionidae (8%, particularly *Phytonomus*), and Scarabaeidae (7%, particularly *Lachnosterna*). Coleoptera were followed in frequency by Lepidoptera (13%) and Hymenoptera (9%). These three orders accounted for over half of all food items (inver-

TABLE 1. The 10 most common fruit and invertebrate taxa recorded in American Robin stomachs in the eastern region, compared with their frequencies in the central and western regions. Frequencies are expressed as a percentage of the total number of occurrences of each food type (fruits or invertebrates).

	East	Central	West
Fruit genera			
Prunus	0.23	0.05	0.08
Cornus	0.07	0.01	0.0
Rhus	0.07	0.01	0.0
Rubus	0.06	0.01	0.01
Smilax	0.06	0.04	0.005
Vaccinium	0.04	0.01	0.005
Ilex	0.04	0.03	0.0
Morus	0.04	0.04	0.0
Celtis	0.03	0.13	0.0
Juniperus	0.03	0.02	0.0
Invertebrate taxa			
Lepidoptera (unidentified)	0.12	0.12	0.07
Carabidae	0.10	0.13	0.11
Curculionidae	0.08	0.10	0.09
Scarabaeidae	0.08	0.07	0.05
Formicidae	0.07	0.05	0.04
Elateridae	0.05	0.05	0.05
Acrididae	0.05	0.04	0.02
Coleoptera (unidentified)	0.04	0.05	0.11
Arachnida	0.04	0.04	0.02
Pentatomidae	0.03	0.01	0.01
No. of individual birds	1,260	240	436
No. of individual prey items	5,141	1,595	1,104
Total no. of fruit genera	50	27	23
Total no. of invertebrate families	91	66	48

TABLE 2. ANOVA of relative amount of fruit eaten by American Robins.

	Source of variation[a]					
Region	Month	Habitat	Sex	Time	Decade	*n*
Entire United States	***	***	NS	*	*	568
East	***	***	NS	NS	*	350
Central	***	NS	NS	**	NS	144
West	*	NS	NS	NS	NS	74

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant.

tebrates plus vertebrates, fruits, seeds, and vegetable matter; $n = 7{,}840$). Lepidopteran prey were almost exclusively caterpillars. Prey of other invertebrate orders were chiefly adults, although larval Scarabaeidae commonly were eaten. Caterpillars and other soft-bodied insect larvae, like earthworms, may be underrepresented in stomach-sample records, although unlike earthworms they have head capsules and mouthparts resistant to digestion.

Even within a restricted geographical area, such as the northeast, robins consumed fruits from at least 37 plant genera and 12 plant families. They preyed on invertebrates of 72 families and insects of 12 orders. In New York State alone, robins were recorded eating fruits from 31 genera and insects from 59 families; in the vicinity of Ithaca, New York, robins ate fruits from at least 17 genera and insects from at least 43 families. The most common fruit families in the northeast were Rosaceae (43% of fruit records), Cornaceae (12%), Ericaceae (9%), and Anacardiaceae (7%) ($n = 481$ fruit records). The commonest insect families in the northeast were Carabidae (9% of invertebrate records), Formicidae (8%), Curculionidae (7%), Scarabaeidae (6%), and Elateridae (6%) ($n = 1{,}943$ invertebrate records).

The same invertebrate taxa proved to be important in diets within each geographical region. For example, of the 10 most frequent taxa of invertebrate prey eaten in each region, 7 taxa were common to all three regions (Table 1). Their relative and absolute frequencies were almost the same. These same invertebrate taxa appeared in robins' diets in approximately the same order of frequency in a comparison of records from natural, agricultural, and suburban habitats. In all three regions and in most habitat types Rosaceae was the first or second (central region) most common family of fruits eaten by robins, followed in frequency by Anacardiaceae. Fruit diets were more variable between regions than invertebrate diets, however. Of the 10 fruit genera most frequently represented in the eastern subsample, only *Prunus* was commonly eaten elsewhere (Table 1).

The effect of season, habitat, time, and sex on diet.—The proportion of fruit in robins' diets

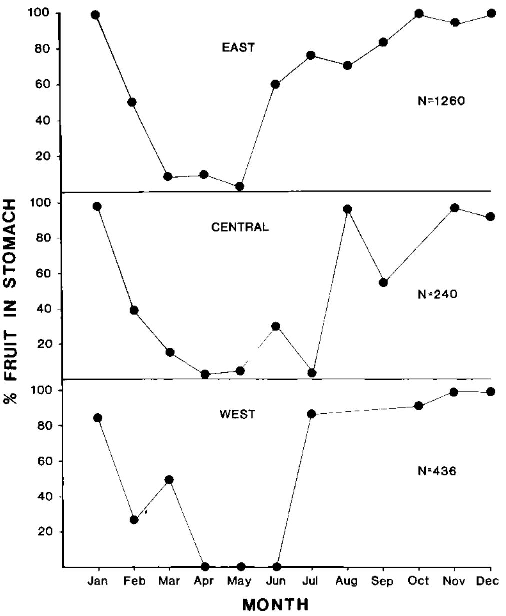

Fig. 1. Proportion of fruit (by volume, vs. animal prey) in the stomachs of robins collected in different months in three geographical regions of North America. Each point represents the median value for percentage of fruit for at least 5 individuals. Sample sizes (N) represent the number of individuals collected within each region over all months of the year.

was influenced by several factors. Most important was time of year (month when robins were collected), according to an ANOVA of the entire sample (Table 2). The same main effect was important in each of the regional samples (Table 2). For the entire sample and for certain regional samples, habitat and, to a lesser degree, time of day also affected the extent of fruit eating. Decade of collection had a minor effect, which could reflect long-term sampling biases, differences in methods of describing stomach contents used by different Biological Survey personnel, or actual long-term changes in the diets of robins (Table 2). Sex was an insignificant factor. In an ANOVA of records from the northeast, only month accounted for significant variation in the degree of fruit eating; interactive effects (habitat by month, sex by month, and sex by habitat) were not significant ($P > 0.05$).

The number of different food types in robin stomachs was also strongly affected by time of year in an ANOVA of all regions (Table 3). Habitat, time of day, and decade had significant effects in certain regions, but nowhere were they of major importance. Once again, there were no differences due to sex. In the northeast sample, time of year was apparently less important ($P = 0.09$) than time of day ($P < 0.01$) in explaining variation in number of food types. This inconsistent result probably is due to the fact that robins are scarce in the northeast during the late fall and winter (when fruits dominate their diets; Fig. 1), thereby affecting the ANOVA. All other factors, including interactive effects, were insignificant sources of variation in number of food types eaten at one time in the northeast.

TABLE 3. ANOVA of number of different food items in American Robin stomachs.

	Source of variation[a]					
Region	Month	Habitat	Sex	Time	Decade	*n*
Entire United States	***	**	NS	**	***	572
East	***	*	NS	**	***	350
Central	**	NS	NS	NS	NS	148
West	*	*	NS	NS	*	74

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant.

The volume of stomach contents (fullness of the stomach) depended to some degree on time of year and time of day (Table 4). Habitat, sex, and decade were unimportant factors. In the northeast, only time of day approached statistical significance as a factor that accounted for variation in stomach fullness ($P = 0.06$). The results of the ANOVAs suggested that further analysis of individual factors was warranted.

TABLE 4. ANOVA of fullness of stomach in American Robins.

	Source of variation[a]					
Region	Month	Habitat	Sex	Time	Decade	*n*
Entire United States	*	NS	NS	**	NS	571
East	**	NS	NS	*	NS	349
Central	*	NS	NS	NS	NS	148
West	NS	NS	NS	NS	NS	74

[a] * = $P < 0.05$, ** = $P < 0.01$, NS = not significant.

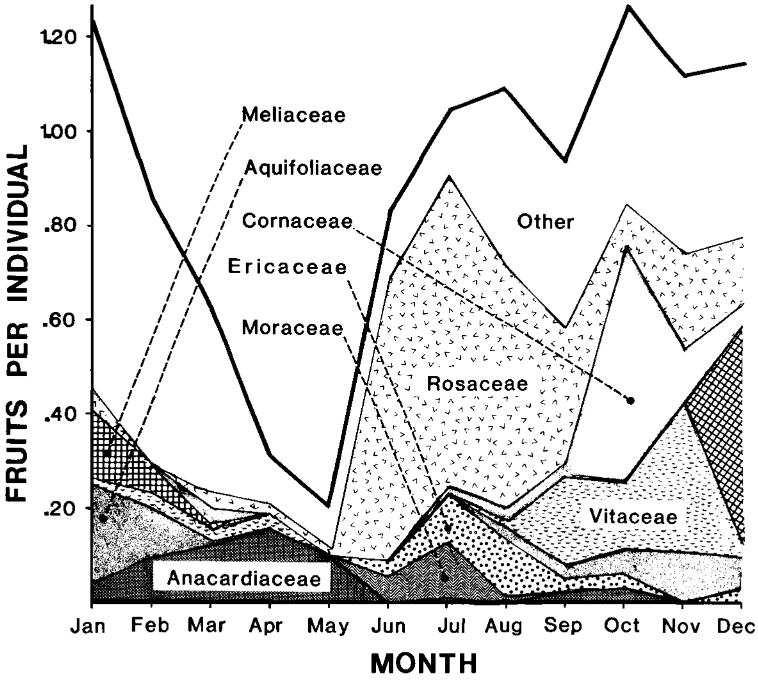

Fig. 2. Average occurrence of fruits of various plant families in the stomachs of robins in eastern North America in different months.

Each of these factors and their effects on the proportion of fruit, number of food types, fullness, and prey frequencies are considered in greater detail below.

Seasonal trends.—Robins ate fruits in every month of the year (Fig. 1). Most fruits eaten by birds that remained at high latitudes during the winter or returned in the spring were fall-ripening species that persist over the winter on plants. Perhaps the best examples are *Rhus* spp., whose fruits are eaten by robins in New York in every month of the year except August (pers. obs.); *Rhus* seeds were recorded in stomach samples in most months (Fig. 2). Different families of fruiting plants were prominent in robins' fruit diets at different times of year (Fig. 2). Species of Rosaceae dominated the fruit diet in mid- to late summer and were replaced in fall by species of Cornaceae and Vitaceae. The family Anacardiaceae was most conspicuous as a spring food. Genera within families also varied in importance over time. For example, within the Rosaceae, fruits in the genera *Prunus* and *Rubus* were eaten commonly in June, July, and August, whereas hawthorn fruits (*Crataegus* spp.) were eaten in late fall and again in spring (Fig. 3).

Although robins fed on fruits year-round, there was a clear seasonal pattern in fruit eating (cf. Jordano and Herrera 1981). The median percentage of fruit (by volume) in robins' stomachs was relatively low in the months immediately preceding breeding and during the breeding season; it declined to less than 10% in April and May in all three regions of North America (Fig. 1). (I use medians rather than means because values for the proportion of fruits eaten were bimodally distributed; means, however, showed similar seasonal trends despite being less extreme than medians.) During the fall and early winter (August through January), in contrast, over 80–99% of the diet (by volume) comprised fruits (Fig. 1). The change in diet occurred abruptly, with the proportion of fruit climbing from less than 10% to over 80% within 1–2 months (Fig. 1). The frequency of fruits in robins' stomachs was significantly lower in the breeding season (April through July) than in the nonbreeding season (Wilcoxon two-sample test, $P < 0.001$ in each region).

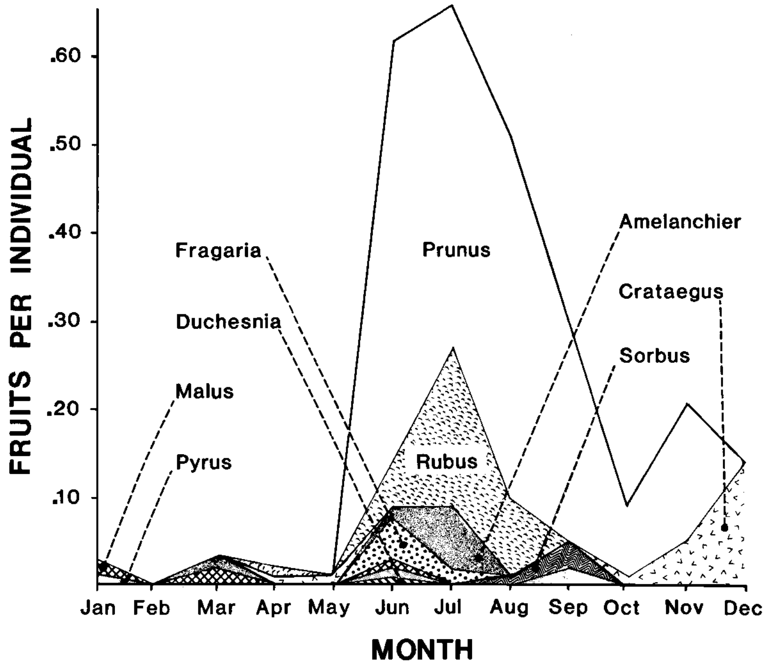

Fig. 3. Average occurrence of fruits of various genera in the Rosaceae (the plant family whose fruits were eaten most commonly by robins) in the stomachs of robins in eastern North America in different months.

In all regions, fruits were eaten most commonly in fall (median proportion eaten = 96%, mean = 77.2%, both sexes combined), with decreasing amounts eaten in winter (median = 93%, mean = 67.2%), summer (median = 66%, mean = 38.6%), and spring (median = 6%, mean = 37.7%) (Kruskal-Wallis test, $P < 0.001$; seasons defined as in Martin et al. 1951).

The number of distinct food types also varied seasonally. During the breeding season 4-6 taxa occurred on average in stomach contents. During winter months the mean number of distinct food types dropped by half (Fig. 4). The number of food items per stomach was significantly higher in the breeding season than in the nonbreeding season (Wilcoxon two-sample test, $P < 0.001$ in all regions). Consequently, the number of distinct food types and the degree of fruit eating were negatively correlated [Spearman rank test, $r_s = -0.49$, $P < 0.001$; linear regression: (percentage of fruit) = -6.5(number of distinct food types) + 78.0, $r^2 = 0.19$, $P < 0.001$, $n = 1{,}919$].

The fullness of stomachs varied with region. In the eastern sample, stomachs tended to be less full in the breeding season than in the nonbreeding season (Fig. 5; Wilcoxon two-sample test, $P < 0.001$). The opposite was true of the sample from the central region ($P < 0.001$), whereas there were no significant differences in fullness between seasons in the western region ($P = 0.12$). Within the sample as a whole, fullness of the stomach correlated positively with number of food types (Spearman rank test, $r_s = 0.19$, $P < 0.001$, $n = 1{,}919$) but not with proportion of fruit in the stomach ($r_s = 0$, $P = 0.92$).

Differences between sexes.—Male and female robins did not differ significantly in the proportion of fruit eaten in any month in any region, including New York State (Wilcoxon two-sample test, $P > 0.05$; Fig. 6). Both sexes showed similar seasonal trends in frugivory.

The sexes differed in the number of distinct food types (Wilcoxon two-sample test, $P > 0.15$) only in October in the eastern sample, July in the central sample, and November in the western sample. In these three months, the stomachs of females held more food types than the stomachs of males ($P < 0.05$). In 31 monthly comparisons from the three regions (12 months in the east, 9 months in the central region, 10

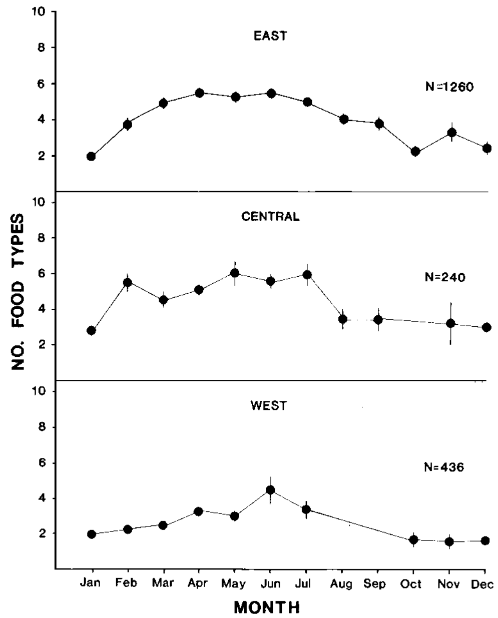

Fig. 4. Number of distinct food taxa in the stomachs of robins collected in different months in three geographical regions of North America. Each point represents the mean value of number of food types for at least 5 individuals; bars represent 1 SE of the mean.

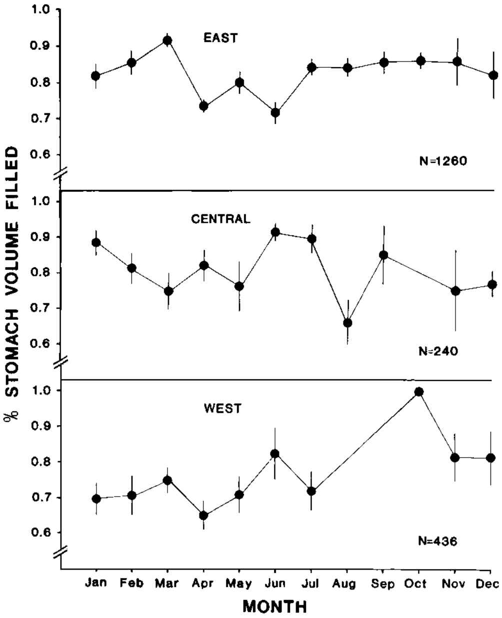

Fig. 5. Fullness of the stomachs of robins collected in different months in three geographical regions of North America. Each point represents the mean value of percentage of stomach volume filled for at least 5 individuals; bars represent 1 SE of the mean.

months in the west; not all months had sample sizes adequate for statistical comparisons), the number of food types per stomach in females exceeded that of males in 18 cases. The reverse was true in the remaining 13 cases, although, as noted above, differences were statistically significant in only 3 of these comparisons.

In 21 of 30 monthly comparisons, females had slightly fuller stomachs on average than males, although these differences were not significant in any month in any region (Wilcoxon two-sample test, $P > 0.05$).

The diet of the sexes was indistinguishable with regard to specific taxa of food items (vs. proportion of fruits, meal diversity, or volume of stomach contents). In most cases, sample sizes for particular taxa were too small to permit statistical tests of differences between sexes while controlling for time of year. However, the sexes did not differ in prey consumption in any month (Chi-square test, $P > 0.64$) in the four most commonly eaten insect orders (Coleoptera, Lepidoptera, Hymenoptera, Hemiptera) in the eastern region (which had the largest sample sizes). In the whole sample, without regard to time of year, the sexes did not differ in their consumption of these four insect taxa ($P = 0.66$, $n = 1{,}703$ prey items). Males and females ate similar numbers of taxa of invertebrates, fruits, and other vegetative matter (Table 5). Differences between the sexes in prey consumption of the most commonly eaten invertebrate orders and beetle families in the homogeneous New York sample during the four breeding-season months were slight or nonexistent (Fig. 7). At the prey-species level, sample sizes in homogeneous regions were too small to test for significant differences between males and females, but no such differences were suggested by the data.

Differences between age classes.—Stomachs of juvenile robins generally contained a higher proportion of fruit than stomachs of adults, at least in the eastern region where sample sizes were sufficiently large for statistical tests. In monthly comparisons from June through September (the period when juveniles can be easily distinguished by plumage), eastern juveniles consistently ate a higher proportion of

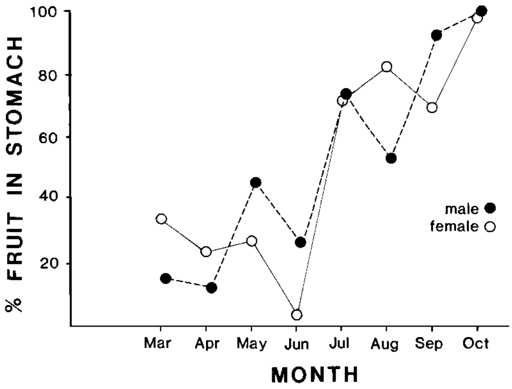

Fig. 6. Proportion of fruit (by volume, vs. animal prey) in the stomachs of male and female robins collected in different months in New York. Each point represents the median value for percentage of fruit for at least 5 individuals.

TABLE 5. Number of taxa of fruits, invertebrates, and grasses/seeds/leaves recorded eaten by adult male and female American Robins, and by juveniles in each geographical region.

	Region		
Food type	East	Central	West
Fruits			
Males	49	30	23
Females	46	28	23
Juveniles	21	9	2
Invertebrates			
Males	77	41	43
Females	60	45	43
Juveniles	54	36	9
Grasses/seeds/leaves			
Males	16	8	5
Females	12	8	5
Juveniles	11	3	0

fruits than did adults. The differences were significant in three of the four months (Wilcoxon two-sample test, $P < 0.01$, $n = 142$ juveniles and 405 adults).

The stomachs of juveniles in the eastern region contained significantly more food types on average than those of adults in June and August. This was reversed in July and September (Wilcoxon two-sample test, $P < 0.01$). In the central and western regions, juveniles' stomachs contained more food types than adults' in half of the monthly comparisons and fewer food types than adults' in the other half of the monthly comparisons, but none of these differences was significant ($P > 0.05$).

Eastern juveniles had fuller stomachs than adults in comparisons in June, July, and August, significantly so in June and August ($P < 0.01$). Adults, in contrast, had fuller stomachs in September ($P < 0.05$). There were no significant differences in the volume of stomach contents in monthly comparisons of juveniles and adults in the central and western regions, possibly due to smaller sample sizes. In terms of total numbers of taxa of fruits, invertebrates, and vegetation, fewer taxa were recorded for juveniles than for adults (Table 5). This pattern probably emerged because far fewer juveniles were sampled than adults. Furthermore, juveniles were collected chiefly in fall, when diets tend to be less diverse than in spring or summer.

Habitat effects.—Robin stomachs contained different proportions of fruit depending on the habitats in which birds were collected (Table 6). In the sample as a whole, the proportion of fruit per stomach was higher among birds collected in orchards (median percentage of fruit = 96.0%), native fruiting trees (90.0%), and forests (80.0%) than in agricultural fields collectively (10.5%). Birds found in meadows and edge habitats ate intermediate amounts of fruit (60.0% and 31.0%, respectively). Note that these figures are not adjusted for monthly biases. Habitat differences in fruit eating were greatest in the spring and early summer. In August, the extent of fruit eating began to converge in distinct habitats, and by October stomachs of birds collected in all habitats contained similar proportions of fruit (80–99%). Although the major habitat types were not represented in the same proportions in the three geographical regions (Chi-square test, $P < 0.02$), the same associations between fruit eating and habitat were found everywhere.

The number of distinct food types and the volume of stomach contents showed few consistent trends among habitats (Table 6). The consumption of insects from the four most commonly eaten orders depended on habitat (Chi-square test, $P < 0.001$). Coleoptera were eaten with disproportionate frequency in open habitats (fields, lawns) and relatively infrequently in edge habitats. The reverse was true for Hymenoptera and Lepidoptera. Hemiptera were preyed on more commonly than expected

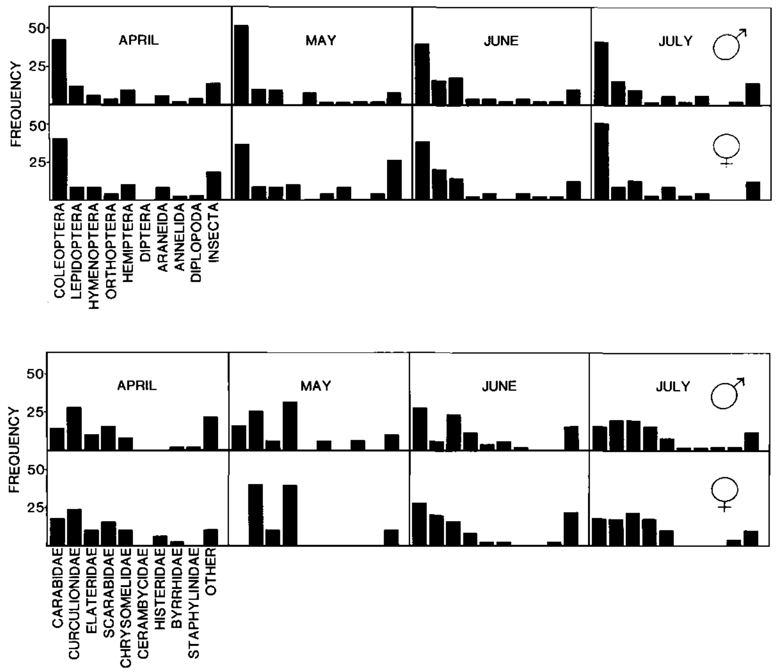

Fig. 7. Frequency (as a function of the number of all records of invertebrates eaten) of different invertebrate taxa (top) and beetle families (bottom) in the stomachs of male and female robins during the 4-month breeding season in New York.

by chance in forested habitats and less commonly than expected in open habitats ($P < 0.05$).

The influence of time of day.—Robin stomachs contained a smaller proportion of fruits in the morning ($n = 1{,}499$) than in the afternoon ($n = 423$) for the whole sample (Wilcoxon two-sample test, $P < 0.001$). In monthly comparisons, however, diurnal differences disappeared. Robins ate a greater percentage of fruits in the afternoon in 19 of 33 monthly comparisons, considering the three regions separately (sample sizes were too small in certain regions in certain months to permit statistical tests).

Neither the number of food types nor fullness of the stomach differed between morning and afternoon. Thus, in 18 of 33 monthly comparisons, robin stomachs contained more distinct food items in the afternoon than in the morning. Stomachs were fuller, on average, in the afternoon in 15 of 32 monthly comparisons. When considering only monthly comparisons that showed a significant difference between morning and afternoon ($P < 0.05$), there was somewhat better support for diurnal differences in diet. Relative to the morning, in the afternoon robins ate a significantly higher proportion of fruit in 5 of 7 monthly comparisons, their stomachs contained significantly more different food items in 4 of 5 comparisons, and their stomachs were significantly fuller in 4 of 5 comparisons.

Associations of food types within meals.—When two or more different prey types were found in stomachs, invertebrates were more likely to be associated with invertebrates, and fruits with fruits, than expected by chance (Chi-square test, $P < 0.001$, $n = 19{,}409$ associations of food items). Certain insect taxa co-occurred with greater frequency than expected by chance; others co-occurred relatively infrequently. A more detailed summary of prey associations within stomachs is given in Appendix 2. No general properties or associations emerged that could define a single feeding niche (Root 1967) for American Robins.

DISCUSSION

This study documents three distinct features of the diet of American Robins. First, robins eat

TABLE 6. Median proportion of fruit, mean number of distinct food types, and mean fullness of the stomach in American Robins collected in different habitats with $n > 30$ individual birds. These figures are not corrected for time of year.

Habitat	Percentage of fruit	No. of items	Fullness	n
Wheat fields	0.0	2.48	0.64	46
Alfalfa fields	3.5	5.67	0.87	72
Fields (general)	16.0	5.34	0.82	39
Pastures	52.0	4.35	0.82	97
Grain fields (miscellaneous)	72.0	2.16	0.65	73
Lake edges	0.0	4.64	0.47	47
Swamps	81.0	3.69	0.78	54
River edges	99.0	3.21	0.79	39
Lawns	81.0	3.50	0.79	34
Orchards (large fruits)	72.0	3.33	0.78	165
Vineyards	83.5	3.12	0.73	42
Cherry trees	90.0	5.29	0.83	127
Coniferous forests	51.0	5.18	0.78	34
Deciduous forests	77.0	3.79	0.85	182

a wide range of invertebrates and fruits throughout their range. Second, the nature of the diet changes dramatically and rapidly over time (Fig. 1). Robins rely on fruit during the fall and winter throughout their range. At the beginning of the breeding season, fruits comprise less than 10% of their diet. Third, the sexes do not differ in diet in any season. The first two results were recognized previously (Forbes 1879, Beal 1915a, Bent 1949, Brown 1976), although the abruptness and magnitude of the shift in diet were unanticipated. My study, however, provides a quantitative assessment of the breadth and seasonal variation in taxonomic composition of the diet in robins. The third result, the lack of differences between sexes, was unexpected because of sexual differences in reproductive roles and projected nutritional requirements (see below). These results raise several questions about seasonal changes in the diet of robins and other fruit-eating birds.

Both opportunity and choice probably determine diet depending on the time scale considered. On a daily basis diets do not appear to change with respect to amount of fruit eaten, diversity of meals, or fullness of the stomach, which could reflect relatively constant nutritional needs, nonselective foraging, and no differential depletion of distinct food types over short time periods. In contrast, during the year diets change markedly. Fruits in all habitats sampled varied seasonally in availability (Snow 1971, Morton 1973, Wheelwright 1985). In the Temperate Zone fruits tend to increase in abundance in the fall (Thompson and Willson 1979), which is when they dominate in robins' diets. The change in diets is far more sudden, however, than the change in relative availability of fruits. Insects are certainly common in most habitats in June, July, and August when robins begin to feed heavily on fruits. Furthermore, juveniles and adults differed in the amount of fruits consumed at the same times of year, suggesting that seasonal differences in diet reflect preferences (Brown 1976), age-related foraging skills (Gochfeld and Burger 1984), or nutritional needs as well as feeding opportunities.

Shifts from a cryptic, indigestible, nutritious insect diet to an accessible, easily digested, low-nutrition fruit diet presumably require major shifts in morphology and are constrained even over evolutionary time (Milton 1981, Demment and Van Soest 1985). Some species solve the problem by handling fruits and invertebrates in the stomach in distinct ways (Walsberg 1975). Other species may exhibit seasonal changes in gizzard thickness (Spitzer 1972), intestine length (Al-Jaborae 1980), cecum length (Pendergast and Boag 1973), or gut microflora (Jayne-Williams and Coates 1969). Conceivably, digestive enzymes could be adjusted to seasonal changes in diet, although this has not been documented. In any event, robins and other Temperate Zone fruit-eating birds must process fruits effectively, for molt and migration occur during periods when their diet is dominated by fruits. These events are presumably energetically and nutritionally expensive (Robbins 1983).

Another potential problem raised by these results is to account for the lack of detectable differences in diet between the sexes. Females of all bird species generally require elevated levels of protein, minerals, and energy during egg laying (Robbins 1983). Caloric intake and nitrogen requirements, for example, may quadruple during reproduction (Robbins 1981, Walsberg 1983). In contrast, males of most species invest relatively little in the early stages of reproduction, including egg laying, nest building, and incubation (Howell 1942). Such ecological differences would be expected to demand different diets for male and female robins. Yet I found no evidence that female robins eat a wider range or distinct taxonomic distribution of food items, that their stomachs contain a greater volume of food or more food types, or that they consume less fruit than males at any season or in any region. Female robins seem to eat the same things as males. If this is true, it is possible that female robins meet their nutritional requirements by eating more earthworms or other soft-bodied prey that are underrepresented in the sample, process foods at a faster rate, are more efficient at nutrient uptake, or forage for more hours per day than males. There is no published evidence for any of these possibilities, however. Conceivably, females select more nutritious individual prey items than males, or feed on distinct species (vs. genera or families) than males, differences that would not have been detected in this study (see Green and Jaksic 1983). Males may supplement females' diets through courtship feeding (E. Jones pers. comm.).

Differences in the amount of fruit eaten by adult and juvenile robins may be explained by age-specific differences in foraging ability. Because of their inexperience, juveniles have inferior foraging success when hunting invertebrates (Gochfeld and Burger 1984) and must turn to fruits to meet their caloric needs. Fruits, despite their nutritional limitations, are acquired more easily than invertebrates (Snow 1971, Wheelwright 1983). Thus, even though developing juveniles presumably have greater protein requirements than adults (Robbins 1983), they may have to sustain their growth on a nutritionally inferior diet high in fruits until they have learned to forage efficiently.

Diet breadth and the distribution of American Robins.—American Robins have an extremely broad diet, and it is tempting to relate this to their broad geographic range and population size. It is important to distinguish diet breadth from diet plasticity, however. Even though robins eat invertebrates from over 100 families, the same taxa predominate in stomach samples throughout the robins' range, irrespective of habitat. Robins may owe their success to their ability to feed predominately on terrestrial invertebrate taxa that happen to be widespread and abundant, not to any behavioral flexibility that has enabled them to learn new foraging skills. Although robins are generalists in one sense, they appear specialized in another sense because they are tied to certain food types.

Robins appeared more flexible with respect to fruit diet than to invertebrate diet. Only rosaceous fruits were eaten commonly in each region. The consistently high frequency of the Rosaceae in robins' diets reinforces a growing perception that fruit-eating birds may feed opportunistically on many fruit species but tend to specialize on the fruits of a few plant families, indicating selective foraging and possible coevolution at taxonomic levels above the species (Wheelwright 1983, Moermond and Denslow 1985).

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APPENDIX 1. Fruit and invertebrate taxa eaten by American Robins. Families and genera are listed for fruits; orders and families are listed for insects. Taxa are arranged alphabetically.

Fruits

- Anacardiaceae
  - *Rhus*
  - *Schinus*
- Aquifoliaceae
  - *Ilex*
  - *Nemopanthus*
- Berberidaceae
  - *Berberis*
- Caprifoliaceae
  - *Lonicera*
  - *Sambucus*
  - *Symphoricarpos*
  - *Viburnum*
- Celastraceae
  - *Celastrus*
  - *Euonyumus*
- Cornaceae
  - *Cornus*
  - *Nyssa*
- Ebenaceae
  - *Diospyros*
- Elaeagnaceae
  - *Elaeagnus*
- Empetraceae
  - *Empetrum*
- Ericaceae
  - *Gaylussacia*
  - *Oxycoccus*
  - *Vaccinium*
- Lauraceae
  - *Lindera*
  - *Persea*
  - *Sassafras*
- Liliaceae
  - *Smilax*
- Loranthaceae
  - *Phoradendron*
- Meliaceae
  - *Melia*
- Menispermaceae
  - *Menispermum*
- Moraceae
  - *Ficus*
  - *Morus*
- Myricaceae
  - *Myrica*
- Oleaceae
  - *Olea*
- Palmae
  - *Sabal*
- Pinaceae
  - *Juniperus*
- Phytolaccaceae
  - *Phytolacca*
- Rhamnaceae
  - *Berchemia*
  - *Rhamnus*
- Rosaceae
  - *Amelanchier*
  - *Crataegus*
  - *Duchesnia*
  - *Fragaria*
  - *Malus*
  - *Prunus*
  - *Pyrus*
  - *Rubus*
  - *Sorbus*
- Rubiaceae
  - *Mitchella*
- Saxifragaceae
  - *Ribes*
- Solanceae
  - *Solanum*
- Ulmaceae
  - *Celtis*
- Vitaceae
  - *Ampelopsis*
  - *Parthenocissus*
  - *Vitis*

Invertebrates

- Amphipoda
- Annelida
- Arachnida
  - Araneida
  - Pseudoscorpionida
- Chilopoda
- Coleoptera
  - Anthicidae
  - Buprestidae
  - Byrrhidae
  - Cantharidae
  - Carabidae
  - Cerambycidae
  - Chrysomelidae
  - Cicindelidae
  - Coccinelidae
  - Curculionidae
  - Dermestidae
  - Dytiscidae
  - Elateridae
  - Erotylidae
  - Haliplidae
  - Histeridae
  - Hydrophilidae
  - Lampyridae
  - Languridae
  - Miridae
  - Nitidulidae
  - Scarabidae
  - Scolytidae
  - Silphiidae
  - Staphylinidae
  - Tenebrionidae
- Decapoda
- Diplopoda
  - Julida
  - Polydesmida
- Diptera
  - Anthomyiidae
  - Bibionidae
  - Chironomidae
  - Chloropidae
  - Empididae
  - Ephydridae
  - Lonchaeidae
  - Micropezidae
  - Muscidae
  - Mycetobiidae
  - Otitidae
  - Stratiomyidae
  - Tabanidae
  - Tachinidae
  - Tipulidae
  - Sarcophagidae
- Gastropoda
- Hemiptera
  - Anthocoridae
  - Coreidae
  - Corimelidae
  - Corizidae
  - Cydnidae
  - Lygaeidae
  - Miridae
  - Nabidae
  - Pentatomidae
  - Piesmidae
  - Reduviidae
  - Rhopalidae
  - Scutelleridae
- Homoptera
  - Aphidae
  - Cicadellidae
  - Cicadidae
  - Fulgoridae
  - Membracidae
- Hymenoptera
  - Apidae
  - Braconidae
  - Chalcidae
  - Cynipidae
  - Formicidae
  - Halictidae
  - Ichneumonidae
  - Sphecidae
  - Symphyta (misc.)
  - Tenthredinidae
  - Tiphiidae
  - Vespidae
- Isopoda
- Isoptera
- Lepidoptera
  - Arctiidae
  - Bombycidae
  - Geometridae
  - Noctuidae
  - Notodontidae
  - Olethreutidae
  - Psychidae
  - Tortricidae
- Mallophaga
- Mecoptera
  - Meropidae
- Neuroptera
  - Chrysopidae
  - Corydalidae
  - Myrmelionidae
  - Raphidiidae
- Odonata
  - Anisoptera (misc.)
  - Zygoptera (misc.)
- Orthoptera
  - Acrididae
  - Blattidae
  - Gryllidae
  - Tetrigidae
  - Tettigoniidae
- Phalangida
- Trichoptera

APPENDIX 2. Frequency of co-occurrence of the most common taxa of fruits and invertebrates in American Robin stomachs.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
1. Arachnida	—																														
2. Diplopoda	21	—																													
3. Acrididae	55	25	—																												
4. Pentatomidae	44	21	37	—																											
5. Unidentified Hemiptera	42	21	32	18	—																										
6. Carabidae	117	63	167	87	79	—																									
7. Chrysomelidae	22	13	20	18	21	57	—																								
8. Curculionidae	92	60	70	82	73	258	58	—																							
9. Elateridae	67	32	45	50	27	164	36	144	—																						
10. Scarabidae	81	38	82	73	59	222	45	196	135	—																					
11. Unidentified Coleoptera	38	31	42	24	31	111	20	102	64	76	—																				
12. Noctuidae	11	3	11	5	9	54	10	40	19	28	47	—																			
13. Unidentified Lepidoptera	140	68	112	94	99	330	64	258	161	256	132	17	—																		
14. Unidentified Diptera	14	18	8	12	13	46	16	40	24	32	32	13	49	—																	
15. Formicidae	72	34	74	50	53	164	38	169	105	140	96	21	179	22	—																
16. Unidentified Hymenoptera	23	15	28	17	33	67	16	61	35	41	27	3	71	13	49	—															
17. Unidentified insects	262	118	201	199	153	616	160	519	326	418	267	100	614	121	315	126	—														
18. *Smilax*	7	8	9	3	3	23	1	21	7	5	18	1	14	1	3	1	28	—													
19. *Celtis*	0	1	0	1	0	6	3	4	0	1	5	0	5	1	0	0	9	3	—												
20. *Morus*	7	3	10	6	0	19	6	14	9	10	8	2	14	2	10	3	29	0	0	—											
21. Unidentified *Prunus*	19	7	38	11	18	88	25	69	43	63	41	10	76	10	74	21	160	0	0	14	—										
22. *Rubus*	12	0	21	7	7	22	4	13	15	13	8	1	33	1	20	8	43	1	0	2	19	—									
23. *Melia*	1	3	2	0	2	25	3	1	0	2	8	0	14	2	0	0	34	2	4	0	0	0	—								
24. *Rhus*	18	7	16	14	13	19	4	25	12	17	9	2	37	2	12	6	51	4	2	0	0	0	0	—							
25. *Schinus*	0	1	1	1	1	5	1	2	2	2	2	6	2	0	1	1	7	0	0	0	0	0	0	0	—						
26. *Ilex*	0	0	1	0	1	4	1	2	3	1	6	0	6	1	1	0	10	7	7	0	0	0	0	1	0	—					
27. *Vitis*	3	2	9	3	8	17	2	8	1	9	4	1	20	1	6	0	39	0	0	0	1	0	0	1	1	1	—				
28. *Cornus*	3	1	2	1	4	3	1	2	2	1	3	1	5	1	4	2	9	0	0	0	1	2	0	2	0	1	4	—			
29. *Vaccinium*	8	3	9	7	2	15	1	9	15	13	6	0	23	2	13	3	26	0	0	0	3	4	1	0	0	0	0	0	—		
30. Unidentified fruits	158	100	132	106	90	405	68	314	196	247	197	43	407	66	231	104	844	25	10	14	86	25	8	30	2	17	16	17	11	—	
Total	1,337	696	1,179	889	799	2,740	583	2,013	1,174	1,375	916	221	1,569	246	739	275	1,992	42	23	30	110	31	9	34	3	19	20	17	11	294	—

DAILY ACTIVITY PATTERNS OF SOUTH POLAR AND BROWN SKUAS NEAR PALMER STATION, ANTARCTICA

PAMELA J. PIETZ
*Department of Ecology and Behavioral Biology, University of Minnesota,
Minneapolis, Minnesota 55455 USA*

ABSTRACT.—I conducted a behavioral study of sympatrically nesting South Polar (*Catharacta maccormicki*) and Brown skuas (*C. lonnbergi*) near Palmer Station, Antarctica. A total of 4,058 bird-hours of observations was made on eight South Polar, three Brown, and one mixed-species pair during the 1979–1980 and 1980–1981 austral summers. I used subsets of these data to analyze various aspects of skua activity patterns.

South Polar Skuas exhibited maximum resting and minimum foraging activity during the twilight period around 2400. Brown Skuas appeared to rest and forage more randomly. Members of the mixed pair exhibited patterns similar to those of their respective species. Several hypotheses are suggested to account for species differences in activity patterns; most of these relate dietary differences and differential foraging abilities at low light levels.

In both species, agonistic and preening activities occurred at all hours. South Polar Skuas, however, were most often observed bathing in early afternoon and preening in afternoon and twilight. Pairing activity showed no discernible relationship with time.

Foraging bouts averaged 13 min for Brown Skuas with feeding territories and about 1 h for those without. South Polar Skuas averaged feeding trips of 2–3 h when the sea was open and over 7 h during heavy ice cover.

The timing of an individual's activity was correlated negatively with that of its mate during incubation, brooding, and postbrooding. A nonbreeding pair and breeders that had suffered nest failure showed more positive correlations. Thus, individual activity patterns were shaped by reproductive priorities as well as by feeding ecology and light levels. *Received 13 March 1985, accepted 18 March 1986.*

AN extensive literature exists on the relationship between daily activity patterns of birds and various light regimes (see reviews by Aschoff 1967, Daan and Aschoff 1975, Gwinner 1975, Rusak 1981). Nevertheless, little research has been done on activity patterns of birds under natural conditions of continuous light, as occurs in polar regions in summer. Three decades ago, Armstrong (1954) noted that such information from arctic regions was meagre, while that from the Antarctic was too scarce to warrant discussion. Since then, antarctic researchers have examined activity patterns of Adélie Penguins (*Pygoscelis adeliae;* Muller-Schwarze 1968), Blue-eyed Shags (*Phalacrocorax atriceps;* Bernstein and Maxson 1984), and Southern Black-backed Gulls (*Larus dominicanus;* Maxson and Bernstein 1984, Fraser pers. comm.). Literature on skuas in Antarctica contains only an incidental comment on timing of activity (Spellerberg 1969).

At Palmer Station (64°46'S, 64°03'W) on Anvers Island, Antarctica, I had an opportunity to observe South Polar (*Catharacta maccormicki*) and Brown skuas (*C. lonnbergi*)[1] where they nest sympatrically and occasionally form mixed pairs. Investigations of allopatric populations suggest that the activity patterns of these species are very different. Spellerberg (1969) noted that South Polar Skuas on Ross Island (77°33'S, 166°09'E), the southern extreme of their breeding range, showed a 24-h cycle of activity even during continuous daylight: "Between 01:00 and 05:00 . . . all breeding pairs are roosting, incubating, or brooding and little or no foraging takes place." On the other hand, Young (1978) documented Brown Skuas feeding regularly during hours of darkness on the Chatham Islands, New Zealand (44°22'S, 176°11'W).

STUDY AREA AND METHODS

This study was conducted during the 1979–1980 and 1980–1981 austral summers on several small is-

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[1] Pending resolution of their taxonomic status, I refer to these as separate species. For discussions of skua systematics and nomenclature, see Pietz (1984, 1985).

lands and peninsulas within 5 km of Palmer Station, Antarctica. The ice-free areas provided nesting sites for nearly a dozen bird species (Parmelee et al. 1977), including South Polar Skuas (approx. 250 pairs) and Brown Skuas (up to 12 pairs). From late November to late January there is enough light at Palmer to conduct fieldwork 24 hours a day, despite the fact that the sun dips below the horizon for a short period around 2400.

Skuas were color-banded to allow recognition of individuals at a distance. Most of these birds had been banded in previous years and thus had documented breeding histories. Sexes of birds were determined by copulatory position and courtship feeding.

Skua feeding habits also had been documented at Palmer in previous years (Parmelee et al. 1978, Neilson 1983). Brown Skuas here, as in many other areas (e.g. Stonehouse 1956, Moors 1980, Sinclair 1980, Trivelpiece et al. 1980), concentrated on penguin eggs and chicks and sometimes defended penguin colonies near their nests as feeding territories. Some South Polar Skuas feed on penguins in areas where Brown Skuas are few (Parmelee pers. comm.) or absent (e.g. Eklund 1961, Le Morvan et al. 1967, Trillmich 1978). At Palmer, however, most South Polars fed at sea on fish and krill, a common habit in much of their range (Eklund 1961, Young 1963, Trivelpiece and Volkman 1982).

Between 8 December 1979 and 22 January 1980, we documented the behavior of 4 South Polar Skua pairs, 2 Brown Skua pairs, and 1 mixed-species pair. A total of 50 bird-days of observations was obtained for South Polar Skuas, 14 for Brown Skuas, and 8 for the mixed pair. All were observed for 24-h periods.

Between 27 January and 9 March 1980, when increasing darkness prevented 24-h observations, we watched each of the 7 pairs for 6 dawn-to-dusk periods. From 7 January to 6 March 1981, I made additional observations using sample periods of 3–14 h. Eight South Polar Skua pairs, 2 Brown Skua pairs, and 1 mixed pair constituted the sample in the second season. The mixed pair, 1 of the Brown, and 4 of the South Polar pairs were observed in both years.

During all observation periods, the behavior of each bird was noted every 30 s using a metronome (Wiens et al. 1970). From these observations hourly and daily time budgets were constructed for each individual.

Only data collected during 24-h observation periods of the 1979–1980 season (1,691 bird-hours) were used for assessing relationships between activities and time of day. For resting and foraging behaviors, the mean and standard error were calculated by hour for each individual and for each pair. Weighted hourly means were determined for both species using pair data, and for each sex of both species using individual data. Mean hourly standard error estimates were weighted across individual or pair standard errors that had been pooled over the 24 h. Finally, weighted hourly means were used to calculate angular-linear correlations (Johnson and Wehrly 1977), in a test for 24-h patterns related to either sine or cosine functions.

Agonistic, preening, bathing, and pairing behaviors occurred too rarely to examine variation among individuals or pairs. For each of the first three of these behavioral groups, data on all individuals from all observation days were combined by hour within species. For pairing behaviors, only data for the male of each pair were combined.

Dawn-to-dusk observations from 1980 (1,406 bird-hours) and the shorter observation periods of 1981 (805 bird-hours) were included only in calculating lengths of foraging trips (or time away from the nest territory) and in evaluating correlations of activity between pair members.

Activity correlations between pair members were assessed for 3,860 bird-hours of observations on 8 South Polar, 3 Brown, and 1 mixed skua pairs over two seasons. Behavioral data were sampled from the time budgets once every 30 min, at the end of each 30-min interval. For each pair at each stage of the breeding cycle, I constructed a 2 × 2 contingency table and tabulated presence or absence of a specified behavior by the male and the female. Product moment correlation coefficients and their standard errors were calculated for each table (Bishop et al. 1975); the weighted means of these coefficients, with their associated error terms, were calculated across pairs for each species.

For the purposes of these analyses, the breeding season was divided into (1) pre-egg-laying, (2) incubation (from the time the first egg was laid), (3) brooding (from the hatching of the first chick until it was no longer regularly brooded), (4) postbrooding (until the time the first chick flew well enough to avoid capture), and (5) fledging. A sixth category (failed-nest) contained observations on pairs following loss of eggs or chicks.

Of the 4 South Polar Skua pairs observed in 1979–1980, 1 courted and defended a territory but failed to produce eggs. For purposes of comparison with the three breeding pairs, this pair's season was divided into sections reflecting the average timing of incubation and brooding observed in the breeders.

In several cases, related behaviors were combined before analysis. Grouped behaviors included resting (i.e. sitting, incubating, brooding), foraging (i.e. procuring, transporting and eating prey, activity out of view off the nest territory), pairing (i.e. courtship and courtship feeding, copulation, attempted copulation), agonistic displays (i.e. long call, alarm call, bent neck, wing raising), and agonistic encounters (i.e. running or flying displacement, swooping, aerial chasing, fighting).

Assessment of foraging behavior presented special

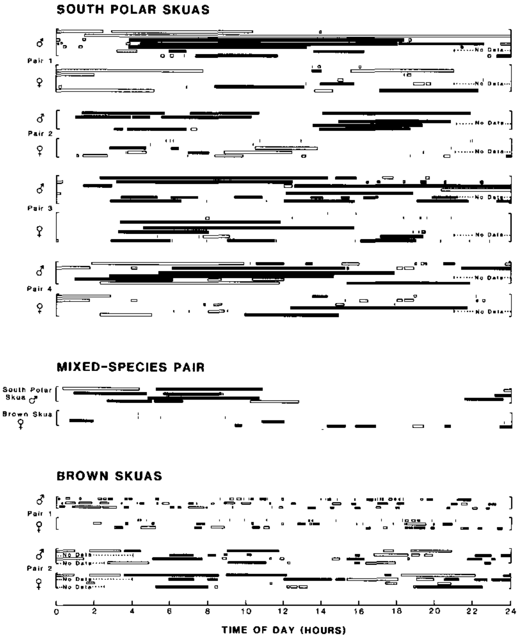

Fig. 1. Daily foraging activity of skua pairs. Each row represents one individual during one 24-h observation period. Horizontal bars denote time spent away from the nest area; solid bars indicate evidence of foraging (see Methods) and open bars indicate unknown location off territory.

problems. Direct observations could be made in the vicinity of each pair's territory, but foraging at sea or at penguin colonies on other islands could only be inferred from flight direction or regurgitation of food when the bird returned. Periods when the birds were off their territories and out of view were divided into those for which there was evidence of foraging (from flight direction or food regurgitation) and those for which there was not. While both types of absences were included in total foraging time, they were distinguished in the representation of daily foraging activity (Fig. 1). In calculating lengths of foraging bouts, absences of the latter type were excluded. Courtship feedings were included in Fig. 1 because, for much of the early season, this constituted the females' primary means of food intake. These feedings were not included in measures of foraging bouts.

RESULTS

Resting and foraging behaviors comprised the two largest components of skua time budgets. The timing of these behaviors varied greatly from day to day for each individual (Fig. 1). There was no hour in which all birds were always foraging or always at rest.

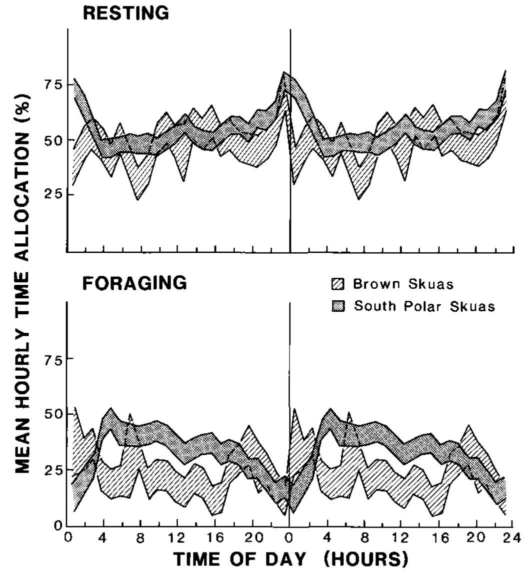

Fig. 2. Daily patterns of resting and foraging. Band width indicates ±1 SE of hourly means weighted across pairs. The 24-h pattern is repeated to facilitate imaging.

Despite this variation, the activity of South Polar Skuas exhibited a significant correlation with time of day (Table 1). On average, both breeding and nonbreeding pairs showed a short peak in resting behaviors around 2400 (Fig. 2); foraging activity moved from lowest to highest levels between 0000 and 0500, then gradually declined toward midnight.

Resting and foraging of Brown Skuas was not correlated with time of day (Table 1). An abrupt peak in resting levels at 2300–2400 (Fig. 2) appeared as an outlier in relation to the other 23 h. Although activity seemed to fluctuate more sharply than for South Polar Skuas, this probably was due to the smaller Brown Skua sample size.

Male and female South Polar Skuas both showed the tendencies described for the species as a whole, but the pattern was much stronger in males (Fig. 3A, Table 1). The lack of a significant correlation between resting and time of day in females reflected their propensity to stay on the territory during pre-egg-laying and early incubation, while males procured food at sea for both of them. Because most of the 24-h

TABLE 1. Angular-linear correlations (Johnson and Wehrly 1977) between activity and time of day for South Polar and Brown skuas near Palmer Station, Antarctica.[a]

	Resting	Foraging	Preening	Bathing	Agonistic	Pairing
South Polar Skua pairs	0.67**	0.83**	0.57*	0.62*	0.34	0.19
Males	0.71**	0.77**	—[b]	—	—	—
Females	0.46	0.67**	—	—	—	—
Brown Skua pairs	0.35	0.39	0.42	0.13	0.46	—
Males	0.36	0.43	—	—	—	—
Females	0.07	0.12	—	—	—	—
Mixed-species pair						
South Polar Skua male	0.83**	0.95**	—	—	—	—
Brown Skua female	0.41	0.30	—	—	—	—

[a] * = $P < 0.05$ for F with 2 and 21 df; ** = $P < 0.005$, for F with 2 and 21 df.

[b] Not calculated.

observations of South Polars occurred early in the breeding season, patterns of this period dominated the data set. Nevertheless, females showed an abrupt resting peak at 2300-2400, like that described for Brown Skuas.

In Brown Skuas, activity of both sexes showed the main features noted for the species (Fig. 3B), but a sex-related difference in pattern strength was not apparent. Although some Brown Skua females may fit the South Polar trend, the evidence was inconclusive because relatively few observations were made early in the Brown Skua breeding cycle. In an early-season study on nearby King George Island (62°10′S, 58°30′W), however, Brown Skua females spent more time at the nest site and less time foraging than males (Trivelpiece et al. 1980).

Members of the mixed pair showed tendencies of their respective species and sexes (Fig. 3C, Table 1). The South Polar Skua male exhibited strong time-related patterns, with foraging highs and resting lows in midmorning. Activity of the Brown Skua female was not correlated with time, and her levels of foraging were generally lower than those of her mate.

Foraging bouts, or trips away from the nest territory, were typically shorter for Brown than for South Polar skuas (Table 2, Fig. 1) ($t = -7.83$, df = 6, one-tailed $P < 0.00025$). This difference also was observed in earlier seasons. In 1977-1978 Neilson (1983) recorded Brown Skua foraging bouts that averaged less than 20 min, and in 1976-1977 South Polar bouts that averaged 1-2 h.

Further distinctions occurred within species. During most of the season, Brown Skuas with feeding territories adjacent to their nests foraged for less than 13 min per bout, while birds without adjacent feeding territories averaged over 60 min ($t = -4.58$, df = 2, one-tailed $P < 0.025$). In Fig. 1 these two conditions are illustrated by Brown Skua pairs 1 and 2, respectively. Similarly, Neilson (1983) documented average bout lengths of 8-13 min for a pair with an adjacent feeding territory and 16-21 min for a pair feeding about 1 km away.

After all the penguin fledglings had departed (late February), differences in the length of foraging bouts between Brown and South Polar skuas decreased substantially. Brown Skuas that had maintained feeding territories still made short scavenging trips to the deserted penguin colonies (weighted $\bar{x} = 16.2$ min, SE = 2.05, $n = 3$ pairs; 21 bouts). In addition, like the other skua groups, they now made trips away from their territories that averaged over 3 h (weighted $\bar{x} = 180.3$ min, SE = 28.42, $n = 3$ pairs; 13 bouts). Some observations suggested that these birds searched for penguins on more distant islands. In addition, seaward flight direction and subsequent regurgitation of fish to chicks indicated some foraging at sea. The average duration of these longer trips was an underestimate because of the inclusion of several trips that started before or ended after the observation period. Nevertheless, the long trips significantly increased average bout length in this period (on log-transformed data, paired $t = -8.89$, df = 3, one-tailed $P < 0.0025$). The Brown Skua pair without a feeding territory also showed an increase in bout length ($t = -2.64$, approx. df = 6, one-tailed $P < 0.025$).

For South Polar Skuas, foraging-trip length

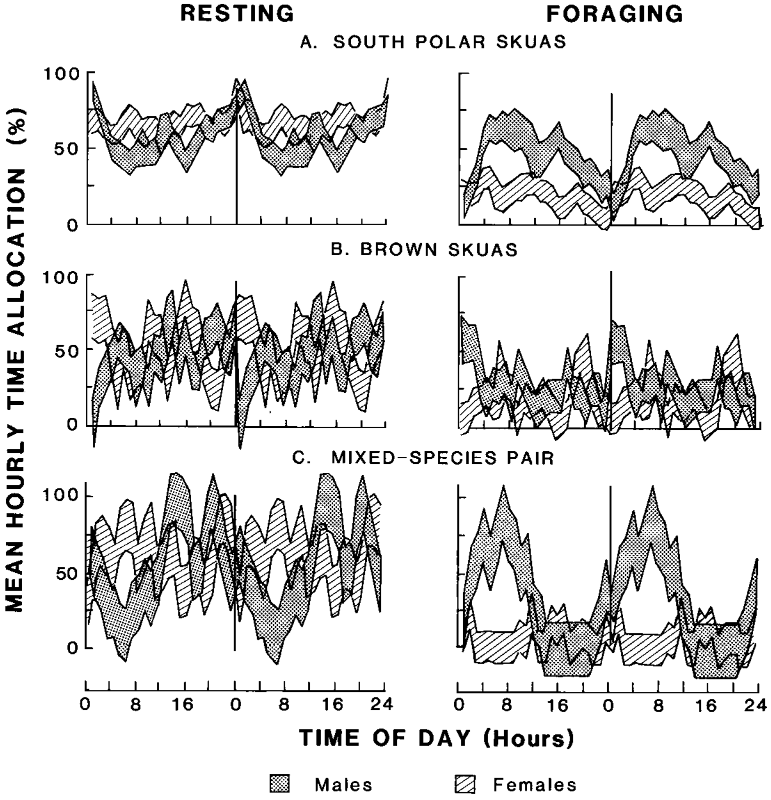

Fig. 3. Daily patterns of resting and foraging for males and females. Band width indicates ±1 SE of hourly means weighted across individuals. The 24-h pattern is repeated to facilitate imaging.

reflected the variable availability of their food resources. Early in the 1979-1980 season, foraging at sea was extremely difficult due to extensive pack-ice cover (Pietz 1984), and trips away from the nest area averaged 7.6 h. Later, when local waters were relatively clear of ice, foraging trips averaged 2.4 h (paired $t = 3.57$, df = 3, one-tailed $P < 0.025$).

Early in the 1980-1981 season, when nest initiation dates, nest densities, and clutch sizes indicated that food was more plentiful (Pietz 1984), average trip lengths were shorter than in the previous year. Because of short observation periods in the second year, accurate estimates of mean trip length could not be calculated; however, 25% of the trips were under 1 h during 1980-1981, compared with 12% in 1979-1980.

Previous investigators noted the impact of ice and storms on the foraging efficiency of South Polar Skuas. In 1976-1977 foraging bouts of three South Polar pairs averaged 58 min in a period of calm weather and 112 min in a period of late-season storms (Neilson 1983). The impact of extensive ice cover was most dramatic in 1977-1978, when birds were sometimes absent from their territories for days, resulting in a total reproductive failure (Parmelee et al. 1978).

Members of the mixed-species pair showed bout lengths and diets characteristic of their respective species. The Brown Skua female, foraging primarily on penguins at neighboring islands, averaged trips of less than 1 h from mid-December to late February, and over 3 h afterwards ($t = -3.57$, approx. df = 4, one-tailed $P < 0.025$). The South Polar Skua male, foraging at sea, averaged trips of about 4 h during the period of extensive ice cover and 2.8 h during periods of open water ($t = 2.4$, df = 23, one-tailed $P < 0.025$).

Finally, female Brown Skuas averaged longer foraging trips than males (on log-transformed data, paired $t = 4.33$, df = 3, two-tailed

TABLE 2. Average duration of foraging bouts for South Polar and Brown skuas near Palmer Station, Antarctica.

	$\bar{x}$[a] (min)	SE (min)	No. of pairs	No. of bouts[b]
Brown Skuas				
Overall	32.3	11.52	4[c]	355
Pairs with feeding territories				
Penguins nesting	12.7	0.74	3[d]	277
Penguins gone	76.7	17.71	3[d]	34
Pair without feeding territory				
Penguins nesting	61.0	10.52	1	38
Penguins gone	239.1	66.73	1	6
South Polar Skuas				
Overall	198.0	17.43	4	123
Heavy ice cover	453.2	77.04	4	24
Ice out	145.1	12.72	4	99
Mixed-species pair				
Brown Skua female				
Penguins nesting	52.8	7.48	1	21
Penguins gone	216.8	45.28	1	4
South Polar Skua male				
Overall	185.0	15.11	1	25
Heavy ice cover	244.1	36.12	1	6
Ice out	166.4	14.33	1	19

[a] Weighted means given where sample includes more than one pair.
[b] Summed for all individuals in sample.
[c] Two pairs for 1 yr and one pair for 2 yr.
[d] One pair for 2 yr and one pair for 1 yr.

$P < 0.05$), but male and female South Polar Skuas showed no consistent differences in length of foraging trips (on log-transformed data, paired $t = -1.32$, df $= 3$, two-tailed $P > 0.20$). This difference may hinge on the sexual size dimorphism that was clearly visible in Brown Skuas (females are larger) but difficult to detect in South Polar Skuas.

Agonistic displays and encounters occurred during nearly all hours (Figs. 4A and 5A). No significant correlations were found between levels of agonistic activity and time of day (Table 1). There was some indication of a lull in agonistic activities during twilight, probably because the fewest potential intruders were active then (Fig. 2).

Episodes of preening activity occurred at all hours in both species, with no decline near 2400 (Figs. 4B and 5B). Some lulls in preening activity coincided with peaks in foraging, suggesting that time spent off territory occasionally constrained the timing of preening as well as resting.

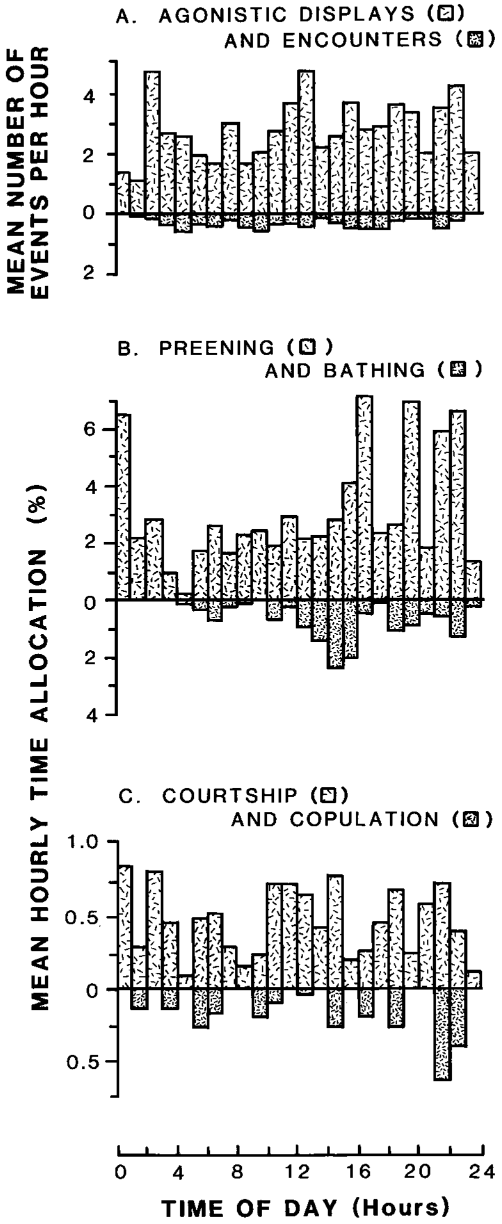

Fig. 4. Timing of agonistic (A), preening and bathing (B), and pairing (C) activities of 8 South Polar Skuas. In A, bar height represents hourly counts of agonistic behaviors, averaged across 50 bird-days of observations. In B and C, bar height represents the percentage of each hour allocated to an activity, averaged across 50 (B) or 25 (C) bird-days.

Among South Polar Skuas, bouts of bathing activity showed highest levels in midafternoon

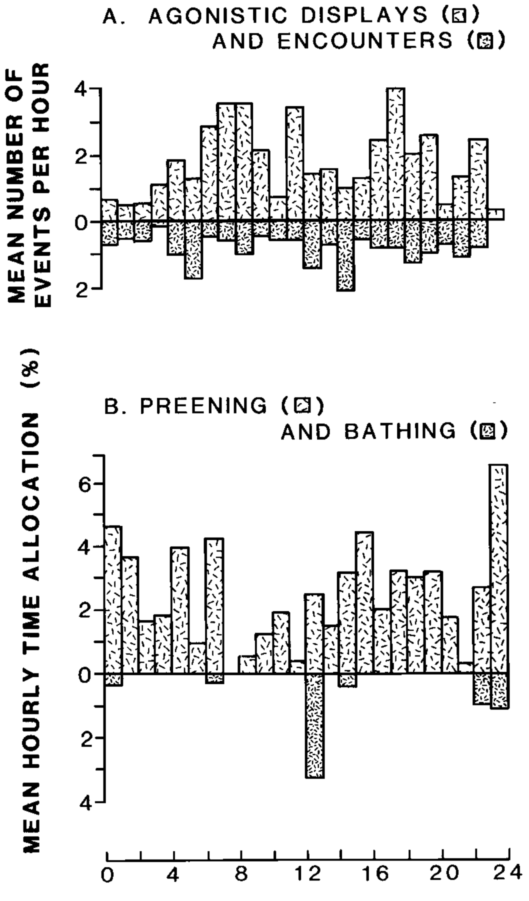

Fig. 5. Timing of agonistic (A) and preening and bathing (B) activities of 4 Brown Skuas. In A, bar height represents hourly counts of agonistic behaviors, averaged across 14 bird-days of observations. In B, bar height represents the percentage of each hour allocated to that activity, averaged across 14 bird-days.

and a sustained low in the early morning (Fig. 4B). Brown Skua bathing patterns could not be assessed because observed bathing was very rare as well as episodic. The six hours in which bathing activity appeared (Fig. 5B) represented only six episodes of bathing.

Pairing behaviors of South Polar Skuas, although among the rarest activities observed, occurred randomly (Fig. 4C, Table 1). Brown Skua pairing could not be evaluated because the pre-egg-laying period, when most courtship and mating occurred, was poorly represented in the sample.

In skuas, as in many seabirds, pair members share the tasks of incubation, brooding, and guarding of young. When one bird leaves, the other must remain until its mate returns or risk losing the eggs or chicks. The activity of male and female skuas appeared to be coordinated in this way. It was most striking in Brown Skuas (Fig. 3B), where a peak in the activity of one sex frequently concurred with lowered activity in the other, but was only weakly visible in South Polar Skuas (Fig. 3A). Presumably, with a larger sample of observation days and observed pairs, these compensatory patterns would average out and disappear. Then only the time-related patterns of each species and sex would be apparent.

Direct examination of activity within pairs showed that the nature and strength of within-pair correlations depended primarily on the stage of breeding (Fig. 6). Most sample correlations were weakly positive during pre-egg-laying and negative during incubation, brooding, and postbrooding. Pairs that lost eggs or chicks again showed more positive correlations.

For both species, the strongest negative correlations between activity and breeding stage occurred in resting behavior during incubation and brooding. This reflected the dominance of incubating and brooding in the time budgets of the skuas at these stages (recall that these two behaviors were part of the resting category in the analyses). Members of a nonbreeding South Polar pair generally showed weak positive correlations all season, further indicating the importance of reproduction to the timing of activity between mates.

The importance of nest attendance for breeding skuas was demonstrated by how seldom both pair members were off the nest territory. For South Polar pairs whose eggs or chicks survived, simultaneous absences occurred less than 0.02% of the observed time during incubation (284 h, 6 pairs), 0.07% during the brooding period (112 h, 5 pairs), and about 4% during postbrooding (182 h, 4 pairs). By contrast, simultaneous absences rose to 13% (92 h, 6 pairs) for pairs that suffered total nest failure, and averaged 14% (169 h) in the nonbreeding pair.

DISCUSSION

During this study near Palmer Station, breeding South Polar Skuas did not show an

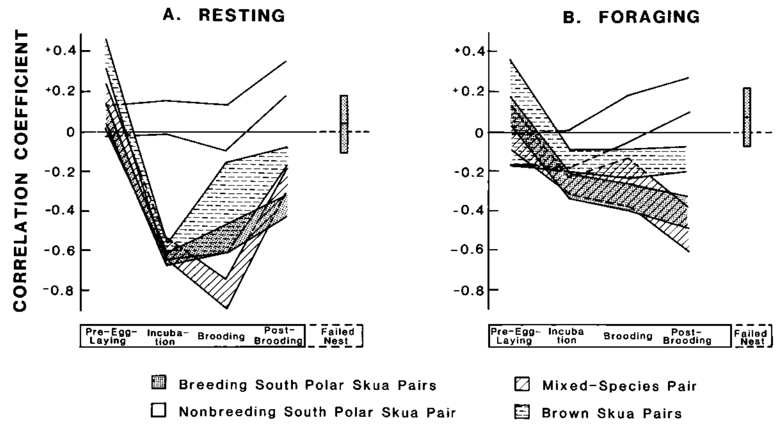

Fig. 6. Correlations between pair members in resting (A) and foraging (B) skuas. Band width indicates ±1 SE of the means weighted across pairs within each group. The "failed nest" category, shown discontinuously from the rest of the breeding chronology, represents 6 pairs of South Polar Skuas.

activity lull from 0100 to 0500 as reported for birds at Cape Royds, Ross Island (Spellerberg 1969). Instead, averaged data for resting and foraging indicated a period of relative quiescence around 2400. In the absence of darkness, one might expect skuas to be equally active at all hours. Instead, South Polar Skuas at Palmer showed a strong relationship between foraging activity and time of day that Brown Skuas did not.

The differences in activity patterns between species most likely stem from differences in their feeding ecology. Searching for fish at sea presents problems for South Polar Skuas that Brown Skuas, feeding on land, do not face.

These problems may relate, directly or indirectly, to diel changes in light intensity. Even during continuous daylight, light intensities may shift markedly; at Ross Island, as much as 8-fold changes in irradiance were measured between 1200 and 2400 under various degrees of cloud cover (Steven Kottmeier pers. comm.). At Palmer, where some twilight occurs even in midsummer, the range of light intensities was greater. Gallardo and Piezzi (1973) recorded January light levels near Palmer (64°53′S, 62°53′W) ranging from 30,000–50,000 lux at noon to less than 1,000 lux at 2200 when twilight began.

At the lowest light levels there are several conceivable deterrents to fishing at sea. It is possible that (1) lower temperatures associated with lower light require birds to conserve heat; (2) lower air temperatures freeze water on feathers after birds splash-dive for fish; (3) lower angles of incidence of light rays, which cause more reflection and less penetration of the water surface, make it more difficult for skuas to see prey; (4) prey show behavioral changes related to light (e.g. vertical movements) that make them less available to skuas at certain times of day; or (5) light cues trigger an intrinsic activity "clock" that may have evolved in response to some other, more strongly rhythmic environment.

The first hypothesis was suggested by the observation (Spellerberg 1969) that the lowest atmospheric temperatures at Cape Royds coincided with a 0100–0500 period of skua inactivity. Atmospheric temperatures from November to March ranged between −15°C and 5°C. At Palmer, however, summer temperatures rarely fell below −2°C, and at warmer times incubating skuas sometimes panted to dissipate excess body heat. The high frequency of early morning activity in individuals of both species (Fig. 1) makes it unlikely that heat conservation was a primary concern for Palmer skuas.

The second hypothesis also involves temperature as a deterrent to fishing. Young (1963) noted that

> The plunge into the water immersing much of the head and lower part of the body accounts for the ice masses that encrusted the upper mandible and

> forehead and the jugulum and breast feathers of many birds. This icing was most commonly observed during early and late summer when air temperatures were lower. Some birds had so much ice about the beak and forehead when they returned to the territory that vision was seriously impaired.

This suggests a reason for Cape Royds skuas to avoid fishing during the coldest hours of the day. At Palmer, where the lowest temperatures were often above freezing, I never saw birds with ice on their feathers. Nevertheless, the fact that records of bathing were rare between 2400 and 0400, and peaked from 1400 to 1600, suggests that skuas may have avoided getting wet during the early hours of the day.

The third hypothesis relates light intensity and sun position to the visibility of prey below the water surface. This may be more important at Palmer than Ross Island, because the height of the midsummer sun ranges much more widely at 65°S than at 78°S. As sun position moves toward the horizon, the proportion of light reflected from the water's surface increases and the proportion penetrating the water decreases. If the water surface is disturbed, reflection at low sun angles is even greater (Hutchinson 1957). Coupled with lower light intensities at this time of day, these effects may severely reduce skuas' ability to see underwater prey. The high proportion of cloudy days at Palmer [mean of about 22 cloudy and 8 partly cloudy days/month in December–January of 1979–1980 and 1980–1981 (Anon. 1980, 1981)] may reduce the importance of reflection off the water, but increase the importance of light intensity for seeing prey.

The feeding habits of South Polar and Brown skuas offer circumstantial support for this hypothesis. Penguin colonies provide a closer and more predictable food source than marine prey, allowing Brown Skuas to find their food with less searching and, probably, with less light.

The fourth hypothesis implicates diel changes in marine prey availability; prey are available to skuas only when they occur within 1 m of the water surface. The primary food source for South Polar Skuas at Palmer is the nototheniid fish *Pleuragramma antarcticum* (Neilson 1983, Pietz 1984). Its movements in response to light, food, and other environmental factors are not well known, but other notothenoid fishes migrate vertically to feed on krill (*Euphausia superba*; Permitin 1970, Karl-Hermann Kock pers. comm.). Krill, a secondary food source of the skuas (Pietz 1984) and a major food of *Pleuragramma* (Dewitt and Hopkins 1977), migrate vertically (e.g. Witek et al. 1981). In most areas, krill aggregate in upper water layers at night and disperse to deeper water in the day.

Such movements would indicate that skuas at Palmer feed when krill are least available. The situation is probably more complicated, however. First, diel krill migrations may be much less important when there is continuous light. Witek et al. (1981) observed no distinct dependence of the vertical krill distribution on the intensity of daylight. In addition, Pavlov (1974) observed a second surface migration at noon, and Mauchline (1981) noted several studies that suggest krill move irregularly, perhaps reacting to varying concentrations of phytoplankton.

The fifth hypothesis relates light intensity to skua activity and implies that proximal causes now may be missing but that an internal clock still responds to changing light cues. Experimental evidence of circadian rhythms in skuas is lacking; however, 24-h rhythms in their physiology and behavior may reflect the influences of an internal clock. At Cape Royds, Spellerberg (1969) found that the core body temperature of an adult male skua peaked at 42.4°C at midday and fell to 41.0°C at 0200–0400, implying a daily cycle. On the other hand, Eklund (1942) measured body temperatures of two South Polar Skuas on the Antarctic Peninsula (68°11′S, 67°12′W) and recorded lows of 39.9°C in the hours just before midnight. Eklund mentioned that the South Polar Skuas observed during continual daylight were "more or less active for 24-hour periods, and . . . could always be observed eating and fighting among themselves over seal-meat scraps near the husky sledge-dog kennels."

These findings, together with individual variability noted at Palmer, suggest that the activity patterns of South Polar Skuas are not controlled by one 24-h pattern. A light-synchronized internal clock may be involved in the timing of activity, but use of this clock may depend on local foraging conditions and opportunities. Brown Skuas display this opportunistic flexibility to extremes. Brown Skuas on the Chatham Islands, New Zealand, forage primarily during hours of darkness (Young 1978).

This allows them to prey on locally abundant, night-active petrels, which they catch on the ground near the petrels' burrows. Similarly, Brown Skuas on Gough Island in the South Atlantic (40°S, 10°W) feed primarily at night on Procellariiformes (Furness pers. comm.).

I believe that light levels ultimately influence the activity of South Polar Skuas, although the proximate mechanism may vary. The effect of light on air temperature may cause the activity lull at 0100–0500 on Ross Island (hypotheses 1 and 2), while the effect of light on prey visibility may produce the midnight low at Palmer (hypothesis 3). Alternatively, light may trigger an internal clock that produces both patterns. Diet is a proximate factor influencing South Polar and Brown skua activity patterns at a local level. For both species, the large variance in the timing of individuals' activities suggests a behavioral flexibility suited to an opportunistic life style.

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A **symposium on Birds of Evergreen Forest,** organized by the Southern African Ornithological Society, will be held **8-10 September 1987** at The Wilderness, Cape Province, South Africa. Papers and posters will be presented on the following topics: forest bird communities, biogeography of forest birds, population biology of forest birds, and conservation of forest avifaunas. Prospective participants should contact the **Symposium Organising Committee, E.C.W.B.S., P.O. Box 1305, Port Elizabeth 6000, South Africa.**

The **Third New England Regional Hawk Conference** will be held **4 April 1987** at the Holiday Inn, Holyoke, Massachusetts. Registration forms are available from **HAWKS, P.O. Box 212, Portland, Connecticut 06480.** There are special rates for lodging at the Conference center. Registration will be limited.

The **Third World Conference on Birds of Prey** will be held **22-27 March 1987** at Eilat, Israel. It will be organized by the World Working Group on Birds of Prey in conjunction with the Israel Raptor Information Center and the U.S. Hawk Mountain Sanctuary Association. The conference will consist of 7 paper sessions on conservation, migration, population biology, education, and legislation. For further information write to the Hon. Secretary of the World Working Group: **Mr. R. D. Chancellor, 15 Bolton Gardens, London SW5 0AL, U.K.**

A PHYLOGENETIC ANALYSIS OF RECENT ANSERIFORM GENERA USING MORPHOLOGICAL CHARACTERS

BRADLEY C. LIVEZEY
Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045 USA

ABSTRACT.—A phylogenetic analysis of all Recent genera of the Anseriformes using 120 morphological characters supports much of the current consensus regarding intraordinal relationships. I found that (1) *Anseranas* should be placed in a monotypic family; (2) *Dendrocygna, Thalassornis,* geese and swans, and *Stictonetta* are paraphyletic to the rest of the Anatidae; (3) *Cereopsis* is the sister group to *Anser* and *Branta,* and *Coscoroba* is the sister group to *Cygnus* and *Olor;* (4) *Plectropterus* is the sister group to the Tadorninae (shelducks) and the Anatinae (typical ducks); (5) the shelducks are monophyletic and include *Sarkidiornis* (provisionally), *Malacorhynchus, Hymenolaimus, Merganetta,* and *Tachyeres;* (6) the tribe "Cairinini" ("perching ducks") is an unnatural, polyphyletic assemblage and is rejected; (7) the dabbling ducks (including the smaller "perching ducks") comprise an unresolved, probably paraphyletic group; (8) tribal monophyly of the pochards (including *Marmaronetta* and *Rhodonessa*), sea ducks (including the eiders), and stiff-tailed ducks (including *Heteronetta*) is confirmed; and (9) the retention of *Mergellus* and resurrection of *Nomonyx* are recommended based on clarifications of intratribal relationships. Problematic groups, effects of homoplasy, phenetic comparisons, life-history correlates, biogeographic patterns, and fossil species are discussed, and a phylogenetic classification of Recent genera is proposed. *Received 18 November 1985, accepted 2 April 1986.*

THE order Anseriformes is considered to comprise the families Anhimidae (2 genera, 3 species) and Anatidae (approximately 43 genera and 150 species). The family Anatidae is undoubtedly one of the best-studied groups of birds, owing largely to the historical importance of waterfowl for hunting (Weller 1964a), domestication (Delacour 1964a), and aviculture (Delacour 1964b).

The classification of the Anatidae proposed by Delacour and Mayr (1945) has been followed, with only minor revisions, in recent decades (e.g. Delacour 1954, 1956, 1959, 1964c; Johnsgard 1961a, 1962, 1965a, 1978, 1979; Woolfenden 1961; Frith 1967; Bellrose 1976; Palmer 1976; A.O.U. 1983; Bottjer 1983; Scott 1985). Perhaps the most innovative aspect of this system (inspired by the works of Salvadori 1895; Phillips 1922, 1923, 1925; and Peters 1931) was the erection of "tribes," groups of genera that were considered to be closely related within the subfamilies of the Anatidae. These tribes became the primary focus of subsequent works on anatid classification, many of which addressed the tribal assignments of problematic genera (e.g. Humphrey and Butsch 1958; Johnsgard 1960a, 1961b; Humphrey and Ripley 1962; Davies and Frith 1964; Raikow 1971; Kear and Murton 1973). Most authors assumed the validity of the tribes and used them as working units in phylogenetic analyses of the family (e.g. Johnsgard 1961a, Bottjer 1983). A few workers named additional tribes (Moynihan 1958, Delacour 1959, Woolfenden 1961, Weller 1968b) or attempted to test the naturalness of those originally proposed (Cotter 1957, Woolfenden 1961, Brush 1976).

Behavioral characters have been accorded considerable weight in classifications of waterfowl. Delacour and Mayr (1945) based their revision on characters they considered to be "non-adaptive," including behavioral displays, nesting and feeding habits, and selected morphological characters (e.g. posture, body proportions, head shape, syringeal bulla). Reliance on comparative ethology in anatid systematics was furthered by the studies of Lorenz (1951–1953), McKinney (1953), and Myres (1959) and was increased significantly by Johnsgard (1960a–c, 1961a–d, 1962, 1964, 1965a, b, 1966a, b, 1967, 1978), whose work was largely ethological and influenced profoundly by that of Delacour (1954, 1956, 1959, 1964c). This emphasis, work on interspecific hybridization

(Sibley 1957; Gray 1958; Johnsgard 1960d, 1963), and study of plumage patterns of downy young (Delacour 1954, 1956, 1959; Frith 1955, 1964b; Kear 1967) were prompted in part by the opportunity to observe waterfowl in avicultural collections.

Other data used in the classification of waterfowl include syringeal anatomy (Humphrey 1955, 1958; Johnsgard 1961e), cytogenetics (Yamashina 1952), serology (Cotter 1957, Bottjer 1983), osteology (DeMay 1940, Verheyen 1955, Humphrey and Butsch 1958, Woolfenden 1961, Humphrey and Ripley 1962, Raikow 1971), feather lice (Timmermann 1963), eggshell structure (Tyler 1964), egg-white proteins (Sibley 1960, Sibley and Ahlquist 1972), feather proteins (Brush 1976), myology (Zusi and Bentz 1978), lipids from the uropygial gland (Jacob and Glaser 1975, Jacob 1982), and mitochondrial DNA (Kessler and Avise 1984).

These studies, with the possible exceptions of those by Lorenz (1953) and Kessler and Avise (1984), estimated the evolutionary relationships of groups by assessments of overall similarities; no attempts were made to determine primitive conditions or to distinguish shared primitive characters from shared derived characters ("special" similarity). Moreover, the "evolutionary trees" presented in most of these works lack references to the specific characters used to support the branching patterns (e.g. Delacour and Mayr 1945; Johnsgard 1961a, 1978; Woolfenden 1961).

I performed a phylogenetic (cladistic) analysis of Recent genera of Anseriformes using 120 morphological characters. I present a hypothetical evolutionary tree for the order, consider the taxonomic implications, and discuss selected life-history and biogeographic correlates and the classification of selected fossil species. Many of the characters were described first in the pioneering work of Woolfenden (1961), to whom I dedicate this paper.

METHODS

Taxa and specimens.—Both genera of Anhimidae and all Recent genera of Anatidae were studied. I analyzed separately several subgenera (sometimes considered genera), including *Olor, Lophonetta, Pteronetta, Amazonetta, Callonetta, Mergellus, Lophodytes,* and *Nomonyx.* Several other "subgenera" were found to be identical to the taxa with which they generally are merged and are not labeled separately in the trees: *Casarca* (= *Tadorna*), *Metopiana* (= *Netta*), *Oidemia* (= *Melanitta*), and *Charitonetta* (= *Bucephala*). For *Anas,* species from several subgenera were examined: Mallard (*Anas platyrhynchos*), Northern Pintail (*A. acuta*), American Wigeon (*A. americana*), Green-winged Teal (*A. crecca*), and Northern Shoveler (*A. clypeata*). Other species of *Anas* were studied for certain characters. Salvadori's Duck [*Anas* (*Salvadorina*) *waigiuensis*], provisionally assigned to *Anas* but considered problematic by some (Mayr 1931, Kear 1975), was not included because no skeletal specimens were available (Wood et al. 1982). Except for *Rhodonessa* (monotypic, probably extinct; one complete skeleton) and *Camptorhynchus* (monotypic, extinct; casts of two partial skeletons), all genera analyzed were represented by at least two complete skeletons. For all polytypic genera at least two species were studied, and a number of the common, diverse, or problematic genera were represented by large series.

For *Camptorhynchus,* character states for unavailable elements either were assumed provisionally (for characters invariant within the anatines) or coded as "missing." Assumption of anatine characters for *Camptorhynchus* is conservative (cf. Humphrey and Butsch 1958, Zusi and Bentz 1978) and did not alter its position in the resultant tree (compared with analyses without this assumption), but permitted more efficient computation of trees and a shorter final solution.

Analysis of characters.—For the phylogenetic analysis presented, 120 characters were used (Appendix 1); a majority of the osteological characters were described in Woolfenden (1961) and illustrated in Howard (1929). Some characters were rejected because variation prevented even modal state assignments for some genera or because discrete states could not be distinguished.

Sources for data on the postcranial skeleton were Wetmore (1951), Rand (1954), Verheyen (1955), Woolfenden (1961), Humphrey and Clark (1964), and Raikow (1971). Additional sources were (by anatomical region): integument and molt (DeMay 1940, Siegfried 1970, Palmer 1976), trachea and syrinx (Wetmore 1926; Niethammer 1952; Wolff and Wolff 1952; Humphrey 1955, 1958, unpubl. data; Humphrey and Butsch 1958; Johnsgard 1961b, e; Humphrey and Ripley 1962; Humphrey and Clark 1964; Weller 1968b), and skull (Abbott 1938, Harrison 1958, Raikow 1970a, Olson and Feduccia 1980a). I included only qualitative characters because the polarities and states of mensural characters are especially difficult to determine. Each character is an anatomical trait for which two or more discrete character states were defined.

Derivation of trees.—Polarities of each character (primitive states) were determined by comparison with outgroups—*Burhinus* and *Larus* (Charadriiformes), *Ortalis* and *Meleagris* (Galliformes), *Ciconia*

(Ciconiiformes), and *Phoenicopterus* (Ciconiiformes or Charadriiformes)—each of which has been proposed as closely related to the Anseriformes (Delacour and Mayr 1945; Delacour 1954; Mainardi 1962; Simonetta 1963; Sibley et al. 1969; Sibley and Ahlquist 1972; Brush 1976; Feduccia 1977, 1978; Olson and Feduccia 1980a, b; Olson 1985). Generally, the galliforms were most useful for establishing polarities. Outgroups were used to construct a hypothetical ancestor (a vector of primitive character states) for the Anseriformes, which was used to root the evolutionary tree; the primitive condition of nine characters could not be determined and were coded as missing (Appendix 1). Transformation series were treated as linear unless they appeared to be nonlinear or problematic; the latter were treated as unordered (Appendix 1). The syringeal bulla was given a weight of 2 because it is a locomotion-independent character complex involving enlargement, symmetry, and fenestration; all other characters were assigned unit weight.

The logic and terminology of phylogenetic analysis are discussed in Wiley (1981). The tree was derived using the PAUP program (Swofford 1984), a program that seeks trees of maximum parsimony (i.e. requires the least number of character-state changes; see Kluge 1984) and that permits the examination of series of "equally short" trees. The large size of the data set prohibited an exhaustive search *guaranteed* to find the shortest tree(s), but two thorough methods—alternate and global branch swapping—were employed and produced identical topologies.

A data matrix for all outgroups and the Anseriformes and a list of specimens examined are available from the author on request.

RESULTS

General findings.—Of 50 equally short trees examined that resulted from minor changes in character distributions, only three distinct topologies were found. The tree illustrated (Fig. 1) has the topology of 46 of these trees (consistency index = 0.59). Two trees reversed the order of branching of *Thalassornis* with the geese and swans, and two others altered relationships in the goldeneye-merganser clade (*Bucephala, Mergellus, Lophodytes, Mergus*).

Anhimids and Anseranas.—Monophyly of the Anhimidae and the waterfowl and the early branching of *Anseranas* were confirmed (Fig. 2). The "primitive" status of *Anseranas* has been recognized widely (Miller 1919; Boetticher 1943; Delacour 1954; Johnsgard 1961c, e, 1962, 1978, 1979; Woolfenden 1961; Olson and Feduccia 1980a). Notable exceptions were the placement of *Anseranas* with the superficially similar *Plectropterus* (Peters 1931, Delacour and Mayr 1945) and the proposition that *Anseranas* is an aberrant "true goose" (Davies and Frith 1964, Frith 1967). Both the anhimids and *Anseranas* have undergone substantial autapomorphic change since divergence, much of which is unique in the order.

Geese, swans, and proto-ducks.—I found that the "Anserinae," as currently defined (e.g. Johnsgard 1978), is paraphyletic to the rest of the family (Fig. 2), in contrast to the monophyly depicted by Delacour and Mayr (1945), Boetticher (1952), and Woolfenden (1961). Johnsgard (1961a, e) depicted the group as paraphyletic to the "Anatinae," but later (1978) diagrammed it as monophyletic, as did Bellrose (1976). These variations, however, may reflect different approaches to tree construction as much as changing perceptions of relationships.

The branching sequence (Fig. 2) differs from conventional schemes (Johnsgard 1967, 1978; Kear 1967; Raikow 1971; Brush 1976) in that *Dendrocygna* and *Thalassornis* are not sister genera but instead comprise a grade. In an equally parsimonious topology, *Thalassornis* diverged immediately after the goose-swan branch. Most of the 13 autapomorphies in *Thalassornis* represent adaptations for diving and include several convergences with diving ducks in other clades. Until the works of Johnsgard (1967) and Raikow (1971), *Thalassornis* was considered to be an aberrant stiff-tailed duck and allied with *Oxyura* (e.g. Peters 1931; Delacour and Mayr 1945; Delacour 1959, 1964c), a treatment repeated recently (Howard and Moore 1984, Scott 1985).

Ten character changes confirmed the monophyly of the geese and swans (Fig. 2), as hypothesized by most authorities in recent decades (Delacour and Mayr 1945; Delacour 1954; Johnsgard 1961a, e, 1965a, 1978; Woolfenden 1961; Bottjer 1983). Also, there is a sister-group relationship between *Coscoroba* and the "typical" swans (*Cygnus, Olor;* 6 characters) and between *Cereopsis* and the "typical" geese (*Anser, Branta;* 2 characters). My analysis demonstrated monophyly of *Olor*, but no apomorphies distinguished *Cygnus* from the common ancestor of *Cygnus* and *Olor* (Fig. 2); hence, the topology of *Cygnus* remains unresolved. The generic monophyly of *Anser* and *Branta* also was not established. Traditionally, *Coscoroba* and *Cereopsis* have been considered to be either "links"

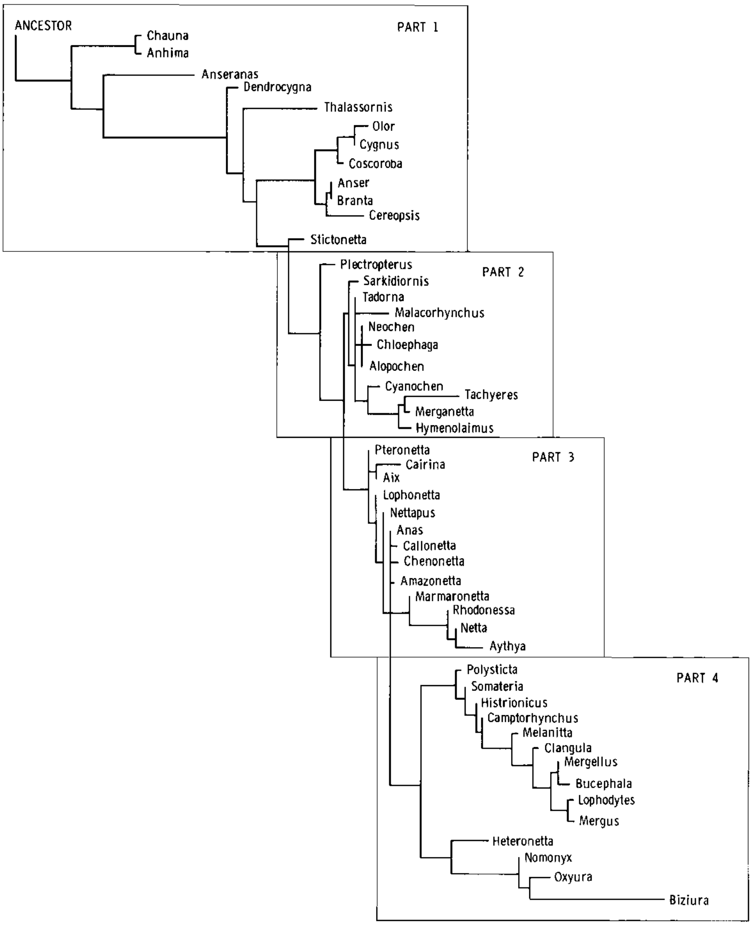

Fig. 1. Phylogenetic tree of Recent anseriform genera and selected subgenera based on 120 morphological characters listed in Appendix 1. Lengths of horizontal lines correspond to the number of character changes (apomorphies) in the lineages. Sections of the tree are detailed in Figs. 2-5.

between tribes, early branches from the common ancestor to the "true" geese and swans, or, for *Cereopsis*, an aberrant shelduck or the sole member of a separate tribe (Peters 1931; Delacour and Mayr 1945; Delacour 1954, 1964c; Johnsgard 1961a, e, 1978; Woolfenden 1961; Frith 1967; Kear and Murton 1973; Bottjer 1983).

My analysis showed *Stictonetta* to be the last branch in the grade of waterfowl with reticulate tarsi (Figs. 1 and 2). *Stictonetta* long was believed to be an aberrant member of the shelducks (near *Tadorna*; Peters 1931, Boetticher 1952) or the dabbling ducks (e.g. *Anas*; Delacour and Mayr 1945; Delacour 1956, 1964c). Based on anatomical comparisons, however, other workers suggested that the genus was derived from an earlier "anserine" branch of the Anatidae (Verheyen 1955; Johnsgard 1960c, 1961a, b, 1962, 1965a, b, 1978; Woolfenden 1961; Frith 1964a, b, 1967; Brush 1976; Olson and Feduccia 1980a).

Plectropterus *and the shelducks.*—I found that *Plectropterus* is not related closely to the "perching ducks" (e.g. *Sarkidiornis, Cairina,* and *Nettapus*) as generally recognized since Delacour and Mayr (1945). Instead, *Plectropterus* is the earliest branch of the waterfowl with scutellate tarsi, and lacks five synapomorphies uniting more-derived members of the family (Fig. 3). Woolfenden (1961) concluded that *Plectropterus* was most similar osteologically to the shelducks, and Tyler (1964) found that egg-

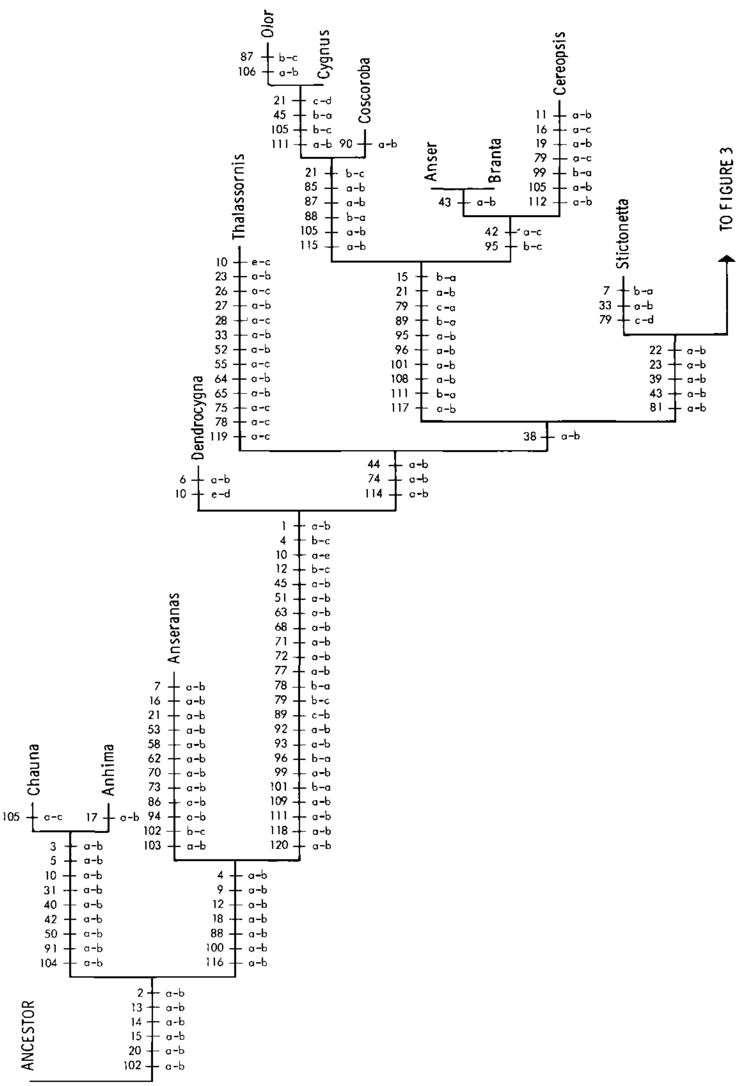

Fig. 2. Detailed diagram of Part 1 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1.

shells of *Plectropterus* were intermediate between those of anserines and shelducks in structure. Bottjer (1983) found that *Plectropterus* differed greatly from other "perching ducks" serologically but attributed the result to experimental error.

My analysis supports the monophyly of the shelducks, although only by a single, possibly convergent character; further study may show the shelducks to be a grade of relatively primitive ducks. The clade includes a polytomy involving *Tadorna, Malacorhynchus,* and two clades containing three genera each (Fig. 3). I found *Malacorhynchus* to be a highly derived shelduck; this genus has been assigned most frequently to the dabbling ducks (e.g. Delacour 1956, Woolfenden 1961, Frith 1967, Johnsgard 1978), although Frith (1955) noted that the pattern of its downy young differed greatly from those of *Anas* and Brush (1976) found that *Malacorhynchus* was distinctly different from *Anas* in its feather proteins. A single synapomorphy

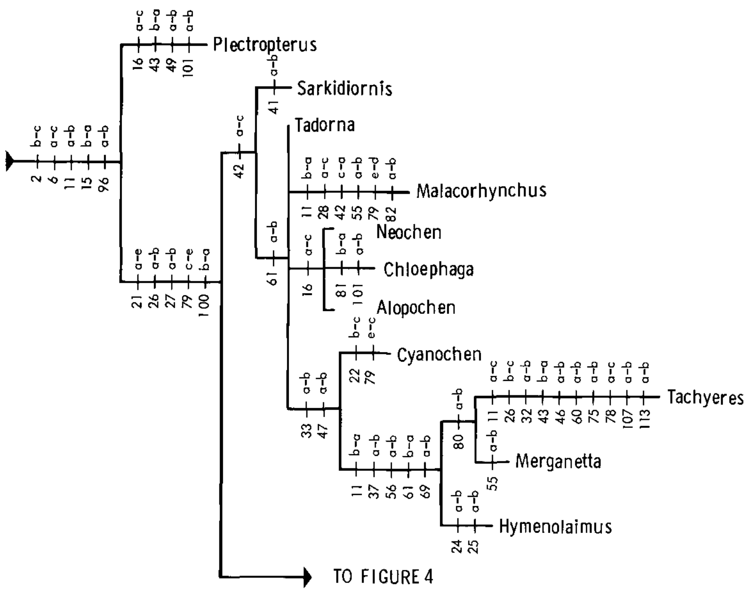

Fig. 3. Detailed diagram of Part 2 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1. Graphical proximity of branches within the polytomy in the shelducks does *not* reflect relatedness.

of the skull supports the monophyly of the three genera of "sheldgeese"—*Alopochen, Chloephaga,* and *Neochen* (Fig. 3).

The Comb Duck (*Sarkidiornis melanotos*), traditionally placed in the "Cairinini" (Delacour and Mayr 1945, Johnsgard 1978), appears to be an early branch of the shelducks. However, three humeral characters that were important in distinguishing the "anserines" and shelducks from the "anatines" [capital shaft ridge (character 22), deltoid crest (25), and external tuberosity (32)] were of equivocal or "intermediate" condition in this species. In addition, the enlarged, uniquely distally directed metacarpal I of *Sarkidiornis*, a character complex herein considered to incorporate two aspects [orientation (41) and length (42)], proved difficult to characterize. Perhaps *Sarkidiornis* branched immediately before *Cairina* or, alternatively, after *Plectropterus* but before the divergence of the shelducks from other "anatines."

Three problematic genera—*Hymenolaimus, Merganetta,* and *Tachyeres*—comprise a highly derived clade of shelducks (Figs. 1 and 3). Several of the characters uniting these genera are evidently related to diving and are shared by diving ducks in other clades (see Discussion). *Hymenolaimus* and *Merganetta* have been treated as allied either with the shelducks, "perching ducks," or as exceptional, possibly primitive dabbling ducks (Delacour and Mayr 1945, 1946; Delacour 1956; Ripley 1957; Johnsgard 1965a, 1966a). Some workers placed *Merganetta* in its own tribe, Merganettini (Woolfenden 1961; Kear and Steel 1971; Kear 1972, 1975; Brush 1976; Johnsgard 1978). My analysis does not support the suggestion (Olson and Feduccia 1980a: 22) that ". . . the typical members of the 'subfamily' Anserinae and the typical members of the 'subfamily' Anatinae are more closely related to one another than to *Stictonetta, Malacorhynchus,* or *Merganetta.*"

The third and most derived member of this clade is *Tachyeres* (Fig. 3), a neotropical genus generally placed in the shelducks or in a separate tribe allied with the shelducks (Delacour 1954; Moynihan 1958; Johnsgard 1965a, 1978; Weller 1976; but see Ripley 1957, Woolfenden 1961). Like all shelducks, *Merganetta* and *Tachyeres* show an enlargement of metacarpal I (adorned with keratin spurs in *Merganetta*) that is sexually dimorphic and age related (Weller 1968a, Livezey unpubl. data). *Cyanochen* is hypothesized to be the sister genus to the *Hymenolaimus-Merganetta-Tachyeres* clade, although this relationship is supported by only two synapomorphies. Bottjer (1983) suggested that *Cyanochen* may have branched before the other shelducks.

"Perching" ducks and "dabbling" ducks.—The sister group to the shelducks comprises four groups (Fig. 1): a poorly resolved grade of "perching" and "dabbling" genera (*Pteronetta, Cairina, Aix, Lophonetta, Nettapus, Anas, Callonetta, Chenonetta,* and *Amazonetta*), which in turn gave rise to the pochards and independently to the sea ducks and stiff-tailed ducks. The first group (Fig. 4), henceforth termed "dabbling ducks," is a paraphyletic group of genera previously allocated to either the "Anatini" or the "Cairinini" (Delacour and Mayr 1945; Delacour 1956; Johnsgard 1960c, d, 1961a, e, 1962, 1965a, 1978).

The polyphyletic character of the "Cairinini" was inferred by Woolfenden (1961). The tribe has been recognized by subsequent workers in spite of the equivocal allocation of several genera (e.g. *Callonetta* and *Amazonetta;* Johnsgard 1960a, 1965a, 1978), the widely recognized heterogeneity of its members in behavior, morphology, and biochemistry (Johnsgard 1960c, 1961a, 1962, 1965a, 1978; Woolfenden 1961; Tyler 1964; Brush 1976; Bottjer 1983), the lower incidence of interspecific hybridization within the tribe than between its members and those of other tribes (Johnsgard 1960d), and the conspicuous lack of a single character (or combination of characters) that uniquely distinguishes its members from other anatines. Johnsgard (1965a, 1978) admitted that retention of the tribe was partly a taxonomic convenience to avoid creation of "a comparatively large tribe" (1978: xxi) and omitted it as a suprageneric taxon in his latest list (Johnsgard 1979).

The genera of dabbling ducks (on the basis of three variable multistate characters) form a grade from relatively primitive (e.g. *Cairina, Lophonetta*) to more-derived forms (e.g. *Anas, Callonetta*). A single osteological synapomorphy supports a close relationship between *Cairina* and *Aix* (Fig. 4), a relationship suggested previously by karyotypic and serological comparisons (Yamashina 1952, Cotter 1957, Bottjer 1983).

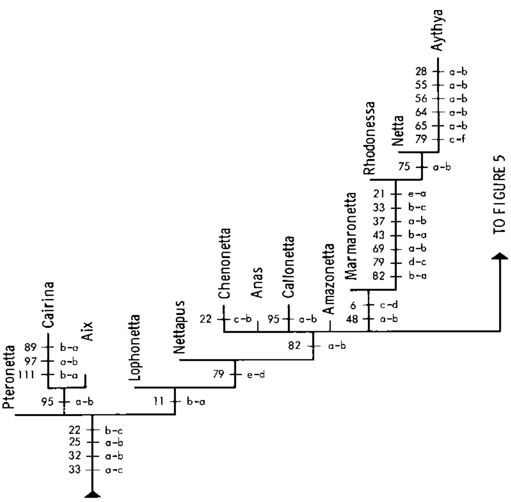

Fig. 4. Detailed diagram of Part 3 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1. Graphical proximity of branches within the polytomy in the dabbling ducks does *not* reflect relatedness.

Pochards.—The pochards are a monophyletic group in an unresolved polytomy that involves *Anas, Callonetta, Chenonetta, Amazonetta,* and the sea ducks and stiff-tailed ducks (Fig. 4), suggesting that the pochards arose independently of other diving ducks. I found that *Rhodonessa* is the sister group to *Netta* and *Aythya,* which agrees with most studies (Verheyen 1955; Johnsgard 1961a, e, 1962, 1978, 1979; Woolfenden 1961; Humphrey and Ripley 1962; Brush 1976) since Delacour and Mayr (1945, 1946) and Delacour (1956) provisionally placed *Rhodonessa* in the dabbling ducks. *Marmaronetta,* a genus believed to "link" the Anatini with the pochards but retained within the Anatini (Johnsgard 1961a, b, e, 1978; Delacour 1964c; Brush 1976), is supported in my study as the sister genus to the pochards by two osteological synapomorphies (Fig. 4). This relationship is corroborated by the secondary loss of metallic coloration in the speculum (Delacour and Mayr 1946).

Sea ducks.—The sea ducks comprise a monophyletic group related to the stiff-tailed ducks, although this relationship is supported by only a few, possibly convergent characters related to diving (Fig. 5). My result contradicts the previously proposed close relationship between sea ducks and "perching ducks" (Delacour and Mayr 1945, Delacour 1959, Bottjer 1983). With

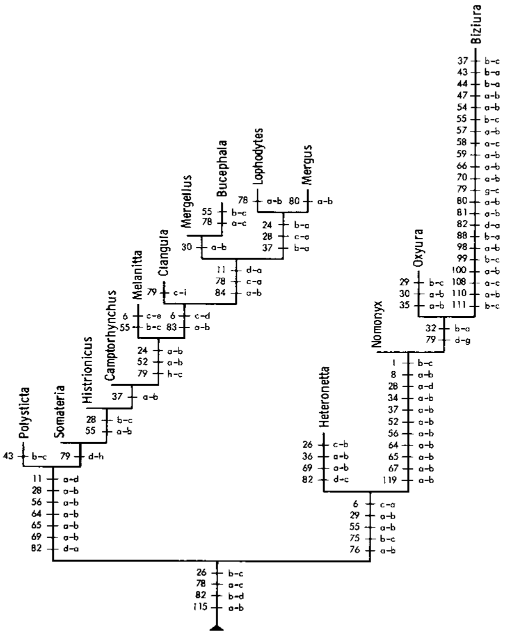

Fig. 5. Detailed diagram of Part 4 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1. Placement of *Camptorhynchus* is tentative.

the possible exception of a few workers who advocated (largely on the retention of primitive *Anas*-like characters) the tribal separation of the eiders (*Somateria* and *Polysticta*) from the other sea ducks (Humphrey 1955, 1958; Delacour 1959; Brush 1976; Todd 1979), the monophyly of the sea ducks has not been questioned recently (e.g. Johnsgard 1960b, 1961a, e, 1964, 1978; Woolfenden 1961; Bottjer 1983).

The proposed sequences of genera within the group has varied (e.g. Delacour and Mayr 1945; Delacour 1959; Johnsgard 1960b, 1961a, 1965a, 1978, 1979). My analysis (Fig. 5) indicates that *Polysticta, Somateria, Histrionicus,* and *Camptorhynchus* comprise a less specialized, basal grade of genera retaining primitive, unfenestrated syringeal bullae. This series of genera gives rise to a well-supported clade of, in order of increasing relatedness, *Melanitta, Clangula,* and the goldeneye-merganser clade. The eiders (*Polysticta, Somateria*) appear to be paraphyletic to the other sea ducks; this paraphyly is supported only weakly, and downy patterns suggest that the eiders may be monophyletic (see Discussion). Placement of *Camptorhynchus* must remain tentative because of the limited material available. Humphrey and Butsch (1958) placed *Camptorhynchus* after *Melanitta* but before *Clangula,* and Zusi and Bentz (1978) allied the genus with eiders, evidently on the basis of shared primitive characters. The very close relationship of goldeneyes and mergansers has had unanimous support in recent decades (e.g. Delacour and Mayr 1945; Boetticher 1952; Humphrey 1955; Delacour 1959; Myres 1959; Johnsgard 1960b, d, 1961a, 1978; Brush 1976).

This analysis shows the Smew (*Mergellus albellus*) to be either the sister genus to *Bucephala* (Fig. 5) or the sister group to the *Lophodytes-Mergus* clade. The former topology is corroborated by the relatively high frequency of *Mergellus* × *Bucephala* hybrids in the wild (Phillips 1925, Ball 1934, Gray 1958, Nilsson 1974, Johnsgard 1978). Previous workers either listed the Smew between the goldeneyes (*Bucephala*) and the mergansers (*Mergus, Lophodytes*) as a monotypic genus (Peters 1931, Woolfenden 1961, A.O.U. 1983), or merged it (with *Lophodytes*) into *Mergus* (Delacour and Mayr 1945; Boetticher 1952; Humphrey 1955; Delacour 1959, 1964c; Johnsgard 1960c, 1961a, d, 1965a, 1978, 1979).

Stiff-tailed ducks.—My study supports the monophyly of the stiff-tailed ducks, wherein *Heteronetta* is the sister genus to the more typical members (Fig. 5). The position of the clade as closely related to the sea ducks and highly derived (especially *Biziura*) agrees with recent orderings of genera by taxonomists (e.g. Johnsgard 1979) but disagrees with suggestions of a pre-dabbling duck (Raikow 1970b, Johnsgard 1978) or pre-shelduck (Johnsgard 1965b, Bottjer 1983) origin for the group. A few workers have expressed doubts about the relationships of *Heteronetta* (Johnsgard 1960c, Brush 1976), and others accepted the relationship between *Heteronetta* and other stiff-tailed ducks but suggested that the genus be accorded tribal rank (Weller 1967, 1968b; Rees and Hillgarth 1984).

My analysis shows that the Masked Duck [*Nomonyx* (*Oxyura*) *dominica*] is the sister group to the highly derived *Oxyura-Biziura* clade (Fig. 5), i.e. *Oxyura* is related more closely to *Biziura* than to the very similar *Nomonyx.* This topology is supported as well by the derived loss of a speculum in *Oxyura* and *Biziura,* which is retained in *Nomonyx* (Delacour 1959). This finding supports the resurrection of *Nomonyx* as advocated by Woolfenden (1961), a recommendation rejected by Delacour (1964c), Johnsgard (1967), and most subsequent workers. I did not examine skeletons of all species of *Oxyura*, so monophyly of the genus was not established with certainty.

DISCUSSION

Diving habit and homoplasy.—Considerable homoplasy (convergence) of characters is shown in the tree (Figs. 1-5) and by the consistencies of characters (Appendix 1). The majority of the convergences are associated with adaptations for diving, and most involve the leg elements (characters 52, 55, 56, 64, 65, 69, 75), pelvis (119), and skeletal pneumaticity (28, 78). These features tend to co-occur, especially within elements. Convergence between *Thalassornis* and the stiff-tailed ducks is particularly pervasive (Figs. 2 and 5). It appears, however, that the moderately large number of characters included in this analysis reduced the impact of such homoplasy on the resultant tree, although deletions or heavy weighting of selected characters can produce topological changes. For example, because of a number of diving-related homoplasies, postulation of the *Hymenolaimus-Merganetta-Tachyeres* clade as the sister group to the sea ducks and stiff-tailed ducks is only slightly less parsimonious than the topology presented (Fig. 1). Similarly, heavier weighting of appendicular characters places *Heteronetta* as the sister group to both the sea ducks and other stiff-tailed ducks.

Patterns of downy young.—Although an analysis of downy patterns for the entire order is not possible at present, a cladistic reevaluation of the downy young illustrated in Delacour (1954, 1956, 1959) permits an independent test of two parts of my phylogenetic hypothesis (using *Anas* as the outgroup). Patterns in downy stiff-tailed ducks agree well, wherein (1) *Heteronetta* retains virtually all dabbling-duck characters; (2) *Nomonyx, Oxyura,* and *Biziura* share a synapomorphic, dark cheek stripe; (3) *Oxyura* and *Biziura* are united by the derived loss of the pale supraorbital stripe; and (4) *Biziura* shares a loss of dorsal and wing spotting with the Peruvian Ruddy Duck (*O. ferruginea*) and dark cheeks with the Australian Blue-billed Duck (*O. australis*). Patterns of downy Mergini also are informative: (1) eiders retain the supraorbital stripe of dabblers but, in contrast to osteological evidence, appear monophyletic in their dusky undersides, obsolete dorsal spots, and dark cheeks; (2) other Mergini lack the supraorbital stripe and dorsal spotting of the dabbling ducks (loral spot and vestigial back spots retained in *Histrionicus*); (3) *Melanitta* and its sister genera are synapomorphic in their dark breast bands, a character secondarily lost in *Mergus*; (4) the Black Scoter (*Melanitta nigra*) and Surf Scoter (*M. perspicillata*) are united by the derived darkening of the lower breast and belly; (5) *Bucephala, Mergellus, Lophodytes,* and *Mergus* share a reversal in (presence of) dorsal spotting; (6) obscured (*Lophodytes*) to dark (*Mergus*) cheeks unite the mergansers; and (7) *Mergus* is derived further in the anteriorly incomplete breast band and pale suborbital stripe.

Similarity vs. relatedness.—Recognition of the different types of character change is important in light of the conspicuously unequal rates of morphological evolution in different lineages, e.g. autapomorphies of *Branta* vs. *Cereopsis* (Fig. 2) and *Oxyura* vs. *Biziura* (Fig. 5). The inadequacy of simple distance techniques was demonstrated using these data through a comparison of phylogenetic relationships with "path lengths" or patristic distances. Selected results were: (1) *Anseranas* is roughly equidistant from the anhimids and other anatids [corroborated immunologically by Bottjer (1983)], but is the sister group to the latter (Fig. 2); (2) *Thalassornis* is most similar to *Dendrocygna* but is more closely related to other anatids, excluding *Anseranas* (Fig. 2); (3) *Heteronetta* appears "nearer" to *Anas* than to *Oxyura*, a member of the sister group of *Heteronetta* (Figs. 4 and 5); and (4) because of autapomorphies in *Oxyura*, *Biziura* is phenetically "closer" to *Nomonyx* than it is to its sister genus *Oxyura* (Fig. 5).

Life-history correlates.—Diving, at least as an escape behavior, occurs throughout the order except in the anhimids and possibly *Anseranas* (Johnsgard 1962, Todd 1979). Groups that routinely dive for food are fewer, but occur in six lineages throughout the family (Weller 1964b): *Dendrocygna, Thalassornis, Hymenolaimus-Merganetta-Tachyeres*, pochards, sea ducks, and stiff-tailed ducks.

Perching habit, the probably primitive character used traditionally to define the polyphyletic "perching ducks," occurs in many genera, including *Anseranas, Dendrocygna, Plectropterus, Sarkidiornis, Tadorna, Malacorhynchus, Cairina, Aix,* *Chenonetta, Rhodonessa,* and *Amazonetta* (Ali 1960, Johnsgard 1978, Todd 1979). A related trait (also used to justify the "Cairinini"), nesting in tree cavities, occurs in *Dendrocygna,* some shelducks (*Sarkidiornis, Neochen, Alopochen, Tadorna, Malacorhynchus*), a number of dabbling ducks (e.g. *Aix,* some *Anas*), and some sea ducks (*Histrionicus, Bucephala, Mergellus, Lophodytes, Mergus*).

Use of terrestrial cavities for nesting also occurs in some shelducks (*Tadorna, Hymenolaimus, Merganetta, Tachyeres*), in some *Anas,* and in the sea ducks cited above (Hobbs 1957, Warham 1959, Johnsgard 1962, Johnson 1963, Weller 1964c, Kear 1970, Moffett 1970, Humphrey and Livezey 1985). Other species nest on the ground or over water (Weller 1964c, Kear 1970). Only the Black-headed Duck (*Heteronetta atricapilla*) is an obligate nest parasite, although infrequent nest parasitism occurs in a number of other genera including *Dendrocygna, Branta, Anas, Aythya,* and *Mergus* (Weller 1959, 1968b). Although ground nesting appears to be primitive for the order (Johnsgard 1965a, Kear 1970), nesting habit is probably unreliable for intraordinal phylogenetic inferences. Clutch size, proportion of yolk in eggs, incubation period, parental carrying of young, and sexual dimorphism also appear to be quite plastic (Johnsgard 1961f, 1966b; Lack 1967, 1968, 1974; Johnsgard and Kear 1968; Kear 1970; Livezey and Humphrey 1984).

Selected reproductive characteristics, however, show distinct primitive-to-derived sequences (Kear 1970). Most change near the divergence of the goose-swan clade but may be confounded by an evolutionary trend toward reduced body size: (1) nest bowl unlined vs. lined with down (secondarily lost in stiff-tailed ducks); (2) biparental nest construction, incubation, and attendance of young vs. female alone responsible; and (3) brooding period and pair bond long ("anserines," roughly 6 months) vs. moderately long (shelducks, roughly 4 months) vs. comparatively short (dabblers and divers, less than 2 months). Participation of males in brood rearing is variable within *Anas,* however, wherein several neotropical species are characterized by protracted, perhaps permanent pair bonds (Johnsgard 1978).

Biogeographic patterns.—Despite the early acknowledgment of the diversity of "aberrant and primitive" genera in Australia (Delacour and Mayr 1945: 51), most previous biogeographers contended that the Anseriformes originated in the Northern Hemisphere, probably the Palearctic (Howard 1950, Weller 1964d). Although the fossil record of waterfowl is more complete for the Northern Hemisphere (Howard 1964), early forms are known from both hemispheres, and the apparent disparity in representation probably reflects intensity of paleontological research. The only essentially northern groups are *Olor, Anser-Branta, Cyanochen, Rhodonessa,* and the sea ducks; genera that have roughly equal distributions in both hemispheres are *Cygnus, Tadorna, Alopochen, Anas, Netta, Aythya,* and *Oxyura.* The remaining 20 genera are limited to or most speciose in the Southern Hemisphere, and, with the anhimids, include most of the early branches in the order. Furthermore, the earliest branches (Fig. 2) in the swan and goose clades are genera limited to the Southern Hemisphere. The numerous holarctic species of *Anas, Aythya,* and the sea ducks (Weller 1964d) may represent radiations hastened by widespread glaciations (cf. Ploeger 1968). Consequently, I agree with Cracraft (1980) that the Anseriformes probably originated in the Southern Hemisphere.

Taxonomic implications.—The tribes of Anatidae originally proposed by Delacour and Mayr (1945) were defined primarily in terms of genera of the Northern Hemisphere. Although most tribes were assigned members from both hemispheres, only the monotypic "Merganettini" was limited to the Southern Hemisphere. A number of "aberrant" southern genera were sorted tentatively among these tribes: *Anseranas* and *Plectropterus* to the Cairinini; *Cereopsis, Tachyeres,* and *Lophonetta* to the Tadornini; *Stictonetta, Malacorhynchus,* and *Hymenolaimus* to the Anatini; and *Thalassornis* to the Oxyurini. Since then four of these genera have been placed in their own subfamilies or tribes, one has been moved to another subfamily, and the others have remained problematic (Wolfenden 1961, Johnsgard 1978). Several findings in my study involve these genera, and suggest a revision of the classification of waterfowl (Appendix 2).

The dabbling ducks are paraphyletic and should be considered a phylogenetically unresolved group. I therefore place these genera in a provisional taxon, the "Anatini" (Appendix 2). If paraphyly of this group is corroborated by further work, the erection of additional tribes corresponding to the branches in the grade would be warranted.

Classification of fossil groups.—Several early fossils can be classified tentatively on the basis of published descriptions (Howard 1964). *Romainvillia* (upper Eocene or lower Oligocene), *Cygnopterus* (upper Oligocene), and *Paranyroca* (lower Miocene) possess the primitive procoracoidal foramen (character 92) retained among Recent genera only by anhimids and *Anseranas.* Conformation of the tarsometatarsal trochlea (68) indicates that at least *Romainvillia* and *Paranyroca* are derived with respect to *Anseranas,* and the hypotarsus (72) of *Paranyroca* shows it to be more primitive than *Dendrocygna.* Accordingly, these fossils should be listed after *Anseranas* and before *Dendrocygna* and sequenced (provisionally by epoch of occurrence) as *Romainvillia, Cygnopterus,* and *Paranyroca;* the fossils may be given familial names or be designated "plesions" (Wiley 1981) at familial rank. Phylogenetic reappraisals of several other fossil Anseriformes [e.g. *Anas*(?) *blanchardi,* the tadornines *Anabernicula* and *Brantadorna,* and *Chendytes;* Howard 1964], and the probable anseriform *Presbyornis* (Olson and Feduccia 1980a), should provide minimum ages of branch points in the phylogeny.

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APPENDIX 1

The 120 characters used in this analysis are listed below and are numbered and grouped anatomically. Character states are lettered and correspond to the character changes in Figs. 2-5. Plesiomorphic (primitive) conditions generally are designated "a" and derived character states are ordered alphabetically thereafter (implying a linear transformation series); characters followed by a "U" were analyzed as unordered. Characters for which the primitive state was not determined are marked with "U*." Characters judged to be unusually variable, generally necessitating determinations of modal conditions, are indicated with a "V." Taxa with problematic state determinations are listed in parentheses after the corresponding character. Consistency indices (CI) follow each character. Anatomical terminology follows Howard (1929) and Woolfenden (1961) unless annotated otherwise.

Integument

1. Molt of remiges: (a) sequential; (b) synchronous, once annually; (c) synchronous, twice annually. (Variable in Phoenicopteridae; Sileo et al. 1977.) CI = 1.0.
2. Tarsal sheath: (a) scutellate anteriorly and posteriorly; (b) reticulate anteriorly and posteriorly; (c) scutellate anteriorly (at least distally) and reticulate posteriorly. CI = 1.0.
3. Spongy subcutaneous layer: (a) absent; (b) present. CI = 1.0.
4. Interdigital webbing of feet (excluding hallux): (a) lacking (slight webbing in anhimids); (b) incomplete (semipalmate); (c) complete (incised in *Cereopsis* and *Branta sandwicensis*). CI = 1.0.
5. Apteria: (a) present; (b) obsolete. CI = 1.0.

Trachea

6. Bulla ossea of males (U, weight = 2): (a) not enlarged; (b) symmetrically enlarged; (c) asymmetrically enlarged, unfenestrated;

(d) asymmetrically enlarged, fenestrated; (e) enlargement reduced and symmetrical, or obsolete. (*Thalassornis, Malacorhynchus, Nettapus.*) CI = 0.67.

7. Extrasternal, subdermal looping of trachea in males (U*): (a) present; (b) absent. CI = 0.33.
8. Inflatable tracheal air sacs: (a) absent; (b) present. CI = 1.0

Skull

9. Occipital fontanelles: (a) absent; (b) present. CI = 1.0.
10. Lacrymals (U): (a) not fused to skull; (b) fused to skull dorsally, small, nonpneumatic; (c) fused dorsally, moderately thick, long, ventrally directed (lacking flange), nonpneumatic; (d) fused to skull dorsally, and (typically) also fused to postorbital process, slightly pneumatic; (e) fused dorsally, of variable shape and pneumaticity, posterioventrally directed, often with flanged ventral terminus. CI = 1.0.
11. Supraorbital process (U; best developed in adult males): (a) absent or small, straight, essentially coplanar with dorsal surface of skull; (b) large, flat, medially appressed to dorsal margin of orbit; (c) large, thick, rugose, dorsolaterally directed; (d) long, slender, dorsally directed, often curved. (*Aythya, Bucephala albeola.*) CI = 0.38.
12. Anterior terminus of premaxillae: (a) strongly ventrally hooked, typically pointed; (b) strongly ventrally hooked, moderately rounded; (c) not ventrally hooked (directed anteriorly), rounded, spatulate. CI = 1.0.
13. Bill lamellae: (a) absent; (b) present. (Nonhomologous lamellae in flamingos, vestigial in anhimids; Olson and Feduccia 1980a.) CI = 1.0.
14. Retroarticular processes of mandible: (a) lacking, small, or recurved and rounded; (b) recurved, pointed, and bladelike. CI = 1.0.
15. Quadrate, lateral view: (a) not squarish, with variably deeply curved dorsal margin between orbital and otic processes; (b) squarish, with dorsal margin straight. CI = 0.33.
16. Frontonasal region of skull (U): (a) essentially continuous with profile defined by premaxillae and frontals; (b) enlarged into conspicuous, laterally compressed, dorsal prominence (larger in males); (c) with rounded, pneumatic swelling (especially in adult males). CI = 0.50.
17. Frontals: (a) without dorsally directed hornlike prominence; (b) with small, ossified "horn" on midline. CI = 1.0.
18. Pterygoid-palatine articulation: (a) a simple abutment; (b) a ball-and-socket arrangement involving two extensions of the pterygoid. CI = 1.0.
19. Dorsum of upper bill in region of external nares: (a) essentially continuous with curvature of skull to somewhat convex; (b) substantially dorsally bowed. CI = 1.0.
20. Basipterygoid processes: (a) lacking or (in Galliformes) present but without basal supports; (b) present, lipped, almost pedicellate. CI = 1.0.

Vertebrae

21. Number of cervical vertebrae (U, V): (a) 17; (b) 18–20; (c) 21; (d) 22–25; (e) 16. (Some Tadorninae.) CI = 0.67.

Humerus

22. Capital shaft ridge: (a) prominent and directed toward head; (b) prominent and directed toward external tuberosity; (c) obsolete proximally or absent completely. (*Sarkidiornis, Cyanochen, Hymenolaimus, Chenonetta.*) CI = 0.50.
23. Capital groove: (a) short, essentially directed distally; (b) extending laterally toward external tuberosity, undercutting head. (*Thalassornis.*) CI = 0.50.
24. Proximo-anconal region: (a) variably rounded by shaft; (b) traversed by a deep, uninterrupted trenchlike depression from under head to internal edge immediately distal to bicipital crest. CI = 0.33.
25. Deltoid crest (V): (a) margin rounded, laterally flaring, concave anconally; (b) margin angular or squared, depressed around shaft toward palmar side, convex anconally. (*Sarkidiornis, Hymenolaimus.*) CI = 0.50.
26. Surface of attachment for anterior articular ligament: (a) not elevated, essentially parallels shaft; (b) elevated, angled distally; (c) elevated, angled medially. CI = 0.40.
27. Internal tuberosity: (a) proximally rotated, exposing completely the pneumatic foramen in anconal view, lacking a distinct, distally directed prominence; (b) produced distally so as to largely or completely obscure pneumatic foramen in anconal view, typically with prominent, distally directed point. CI = 0.50.
28. Pneumatic fossa (U): (a) open, usually containing numerous bony struts; (b) closed by bony shell except for a small central opening; (c) completely closed; (d) closed but perforated by numerous small holes. (*Lophodytes.*) CI = 0.43.
29. Attachment site of M. latissimus dorsi posterioris: (a) well medial to external edge of pectoral attachment; (b) in line with outer edge of pectoral attachment, on anconal surface of shaft; (c) in line with outer edge of pectoral attachment, on raised ridge. CI = 1.0.
30. Distal portion of anconal surface of bicipital crest: (a) poorly developed or shelflike; (b) produced medially with distinct proximal cuplike depression, visible as translucent window in palmar view. CI = 0.50.
31. Distal terminus of deltoid crest: (a) essentially continuous with lateral edge of shaft; (b) produced into prominent tuberosity on palmar surface of shaft. CI = 1.0.
32. External tuberosity: (a) prominent, buttressed, typically with attachment site elevated, parallel to shaft, not sloping away with anconal surface of deltoid crest; (b) reduced, lacking buttress, with attachment site sloping and essentially flush with anconal surface of deltoid crest. (*Stictonetta, Sarkidiornis, Cyanochen, Merganetta, Oxyura.*) CI = 0.33.
33. Relative anconal heights of ectepicondyle and entepicondyle: (a) ectepicondyle distinctly higher than entepicondyle; (b) condyles essentially equally high; (c) ectepicondyle lower than entepicondyle. (*Hymenolaimus.*) CI = 0.40.
34. Pit for attachment of M. flexor carpi ulnaris: (a) prominent; (b) reduced to obsolete. CI = 1.0.
35. External condyle and brachial depression (palmar side, distal end): (a) separated by smooth strip of bone; (b) connected by rounded ridge. CI = 1.0.
36. Attachment site for external head of triceps: (a) immediately distal to head, typically in excavation under head; (b) displaced distally on lobe of bone and obscures external terminus of capital groove. CI = 1.0.

Carpometacarpus

37. Distal end of internal rim of carpal trochlea (external view): (a) with prominent swelling; (b) without prominent swelling; (c) deeply excavated. (*Marmaronetta, Hymenolaimus, Clangula, Mergellus, Heteronetta.*) CI = 0.33.
38. External rim of carpal trochlea: (a) essentially continuous, unnotched; (b) with prominent notch distally. CI = 1.0.
39. Dorsal surface of metacarpal II: (a) flattened proximally (can appear angular); (b) rounded proximally. CI = 1.0.
40. Tuberosity of metacarpal II: (a) small; (b) prominent, spurred. CI = 1.0.
41. Angle of process of metacarpal I: (a) perpendicular to or proximally directed relative to shaft; (b) angled distally. (*Plectropterus.*) CI = 1.0.
42. Process of metacarpal I (U): (a) not enlarged, length less than width of trochlea; (b) an enlarged, pointed spur, longer than width of trochlea; (c) enlarged, blunt, typically with rugose-capped spur, longer than width of trochlea. (*Plectropterus, Hymenolaimus, Lophonetta.*) CI = 0.50.
43. Attachment site of M. extensor metacarpi ulnaris (Zusi and Bentz 1978; "flexor" of Woolfenden 1961) (U, V): (a) completely proximal to proximal fornix of metacarpal II and III: (b) opposite, at least partly, fornix; (c) completely distal to fornix. (*Tachyeres.*) CI = 0.29.
44. Lower proximal surface of metacarpal III: (a) ungrooved, rounded; (b) distinctly grooved. CI = 0.50.
45. Facets for digits II and III (U*): (a) facet for digit III extending farther distally than facet for digit II; (b) facets essentially equal in distal extent. CI = 0.33.
46. Cuneiform fossa: (a) shallow to moderately deep; (b) deep, rounded, ovate, with distinct rim. CI = 1.0.

APPENDIX 1. Continued.

47. Distal portion of internal rim of carpal trochlea: (a) of uniform thickness with proximal portion; (b) distinctly thickened. CI = 0.50.
48. Internal rim of carpal trochlea (posterior view): (a) in line with internal margin of shaft; (b) sharply deflected laterally. (*Callonetta.*) CI = 1.0.

Radial carpal

49. Size and shape: (a) small, short, and blunt; (b) elongated into large pointed spur. CI = 1.0.

Appendicular pneumaticity

50. Distal alar and pelvic elements: (a) essentially nonpneumatic; (b) pneumatic with one or more large foramina. CI = 1.0.

Femur

51. Head, relative to plane of external surface of shaft: (a) oriented posteriorly; (b) perpendicular. CI = 1.0.
52. Anterior extent of trochanter: (a) relatively great, such that anterior-posterior depth of trochanter substantially exceeds depth of head; (b) reduced, such that depth of trochanter only equals that of head. CI = 0.33.
53. Distal extent of internal condyle: (a) distinctly less than that of external condyle; (b) equal to that of external condyle. CI = 1.0.
54. Rotular depression: (a) shallow to moderately deep, margin relatively indistinct; (b) deep, distinctly bordered proximally. CI = 1.0.
55. Curvature of shaft, lateral view (U): (a) straight to slight; (b) moderate; (c) strong, subangular. CI = 0.22.
56. Popliteal fossa: (a) shallow; (b) deep, typically pitted. CI = 0.25.
57. Lobe at midpoint of posterior surface of shaft: (a) not prominent; (b) prominent. CI = 1.0.
58. Posterior intermuscular line (U): (a) relatively distinct, following internal edge of shaft; (b) relatively distinct, swings laterally toward trochanter; (c) indistinct. CI = 1.0.
59. Internal edge of distal end of shaft: (a) smoothly curving and continuous with proximal portion; (b) leveled by raised ridge to internal condyle. CI = 1.0.
60. Posterior intermuscular line: (a) distinguishable only as fine etching; (b) forming overhanging ridge proximally. CI = 1.0.

Tibiotarsus

61. Proximal articulating surface: (a) in line with shaft, squares with distal condyles; (b) strongly rotated counterclockwise about shaft (proximal view). CI = 0.50.
62. Rim of internal condyle: (a) distinctly notched; (b) lacking notch. CI = 1.0.
63. Inner cnemial crest: (a) not deflected laterally; (b) laterally deflected. CI = 1.0.
64. Anterior extent of condyles: (a) internal distinctly greater than external; (b) approximately equal. (*Aythya.*) CI = 0.25.
65. Inner cnemial crest: (a) lacking distinct ridge extending distally along anterior surface of shaft; (b) continued by distinct ridge distally along anterior surface of shaft to point well beyond proximal terminus of fibular crest. CI = 0.25.
66. Internal condyle, posterior view: (a) with relatively rounded internal edge; (b) flared, with squared medial edge. CI = 1.0.
67. External ligamental prominence: (a) essentially continuous with curvature of shaft; (b) produced laterally, ridgelike. CI = 1.0.

Tarsometatarsus

68. Trochlea for digit II: (a) approximately equal to trochlea for digit IV in distal extent; (b) proximal to trochlea for digit IV. CI = 1.0.
69. Anterior (of two) ligamental passages between trochlea for digits III and IV (in distal wall of distal foramen) (V): (a) obscured from view anteriorly by bone; (b) largely or completely exposed anteriorly because of reduction of bony covering. CI = 0.25.
70. Internal calcaneal ridge of hypotarsus: (a) slightly to moderately exceeds other calcaneal ridges in posterior extent; (b) greatly exceeds other (more external) calcaneal ridges. CI = 0.50.
71. Facet for metatarsal I: (a) deep; (b) obsolete. CI = 1.0.
72. Calcaneal ridges of hypotarsus: (a) 2, lateral to midline of shaft, bordered medially by depression (deep in *Anseranas*); (b) 3 or 4, situated on midline of shaft, without depression on internal margin. CI = 1.0.
73. Wing on trochlea for digit II: (a) not prominent medially; (b) medially prominent, thickened. CI = 1.0.
74. Groove in trochlea for digit II: (a) absent; (b) present, but posterior terminus of groove variable in extent. CI = 1.0.
75. Anterior extent of internal and external ridges of shaft: (a) essentially equal, no twisting of shaft about its long axis; (b) internal ridge less prominent anteriorly than external, becoming flush with shaft immediately distal to proximal foramen, associated with moderate twisting of shaft; (c) internal edge of shaft depressed below level of shaft anteriorly, associated with strong twisting of shaft. (*Hymenolaimus, Merganetta, Amazonetta.*) CI = 0.33.
76. External margin of shaft: (a) concave (in anterior profile), curving smoothly to external surface of trochlea for digit IV; (b) essentially straight, trochlea for digit IV internally deflected. CI = 1.0.
77. Posterior opening of distal foramen: (a) directed posteriorly, flush with surface of shaft; (b) directed distoposteriorly, recessed in depression immediately proximal to symphysis of trochlea for digits III and IV. (*Anseranas.*) CI = 1.0.

Sternum

78. Pneumatic foramen (U*): (a) open, ovoid; (b) pitted, largely occluded by medial bar; (c) closed (sometimes marked by small depression). CI = 0.25.
79. Ventral manubrial region (U*, V): (a) keel-like, laterally compressed medial flange; (b) thick medial wedge; (c) lacking median protuberance(s); (d) long, peglike spine; (e) small lump; (f) a pair of small pointed prominences separated at midline by a deep excavation, typically with an ovoid pit at base; (g) a wide, moderately long, dorsoventrally compressed flange; (h) a pair of points partially separated by a shallow midline excavation; (i) a small, unforked, dorsoventrally compressed flange. (*Cyanochen, Hymenolaimus, Cairina, Lophonetta, Chenonetta, Polysticta.*) CI = 0.50.
80. Carina (keel) shape, lateral profile: (a) well developed, ventral margin curved throughout length; (b) reduced, ventral margin essentially straight for posterior half. CI = 0.33.
81. Posterior-lateral processes (U*): (a) extend well posterior to postpectoral line of sternal plate; (b) approximately equal to postpectoral line in posterior extent. CI = 0.33.
82. Dorsal manubrial region (U, V): (a) rounded notch; (b) rounded notch with small point on midline; (c) rounded notch with moderately large point on midline; (d) even shelf. (*Malacorhynchus, Hymenolaimus, Marmaronetta, Callonetta.*) CI = 0.43.
83. Abdominal plate (dense, symmetrical extension of sternal plate posterior to both post-pectoral line and posterior-lateral processes): (a) absent; (b) present. CI = 1.0.
84. Sternal notches (posterior margin of plate medial to posterior-lateral processes): (a) typically open posteriorly; (b) typically closed posteriorly, forming fenestrae. CI = 1.0.
85. Xiphial area: (a) posterior margin approximately straight or concave; (b) with medial, irregularly shaped, roughly circular extension of thin bone (anterior to posterior-lateral processes). CI = 1.0.
86. Costal margin: (a) comprises less than half of basin length; (b) comprises more than half of basin length. CI = 1.0.
87. Carina: (a) lacking pneumatic foramen in anterior margin, apparently solid; (b) with small pneumatic foramen in anterior edge, but carina uninflated; (c) hollow, containing loop of trachea, with large pneumatic foramen in anterior edge. CI = 1.0.
88. Intermuscular line: (a) angles medially to carinal base well anterior to posterior edge of plate; (b) extends posteriorly to posterior margin of plate. CI = 0.33.
89. Foramina of basin (U*): (a) limited to midline and anterior margin; (b) essentially absent; (c) present on anterior margin, midline, and scattered across plate (often among transverse bony striations). CI = 0.50.
90. Midpoint of coracoidal sulcus: (a) solid; (b) having oval pneumatic foramen. CI = 1.0.

Costae

91. Uncinate processes: (a) present; (b) absent. CI = 1.0.

Coracoid

92. Procoracoidal foramen: (a) present (variable in *Chauna*); (b) absent. CI = 1.0.
93. Pneumatic foramen on dorsal surface anterior to sternal facet: (a) present; (b) absent. CI = 1.0.
94. Dorsal sternal facet: (a) with anterior border essentially smoothly curving; (b) with prominent circular internal lip. CI = 1.0.
95. Brachial tuberosity (U): (a) essentially without foramina under posterior edge; (b) with small foramina under posterior edge; (c) with small foramina, typically contained within larger foramina, under posterior edge. CI = 0.50.
96. Depression on ventral surface anterior to sternal facet (U*): (a) present, typically deep; (b) absent. (*Anseranas.*) CI = 0.25.
97. Furcular facet: (a) with posterior margin complete or slightly reduced; (b) posterior margin deeply notched. CI = 1.0.
98. Angle of head: (a) coplanar to slightly ventral to plane of blade; (b) distinctly ventral to plane of blade. CI = 1.0.
99. Sternocoracoidal process: (a) wide, long, and rounded flange, extending farther laterally than sternal facet; (b) variably shaped, rounded or angular process, approximately equal to sternal facet in lateral extent; (c) long pointed process, extending farther laterally than sternal facet. CI = 0.67.
100. Ventral (external) sternal facet (V): (a) anterior margin moderately raised or continuous with blade; (b) anterior margin with distinct buttress. CI = 0.33.

Furculum

101. Coracoidal tuberosities (U*): (a) present; (b) obsolete. CI = 0.25.
102. Furcular process: (a) a flattened point; (b) variable, but reduced, essentially continuous with curvature of clavicles; (c) swollen truncate lobe. CI = 1.0.
103. Clavicular symphysis: (a) without foramina; (b) with medial foramina. CI = 1.0.
104. Clavicles: (a) roughly circular in cross-section; (b) distinctly flattened antero-posteriorly. CI = 1.0.
105. Lateral surfaces of clavicles: (a) smooth, unperforated; (b) with depressions containing several small foramina; (c) with depression containing large pneumatic foramen. CI = 0.50.
106. Region of clavicular symphysis: (a) a continuous smooth curve; (b) markedly extended posterodorsally, forming a U-shaped accommodation for tracheal loop and associated modification of carina. CI = 1.0.

Scapula

107. Coracoidal articulation: (a) flush with blade; (b) base protruding ventrally as rounded hump. CI = 1.0.
108. Taper (profile) of blade (U): (a) of uniform width or tapering continuously throughout length; (b) width maximal at midpoint; (c) width maximal at terminus. (*Cygnus, Olor.*) CI = 1.0.
109. Coracoidal articulation: (a) equal to acromion in proximal extent; (b) distinctly distal to acromion. CI = 1.0.
110. Internal surface, immediately posterior to glenoid facet: (a) essentially smooth; (b) having deep depression. CI = 1.0.
111. Anterior edge (U*): (a) containing pneumatic fossa; (b) without pneumatic fossa. (*Cairina.*) CI = 0.25.
112. Dorsal surface of neck: (a) marked by single distinct raised attachment scar; (b) marked by two prominent raised attachment scars. CI = 1.0.

Pelvis

113. Preacetabular iliac fossa: (a) smoothly curved surface; (b) containing a deep, irregularly shaped depression. CI = 1.0.
114. Caudal margin: (a) ischium extending well caudad to ilium; (b) variable, but ischium and ilium roughly equal in caudal extent, forming an obliquely sloping margin, with elements typically separated posteriorly by a distinct notch. CI = 1.0.
115. Body of pubis (V): (a) concave dorsally (rarely almost straight); (b) convex dorsally. CI = 0.50.
116. Orientation of postischiac pubis: (a) directed posteriorly; (b) directed ventrally. CI = 1.0.
117. Shape of postischiac pubis: (a) of uniform width or evenly widening caudally; (b) widened into roughly circular flange, especially extensive anteroventrally. CI = 1.0.
118. Dorsolateral crests: (a) distinct to caudal margin of pelvis; (b) becomes obsolete cranial to caudal margin. CI = 1.0.
119. Anterior terminus of shield (posterior terminus of fusion of median dorsal ridge): (a) cranial to acetabula; (b) essentially coincident with acetabula; (c) well caudad to acetabula. CI = 0.67.
120. Recessus iliacus (Baumel 1979; a pneumatic pocket at caudal terminus of renal depression): (a) present; (b) absent. CI = 1.0.

Appendix 2. A Linnean classification of the Recent genera of Anseriformes. I follow the conventions of Wiley (1981), with the exception of the provisional recognition of the paraphyletic "Anatini" (annotated *incertae sedis*). I have retained, where possible, the names and taxonomic ranks of previous classifications. Names of subtribes are given endings of -eae after the names for the "sections" of Boetticher (1952) and are derived from the oldest included genus. *Sedis mutabilis* follows taxa in which the order of included groups is unresolved. * = two subfamilies may be in reverse order; ** = subtribes possibly are sister groups; * = probable sister groups.**

- Order Anseriformes
  - Suborder Anhimae
    - Family Anhimidae
      - Genus *Anhima*
      - Genus *Chauna*
  - Suborder Anseres
    - Family Anseranatidae
      - Genus *Anseranas*
    - Family Anatidae
      - Subfamily Dendrocygninae
        - Genus *Dendrocygna*
      - Subfamily Thalassorninae*
        - Genus *Thalassornis*
      - Subfamily Anserinae*
        - Tribe Anserini
          - Genus *Cereopsis*
          - Genus *Anser*
          - Genus *Branta*
        - Tribe Cygnini
          - Genus *Coscoroba*
          - Genus *Cygnus*
          - Genus *Olor*
      - Subfamily Stictonettinae
        - Genus *Stictonetta*
      - Subfamily Plectropterinae
        - Genus *Plectropterus*
      - Subfamily Tadorninae
        - Tribe Sarkidiornini
          - Genus *Sarkidiornis*
        - Tribe Tadornini *sedis mutabilis*
          - Subtribe Tadorneae
            - Genus *Tadorna*
          - Subtribe Malacorhyncheae
            - Genus *Malacorhynchus*
          - Subtribe Chloephageae *sedis mutabilis*
            - Genus *Alopochen*
            - Genus *Neochen*
            - Genus *Chloephaga*
          - Subtribe Cyanocheneae**
            - Genus *Cyanochen*
          - Subtribe Merganetteae**
            - Genus *Hymenolaimus*

APPENDIX 2. Continued

        - Genus *Merganetta*
        - Genus *Tachyeres*
- Subfamily Anatinae
    - [Tribe] "Anatini" *incertae sedis*
        - Genus *Pteronetta*
        - Genus *Cairina*
        - Genus *Aix*
        - Genus *Lophonetta*
        - Genus *Nettapus*
        - Genus *Anas*
        - Genus *Callonetta*
        - Genus *Chenonetta*
        - Genus *Amazonetta*
    - Tribe Aythyini
        - Genus *Marmaronetta*
        - Genus *Rhodonessa*
        - Genus *Netta*
        - Genus *Aythya*

APPENDIX 2. Continued

    - Tribe Mergini
        - Genus *Polysticta*
        - Genus *Somateria*
        - Genus *Histrionicus*
        - Genus *Camptorhynchus*
        - Genus *Melanitta*
        - Genus *Clangula*
        - Genus *Bucephala****
        - Genus *Mergellus****
        - Genus *Lophodytes*
        - Genus *Mergus*
    - Tribe Oxyurini
        - Genus *Heteronetta*
        - Genus *Nomonyx*
        - Genus *Oxyura*
        - Genus *Biziura*

POPULATION ECOLOGY OF THE LONG-BILLED CURLEW (*NUMENIUS AMERICANUS*) IN WESTERN IDAHO

ROLAND L. REDMOND AND DONALD A. JENNI
Department of Zoology, University of Montana, Missoula, Montana 59812 USA

ABSTRACT.—In western Idaho, a breeding population of Long-billed Curlews (*Numenius americanus*) remained relatively stable over a 7-yr period. Productivity was monitored closely from 1977 through 1979. Clutch mortality rates did not differ significantly among years, and mean clutch survival for a 32-day nesting period (4 days egg laying and 28 days incubation) was 40% for all 3 yr combined. Females laid just one clutch (usually of 4 eggs) each season, and mean clutch size was significantly smaller in 1979 than in 1977 and 1978. Estimated fledging success ranged from 0.40 in 1977 to 0.17 in 1978 and was consistently greater for females that nested early each season. Mean annual adult survival was estimated at 85% based on resightings of color-marked individuals. Limited data for subadult survival precluded complete demographic analysis. Nevertheless, given the estimates of productivity and adult survival pooled for 3 yr, survival of subadults from fledging until first breeding as 3-year-olds needed to be only 58% to maintain the stable population size observed through 1983. *Received 10 June 1985, accepted 7 April 1986.*

THE population ecology of shorebirds (Charadrii) is not well known, probably because many species are wary, breed in remote areas, or both. Most thoroughly studied are species that nest at temperate latitudes such as the Eurasian Oystercatcher (*Haematopus ostralegus;* Goss-Custard et al. 1982, Safriel et al. 1984), Common Ringed Plover (*Charadrius hiaticula;* Laven 1940, Bub 1962, Pienkowski 1984a), and Common Redshank (*Tringa totanus;* Grosskopf 1959, 1964; Yates 1982). Many aspects of breeding biology are known for other shorebirds, especially in Europe and Scandinavia (see Cramp and Simmons 1982, Evans and Pienkowski 1984). But even among calidridine sandpipers (Scolopacidae), a subfamily with diverse social adaptations and mating systems (Pitelka et al. 1974, Myers 1981), detailed demographic parameters have been reported only for the Dunlin (*Calidris alpina;* Soikkeli 1967, 1970a, b) and Temminck's Stint (*C. temminckii;* Hildén 1978). Tringine sandpipers exhibit a wider range of body sizes and tend to breed at lower latitudes than do calidridines (Johnsgard 1981). Hence, they should be more accessible for study, and also more accessible for comparative demographic analyses. Long-term reproductive performance and population dynamics, however, are known for only a few smaller species such as the Spotted Sandpiper (*Actitis macularia;* Oring et al. 1983), Common Sandpiper (*A. hypoleucos;* Holland et al. 1982), and Common Redshank (Yates 1982). Larger species tend to be better studied during the nonbreeding season, and survival estimates based on annual returns to wintering grounds exist for Bar-tailed Godwits (*Limosa lapponica*) and Eurasian Curlews (*Numenius arquata*) (Evans and Pienkowski 1984).

We studied breeding density, clutch size, nesting mortality, reproductive success, and adult survival in a population of Long-billed Curlews (*Numenius americanus*). These demographic data are integrated by life-table analyses, and the longer-term reproductive performance of the population is evaluated.

STUDY AREA AND METHODS

Study area.—The study area was an upland strip of shortgrass rangeland (~21,600 ha) in western Idaho (Redmond and Jenni 1982). We concentrated on a portion of the area (~1,600 ha) that supported high breeding densities of Long-billed Curlews. This smaller plot was grazed intensively by large bands of sheep from late March through early May each year; other portions of the study area were grazed by cattle from November to June.

Methods.—The nesting cycle was divided into prelaying, laying, incubation, and prefledging periods. A standard clutch of 4 eggs was laid in 4–7 days, and incubation began after the last egg was laid. Time from laying to hatching of the last egg was considered the incubation period; it ranged from 28 to 30 days ($\bar{x}$ = 28.4 days).

Population densities were estimated each year by a modified Finnish line-transect method (Redmond et al. 1981), and nests were located during egg laying or incubation according to methods described by Redmond (1986). When found, each nest was marked with a numbered wooden stake (2.5 × 5 × 40 cm) placed 10 m upslope from the nest cup. To deter mammalian predators from following our scent trails, paradichlorobenzene (PDB) crystals were sprinkled at a 1-m radius around each nest cup. On subsequent visits, a nest was always approached directly from the marking stake; when departing, a line of PDB crystals was spread across this path. Because the crystals were small and very volatile, they evaporated quickly and probably had only a short-term effect. Whereas the efficacy of this method for discouraging mammalian predators has never been tested, Lehner et al. (1976) showed that similar chemicals deterred coyotes (*Canis latrans*) and dogs (*Canis familiaris*) from food rewards. Similarly, Knight (1983) found PDB and napthalene to be useful in repelling skunks from specific areas.

Nests found during incubation usually were checked every 2–5 days until the eggs first starred or pipped, and then every day until hatching was completed. Nests located during egg laying were not checked for the first 2–3 weeks of incubation. Clutch size was estimated by the maximum number of eggs found in a given nest.

The diversity of potential predators on and around the study area made it difficult to interpret every act of predation and to identify responsible species. Mammalian carnivores that hunted regularly over portions of the study area included coyotes, feral dogs, feral cats (*Felis domesticus*), badgers (*Taxidea taxus*), and long-tailed weasels (*Mustela frenata*). Red foxes (*Vulpes fulva*), striped skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*) occurred on adjacent agricultural lands but were never seen hunting in upland habitat.

Nest loss was attributed to a badger if the nest cup was damaged and buried under several centimeters of soil. Large, crushed shell fragments often lay beneath this soil or in the immediate vicinity of the destroyed nest. Canids were presumed to be responsible for an empty, undamaged nest cup whenever the previous visit had revealed an intact clutch. In several cases also attributed to canids, the nest cup was damaged but not buried, and large shell fragments lay nearby.

Avian predators usually did not destroy entire clutches; instead, they opened and consumed portions of 1 or 2 eggs. Partially destroyed clutches were abandoned by adult Long-billed Curlews, and remaining eggs were subsequently consumed. Black-billed Magpies (*Pica pica*) were the most abundant avian egg predator. Common Ravens (*Corvus corax*) and several gull species (California Gulls, *Larus californicus*; Ring-billed Gulls, *L. delawarensis*; and Franklin's Gulls, *L. pipixcan*) occasionally passed over the study area during April and May. Only ravens were mobbed by adult curlews.

Grazing livestock also destroyed curlew nests. Characteristically, one or more eggs disappeared from a nest coincident with the presence of sheep or cattle in the vicinity. Sometimes a crushed egg remained in the cup or an egg was dislodged a short distance.

Gopher snakes (*Pituophis melanoleucus*) were the only reptiles capable of preying on curlew eggs or chicks. These snakes were encountered regularly during late spring, but individuals were always relatively small and probably unable to swallow a curlew egg whole. The existence of individual gopher snakes large enough to ingest whole curlew eggs was documented in Nebraska (Tremaine 1975), but we doubt that such predation was frequent on this study area.

Daily mortality rates were calculated for all clutches, for individual eggs within successful nests, and for chicks before fledging according to Mayfield's (1975) method as modified by Willis (1981). When the day of nest destruction was not known, it was assumed to have occurred at 40% of the interval since the last visit (Johnson 1979). Variance estimates of these mortality rates follow Johnson (1979), and rates were compared by *G*-tests of independence (Willis 1981). Capture and marking techniques were described by Redmond and Jenni (1982), and Redmond (1984) provided details about radio-tracking methods.

Resightings of natally philopatric curlews (individuals color-banded as chicks in the study area and resighted there in later years) were made opportunistically along survey routes from 1979 through 1981. By themselves, these resightings represent minimum survival rates for subadults. Because of a significant male bias in natal philopatry (Redmond and Jenni 1982), however, subadult survival for males was estimated as one half the number of color-marked chicks known to fledge and later resighted. Estimates of annual adult survival utilize resighting data from 1978 through 1981 and are based on the maximum-likelihood method of Cormack (1964). To obtain resightings of color-marked adults, their previous nesting territories and adjacent territories were searched regularly during the prelaying and incubation periods.

RESULTS

Breeding density.—Because of high variances, there were no significant differences among annual density estimates of territorial male Long-billed Curlews on the 1,600-ha study plot (Fig. 1). Thus, for the duration of the study, we assumed that the breeding population was relatively stable in size, even though a gradual

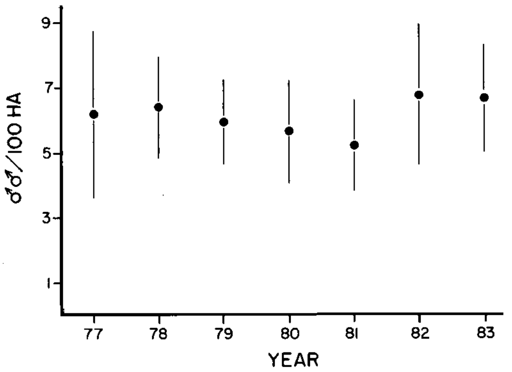

Fig. 1. Annual density estimates (mean ± SD) of male Long-billed Curlews attempting to breed on the study site from 1977 to 1983. Estimates are based on Finnish line-transect method of Järvinen and Väisänen (1975) as modified by Redmond et al. (1981). Actual data are available in Redmond (1984).

Table 1. Clutch size of Long-billed Curlews in western Idaho.

Year	Frequency of clutch size[a] 3	4	5	Mean ± SE[b]
1977	1	24	0	3.96 ± 0.039
1978	1	36	1	4.00 ± 0.037
1979	8	32	0	3.80 ± 0.063
1977–1979	10	92	1	3.91 ± 0.000

[a] Clutch size could not be determined for 16 additional nests because they were either destroyed during laying or found during hatching.

[b] ANOVA among years: $F = 4.56$, 2,100 df, $P = 0.01$.

decline in males attempting to breed probably occurred between 1978 and 1981 (see Discussion).

Clutch size.—Female Long-billed Curlews commonly laid a single clutch of 4 eggs in 1977 and 1978 (Table 1). In 1979, however, the frequency of 3-egg clutches increased dramatically, and mean clutch size was significantly less than in the previous 2 yr (GT-2 multiple comparison test, $P < 0.05$). There was no evidence of renesting by any color-banded or radio-marked female in any year.

Egg and clutch mortality.—Mean clutch mortality rate for all years was 0.029 nests lost per day (Table 2). Daily clutch mortality rates were remarkably constant in 1977 and 1978, and increased insignificantly in 1979 ($G = 0.02$, 2 df, $P = 0.90$).

Mammalian carnivores were the most important predators of Long-billed Curlew eggs and clutches (Table 2). The relative intensity of predation by canids and badgers differed significantly among years ($G = 6.10$, 2 df, $P < 0.05$). During 1977 badgers were particularly destructive of curlew eggs in an area of high Townsend ground squirrel (*Spermophilus townsendii*) density, where 67% of all nests were found. During 1978 and 1979, when only 15% of all nests were found in this area, canids were the dominant egg predator (Table 2).

It is difficult to identify any specific canid as the most important egg predator. Dogs (unattended, abandoned, or wild) were the most frequently seen. Coyotes were seen infrequently, and red foxes were sighted occasionally in agricultural fringe areas within 3–5 km of curlew nesting habitat.

Other causes of clutch loss were grazing livestock, other birds, and investigator disturbance (Table 2). When large bands of sheep passed through an area, chance seemed to play a role in the actual destruction of Long-billed Curlew nests. On two occasions in 1977, bands of more than 500 ewes and lambs trampled past the same two neighboring nests en route to a water trough. Neither clutch was damaged, but both times one of the wooden marking stakes was snapped off and crushed. Soon after each incident, the adult curlews returned and resumed incubation. Similar, but less dramatic, interactions resulted in several broken eggs and 4 nest desertions in 1978 and 1979.

Adult Long-billed Curlews could readily defend their nests against magpies and other avian egg predators. We therefore suspect that these birds probably gained access to curlew clutches only as a result of nest desertion or abnormal inattendance by the adults. Two unusual cases of egg damage and nest abandonment were attributed to birds (1 each in 1977 and 1979) and may have been caused by other Long-billed Curlews. All eggs in both clutches were pecked, but their contents were not eaten. The holes, approximately 15–30 mm in diameter, were considerably smaller than those made by magpies. Both of these nests were within 40 m of other active curlew nests.

Individual egg losses or hatching failures were recorded each year in nests that produced one or more chicks (Table 3). This mortality

TABLE 2. Losses of Long-billed Curlew clutches.

	1977	1978	1979	Total	Percent
Clutches	30	40	49	119	
Losses to:					
Canids	3	8	10	21	17.7
Badgers	7	3	3	13	10.9
Birds	2	2	4	8	6.7
Livestock	0	3	2	5	4.2
Trapping	0	0	2[a]	2	1.7
Unknown	0	0	1	1	0.8
Total	12	16	22	50	42.0
Nest-days	449	592	705	1,749	
Mortality/day	0.0277	0.0280	0.0294[a]	0.0285	
SE	0.00761	0.00666	0.00625	0.00391	

[a] Two clutches were abandoned because of trapping efforts in 1979; mortality rate assumes these would have hatched successfully.

was a result of addled eggs ($n = 7$), parental abandonment of late, asynchronously hatching eggs ($n = 5$), and grazing livestock ($n = 6$). Patterns of single egg losses or hatching failures in otherwise successful nests did not differ significantly among years ($G_{adj} = 6.00$, 4 df, $P = 0.20$).

Hatching success.—Probabilities of clutch survival for a 32-day nesting period were remarkably constant each year (Table 4). Egg survival in successfully hatching nests showed more variability among years (Table 4), probably because of the absence of livestock damage in 1977; nevertheless, these differences were not significant ($G = 4.47$, 2 df, $P > 0.80$).

Chick mortality.—Each year individual chicks that had not survived more than a few hours were found in or near a nest cup ($n = 3$ of 79 color-marked chicks in 1977, 1 of 69 in 1978, and 2 of 62 in 1979). The 3 nonviable hatchlings in 1977 were from 3 different 4-egg clutches, and each weighed 20–25% less than their siblings. All had poorly healed umbilical regions and incomplete yolk sac retention, with small pieces of dried shell or membranes adhering to the yolk sac. There was nothing peculiar about the appearance of nonviable hatchlings in 1978 or 1979, and they may have perished from inadequate brooding.

Long-billed Curlew chicks have cryptic plumage and behavior, which makes them very difficult to locate after they leave the nest. Consequently, we relied heavily on the fates of radio-marked individuals to determine chick mortality rates. The average age when chicks were radio-marked decreased each year from 15.8 (1977), to 14.0 (1978), to 6.0 days (1979). We found no mortality of radio-marked chicks

TABLE 3. Egg losses and hatching failures from successful Long-billed Curlew nests.

	1977	1978	1979	1977–1979
Eggs in successful nests	68	95	91	254
Number of eggs				
Addled	1	3	3	7
Abandoned	3	1	1	5
Damaged[a]	0	4	2	6
Egg-days	1,258	1,702	1,743	4,703
Loss rate[a]/day ± SE ($\times 10^3$)	0.00 ±0.000	2.42 ±1.174	1.18 ±0.811	1.31 ±0.521
Percentage surviving 32 days[b]	100.0	92.5	96.3	95.9
Percentage addled or abandoned	5.88	4.40	4.49	4.84

[a] Caused by grazing livestock only. It is assumed the 4 other eggs damaged in 1979 because of trapping efforts would have hatched.

[b] Four days for egg laying and 28 days for incubation.

TABLE 4. Estimates of hatching and fledging success per breeding adult.

Year	Nesting class[a]	Hatching success		Fledging success[c]	Mean clutch size	No. of young fledged/adult
		Clutches	Eggs[b]			
1977	Early	0.408	0.972	0.565	4.00	0.45
	Late	0.408	0.906	0.437	3.91	0.32
	All	0.408	0.941	0.495	3.96	0.38
1978	Early	0.403	0.878	0.293	4.00	0.21
	Late	0.403	0.890	0.100[d]	4.00	0.07
	All	0.403	0.884	0.229[e]	4.00	0.16
1979	Early	0.385	0.856	0.485	3.77	0.30
	Late	0.385	0.978	0.216	3.86	0.16
	All	0.385	0.920	0.318	3.80	0.21
1977-1979	Early	0.397	0.896	0.436	3.92	0.30
	Late	0.397	0.927	0.262[e]	3.92	0.19
	All	0.397	0.913	0.350[e]	3.91	0.25

[a] Early clutches were completed before the median date of clutch completion each year; late clutches were completed on or after the median date.

[b] Hatchability of eggs in successful clutches (i.e. those in which at least 1 egg hatched).

[c] Based on chick survival estimates from age 6 days to fledging (Table 7) times 75% in 1977 and 1978 and 65% in 1979, except as noted below (see text).

[d] Fraction of color-marked, late-hatching nestlings that were resighted postfledging in 1978 (2/20).

[e] Based on adjusted chick loss ($n = 1.87$ rather than 8) among late-nesting females in 1978; see Table 6 and text.

in the 0-5-day-old age class during 1977 or 1978, but our sample sizes were only 3 and 4 for each year. In 1979, when our sample was much larger, mortality in this very young age class was 57% (12/21). Six conspicuously feeble chicks perished within a few hours of hatching. Two others died on their fourth and fifth day, respectively. Neither gained weight nor showed signs of feeding; we inferred that both starved. One chick died mysteriously on its second day, and the radio signal from another disappeared when the chick was 5 days old. Finally, 2 siblings may have succumbed to heat stress on their fourth day. They hatched late in the season (18 June) within 100 m of a well-traveled road. The female parent disappeared just after hatching, leaving the male to provide all parental care. The family crossed the road on 20 June and entered a sparse, crested wheatgrass (*Agropyron cristatum*) planting where grasshoppers were abundant and shade was scarce. Excessive traffic along this road on 21-22 June (both clear, hot days) may have interfered with the male's ability to provide needed shade to the chicks.

Predation on radio-marked chicks varied dramatically among years (Table 5). In 1977, 75% (9/12) of these chicks survived through fledging. One chick was eaten by a long-tailed weasel, and the fates of 2 others were unknown. In 1978, only 2 of 13 radio-marked chicks (15%) survived to fledge, and both were killed soon thereafter. Raptors were responsible for at least 73% (8/11) of all prefledging losses in 1978, and no mortality was attributed to mammalian carnivores. The fate of 1 individual was unknown, however, and it may have been captured by a mammal and carried underground. In 1979, predation was again light,

TABLE 5. Mortality of radio-marked Long-billed Curlew chicks aged 0-45 days.

	1977	1978	1979	Total	Percent
Chicks	12	13	26	51	
Losses to:					
Raptors	0	8	1	9	17.7
Mammals	1	0	2	3	5.9
Aspergillosis	0	2	0	2	3.9
Other factors[a]	0	0	12	12	23.5
Unknown[b]	2	1	2	5	9.8
Total	3	11	17	31	60.8

[a] See text for fates of these 12 chicks aged 0-5 days in 1979.

[b] Radio signals were lost, and chicks almost certainly were depredated.

TABLE 6. Survival of radio-marked Long-billed Curlew chicks from age 6 days to fledging.

Year	Nesting class[a]	No. of chicks	No. lost	Chick-days	Mortality rate/day ± SE	P[b]	Days to fledge[c]	Percent survival
1977	Early	5	1	116	0.009 ± 0.0086	0.60	32.0	75.3
	Late	7	2	123	0.017 ± 0.0114		32.0	58.3
	All	12	3	239	0.013 ± 0.0072		32.0	66.0
1978	Early	5	3	130	0.024 ± 0.0132	0.001	39.5	39.1
	Late	8	8	42	0.211 ± 0.0606		40.0	0.01
	All	13	11	172	0.066 ± 0.0187		39.8	6.5
1979	Early	6	1	120	0.009 ± 0.0083	0.15	34.3	74.6
	Late	8	4	122	0.034 ± 0.0161		32.0	33.2
	All	14	5	242	0.021 ± 0.0091		33.2	48.9
1977-1979	Early	16	5	366	0.014 ± 0.0061	0.01	35.3	60.8
	Late	23	14	287	0.051 ± 0.0127		34.7	16.4
	All	39	19	653	0.030 ± 0.0066		35.0	34.4

[a] Early clutches were completed before the median date each year; late clutches were completed on or after median dates.

[b] Probability that daily mortality rates do not differ between early and late clutches; obtained by G-tests (Willis 1981).

[c] Means for each period in each year.

with just 4% (1/26) of the sample being lost to raptors and 8% (2/26) to mammals.

The only other known cause of mortality to radio-marked chicks was aspergillosis, a pulmonary mycotic infection from which 15% (2/13) perished in 1978 (necropsies and diagnoses by Dr. B. W. O'Gara, Montana Cooperative Wildlife Research Unit). Aspergillosis has been reported for a wide range of free-living, avian species, particularly waterfowl and gamebirds (O'Meara and Witter 1971), but never for Long-billed Curlews.

Fledging success.—Survival of very young chicks (aged 0-5 days) probably depends more on their learning to feed effectively and receiving occasional thermoregulatory assistance from parents than on avoiding predation. In 1977 and 1978 few chicks were monitored for this period, and no mortality was detected. From the larger sample in 1979, we estimated 14.1% of chicks lost per day (12 lost over 85 chick-days) or 40.2% survival to age 6 days. These figures were almost certainly biased by stress to very young chicks associated with their carrying a radio transmitter and being disturbed daily. Such stress might have increased mortality as much as 50-100%, which would result in survival values of 60-80% from hatching to age 6 days. Our estimates of fledging success (Table 4) were based on 75% of chicks surviving to 6 days in 1977 and 1978, and 65% in 1979. The estimate for 1979 was lower because smaller eggs were laid that year (Redmond 1986), and in other Charadriiformes there is an inverse relationship between egg size and chick mortality (Lundberg and Väisänen 1979).

The variable intensity of predation on radio-marked chicks aged 6 days to fledging suggests variation among years in either predation pressure or effectiveness of parental care, or both. Because late-hatching chicks tend to receive reduced parental care as a result of early departure by females (Redmond 1984), we compared daily mortality rates from age 6 days to fledging between chicks that hatched early (before median date) and late (on or after the median) each year. In 1977 and 1979 these rates did not differ significantly, but in 1978 late-hatching chicks experienced significantly greater mortality than those that hatched early (Table 6).

Resightings of color-marked juveniles that were marked as nestlings provide a minimum estimate of fledging success. The fractions resighted in 1977 (16/56) and 1979 (1/47) were much lower than the estimates of survival from age 6 days to fledging for radio-marked chicks (Table 6). In 1978, however, we resighted as juveniles 17% (5/30) of the color-marked chicks that hatched early and 10% (2/20) of those that hatched late. This 10% minimum survival of late-hatching chicks was considerably greater than the 0.01% estimated from the sample of

TABLE 7. Resightings of natally philopatric Long-billed Curlews.[a]

			Year resighted			
Sex	Hatch year	No. resighted	1978	1979	1980	1981
Males	1977	5		- - -		
				- - -	———	———
					———	
					———	———
						———
	1978	4				———
						———
						———
						———
	1979	0				
Females	1977	1		- - -		
	1978	0				
	1979	1				———

[a] Each horizontal line represents the resighting of one Long-billed Curlew that was color-marked as a chick; a dashed line indicates nonbreeding status for that year.

radio-marked chicks. To adjust for the possibility that in 1978 mortality was greater among radio-marked chicks than among color-marked chicks (see Discussion), we assigned a 10% fledging success rate to the late-nesting class (Table 4). Based on this adjustment, estimated fledging success in 1978 was 23% for all females.

Because female Long-billed Curlews are monogamous and lay just one clutch each season, the number of young fledged per breeding adult equals half the number fledged per nest. Estimates of young fledged per female varied considerably among years (Table 4). More importantly, early-nesting pairs consistently fledged more young than did late-nesting pairs (from 0.13 to 0.14 more; see Table 4).

Juvenile and adult mortality.—Only 2 radio-marked chicks were known to perish after fledging. Both were taken by raptors in 1978 within a week of fledging. All other radio-marked chicks that were monitored past fledging (8 each in 1977 and 1979) survived.

There was no evidence of nonhuman predation on adult Long-billed Curlews at any time during this study. The fact that many clutches were lost to predators, often in twilight or complete darkness, suggests that incubating adults can effectively detect and escape mammalian carnivores. One unsucceessful attack by a Prairie Falcon (*Falco mexicanus*) was observed in early April 1979.

All adult mortality observed during this study was related to human disturbance activities. Carcasses of 9 adults were found during May and June (8 in 1977, 1 in 1979). Three were shot with small-caliber firearms, but the other 6 were too decomposed and damaged to ascertain the cause of death. We believe that they also were shot because all were found along roads accessible to the public and during late May, when many humans used the upland for recreation and when breeding adults were most vigorous in mobbing intruders (Redmond 1984).

Survivorship.—Because of a significant male bias in natal philopatry (Redmond and Jenni 1982), and the tendency for males not to return and attempt to breed until they are 3 or more years of age (Table 7), subadult survival could be estimated only for males from the 1977 and 1978 cohorts. For these years, 29 and 16 color-marked chicks were sighted postfledging. If half of these were actually males, then subsequent resightings of 21% (3/14) and 50% (4/8) for the respective cohorts provide a minimum estimate of survival for the 33-month period between fledging and the first attempt to breed. These estimates were unreliable because both resighting components (numbers returning to breed and numbers resighted postfledging) represent minimums, and therefore actual survival could be either greater or less than the estimates. Given the relatively stable population size (Fig. 1) and the results of a demographic analysis (see below), both figures probably underestimated subadult survival.

TABLE 8. Resighting data and annual survival estimates[a] for adult Long-billed Curlews of both sexes breeding during 1977-1981.

Year	No. marked	No. resighted	No. seen for last time	Estimated probability of	
				Disappearing	Surviving ± SD
1977	9	—	1		
1978	17[b]	8	9	0.11	0.89 ± 0.10
1979	17	16	12	0.36	0.64 ± 0.10
1980	4[c]	11	6	0.36	0.84 ± 0.16
1981	6[d]	19	—	—	—

[a] Based on maximum-likelihood method of Cormack (1964).

[b] Sixteen adults captured and color-banded + 1 albino male (seen from 1978 to 1980).

[c] All 4 individuals were color-banded as chicks in 1977 and first sighted as adults in 1980.

[d] Another 6 individuals color-banded as chicks in 1978-1979 and first sighted as adults in 1981.

Estimates of annual adult survival based on resightings of color-marked individuals (Table 8) represent minimum values. We believe that survival was substantially higher than 64% in 1979 (see Discussion), and we consider average adult survival to be approximately 85% per year. For an adult just starting to breed, such a figure predicts a mean further expected life span of 6.15 yr (Brownie et al. 1978: 39). Thus, depending on age at first breeding, which appears to be 2-3 yr for females and 3-4 yr for males, the average longevity of Long-billed Curlews may be 8-10 yr.

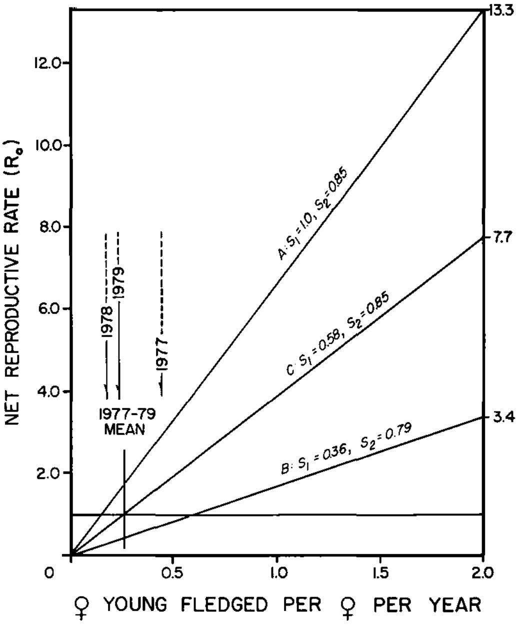

Fig. 2. Net reproductive rate (R_0) as a function of female fledging success and survival of subadults (S_1) from fledging to first breeding at 3 yr (2 yr for line A) and of adults thereafter (S_2). See text for details.

Demographic analysis.—To evaluate the reproductive performance of this population, annual fledging success rates were compared with a range of values for a stable population that assume maximum possible (100%) and minimum observed (36%) survival from fledging until first breeding. These values were obtained by plotting net reproductive rates (R_0, calculated after Ricklefs 1973: 408) as a function of fledging success per female for different rates of subadult survival (Fig. 2). Adult mortality was assumed to be age-constant (Deevey 1947, Lack 1954), and the maximum possible number of female young fledged per female equals 2.0 (or the number of females in the largest mean clutch size, 4.0/2, assuming a primary sex ratio of 1:1). If all eggs and young survive to breed at age 2 yr, and thereafter experience 15% mortality per year, R_0 equals 13.3 (Fig. 2: line A). At the other extreme, if all eggs and young fledge but survival from fledging to first breeding at 3 yr drops to 36%, and minimum adult survival thereafter is set at the observed mean of 79% (Table 8), then R_0 drops to 3.4 (Fig. 2: line B).

By definition, R_0 equals 1.0 in a stable population. For this population of Long-billed Curlews to be stable, with annual survival of 79% for adults (mean observed for all years) and 36% for subadults from fledging to 3 yr, females must fledge on average 0.59 female young per year (where line B crosses R_0 = 1). This did not occur in any year. Estimated fledging success per female in 1978 (0.17) was close to the intercept of line A with R_0 = 1, confirming that this was a year of poor productivity. Depending on actual values of subadult survival and age at first breeding, the 1979 estimate of average fledging success (0.21 female young/female) was probably marginal. In 1977, and especially among early-nesting females, estimated fledging success reached or exceeded 0.38 female young. Such productivity may have been enough to offset the relatively poor success in the following years. Mean fledging success per female pooled for all years was 0.25 female young, which, assuming a stable population size and 85% adult survival, predicts survival from fledging to first breeding at 3 yr to be 58% (Fig. 2: line C).

DISCUSSION

Breeding density.—The modified Finnish line-transect method can be used to estimate densities of territorial male Long-billed Curlews only. Females are less detectable before hatching of their eggs, and consequently their density cannot be estimated reliably (Redmond et al. 1981). Nevertheless, spot-mapping during prelaying and incubation in 1978 and 1979 confirmed that at least 85% of males acquired mates, and there was no evidence of a skewed, breeding sex ratio (Redmond et al. 1981).

The gradual decline in male density from 1978 to 1981 was likely real in spite of the large variances. During August 1981, a range fire burned 142 ha of the study plot. Transect counts during April 1982 were substantially greater, and estimated breeding density increased almost 30% from the previous year (Fig. 1). Territorial males were especially common in the burned area during the spring of 1982, probably because of reduced vegetative cover. Bicak et al. (1982) found a significant negative relationship between vegetative cover and numbers of breeding Long-billed Curlews on this study area.

Clutch size.—Significant annual variation in clutch size has never been reported among scolopacid shorebirds. At north temperate and arctic latitudes nearly all shorebirds (Charadrii) lay clutches of 4 eggs, and especially within Scolopacidae, intraspecific variation is slight (Maclean 1972). Yet in 1979, female Long-billed Curlews laid significantly more 3-egg clutches than in other years. Because clutch size was estimated by the maximum number of eggs found in a nest, it is conceivable that many of these nests in 1979 initially contained 4 eggs, but that 1 egg was lost from each nest before its being found. If this were so, one would expect single egg losses in 1979 to continue after nests were found and to be significantly greater than in other years. Single egg losses were greatest, however, in 1978 (Table 3).

We believe that clutch size actually was reduced in 1979, especially among early-nesting females, and that this was an adaptive response. Unusually dense vegetation covered most breeding territories early that season, and curlews flew considerable distances to find food (Redmond 1986). Clutch size and egg quality are associated with levels of protein reserves stored in the flight muscles of gulls (Houston et al. 1983) and other birds (Jones and Ward 1976, Fogden and Fogden 1979). If female Long-billed Curlews also rely on flight muscles for protein storage, then strenuous use of these muscles before laying might limit protein reserves and thereby affect reproductive effort. We suggest that reduced clutch size was an alternative to delayed laying and reduced egg size for some females in 1979 (see Redmond 1986). We also predict that intraspecific variation in clutch size is more likely to be detected, at least among shorebirds, during seasons of marked environmental contrast that may stress female reproductive physiology.

Reproductive success.—The hatching success of shorebirds is extremely variable among species, and even within species it tends to vary among years (see reviews by Goss-Custard 1981, Evans and Pienkowski 1984). Evidence for a general decline in hatching success with latitude (as proposed by Ricklefs 1969) is mounting for shorebirds (Pienkowski 1984a). Consistent with such a trend, the mean clutch mortality rate of Long-billed Curlews in western Idaho (0.0285/day) was significantly higher than that of Whimbrels (*Numenius phaeopus*) nesting on the Canadian subarctic tundra [0.0150/day, calculated from Skeel's (1983) data for all three habitats combined; $G = 4.34$, $P < 0.05$].

Reports of clutch losses between 20 and 50% are common for shorebirds that nest at temperate latitudes. These figures, however, are biased in many studies (exceptions are Sordahl 1980, Page et al. 1983, Pienkowski 1984a, Lank et al. 1985) and underestimate actual mortality. This is because nests were found throughout incubation, yet rates were not adjusted for unknown losses (Mayfield 1975, Johnson 1979). If this bias is ignored for Long-billed Curlews, the percentage of clutches lost each year was 40–45%, which, although still high, is more comparable to data from these other shorebirds (see Cramp and Simmons 1982).

Survival of shorebird chicks is difficult to determine because of their precocial development and nidifugous habit. Estimates of fledging success are available for only a few species (Safriel 1975, Page et al. 1983, Pienkowski 1984b). Chick mortality between hatching and learning to feed is inferred to be high for many species (Holmes 1966, Soikkeli 1967, Jehl 1973, Hildén 1978, Oring et al. 1983). Among Common Ringed Plovers breeding in northeastern England, 53% of all chick mortality occurred during the first week after hatching, and it was attributable to predation and starvation (Pienkowski 1984b). Mortality of young Long-billed Curlews (age 0–5 days) was most often the result of inadequate parental care (resulting in overheating, chilling, or predation), starvation, or some physical inviability.

In 1977, 5% (3/57) of nestlings handled showed signs of incomplete yolk sac retention and adherence of eggshell fragments. All 3 chicks died within hours of hatching. There was no evidence of similar inviability from 118 nestlings handled in 1978 and 1979. Incomplete yolk sac retention and a poorly healed umbilicus are signs of either inadequate or excessive warming of eggs during incubation (Rol'nik 1968). Adherence of chick embryos to portions of the eggshell occurs under conditions of insufficient humidity (Rol'nik 1968). The drought conditions in 1977 (Redmond 1986) may have reduced humidities in Long-billed Curlew nests, which in turn may have increased egg water loss (Ar and Rahn 1980, Walsberg 1980). The response of Long-billed Curlew embryos to dehydration is not known, but yolk sac adherence to the outer membranes and eggshell proper may have been a consequence of excessive embryonic water loss.

Late-nesting pairs of Long-billed Curlews had lower reproductive success (in terms of number of young fledged per adult) than early-nesting pairs (Table 4). This was due primarily to differences in fledging success between the two groups. Fledging success was greater among chicks that hatched before the median date in all three years. In 1978 this difference was particularly dramatic because of the intense predation of radio-marked chicks by raptors late in the season. Although likely to exist, differences in clutch survival between early- and late-nesting pairs could not be evaluated because laying dates of many destroyed nests were not known. Egg survival, however, was higher among late-hatching than early-hatching nests in 1978 and 1979. This probably reflects the decline in numbers of grazing livestock that occurred throughout May each season.

Abnormally heavy spring rainfall in 1978 produced unusually lush vegetative cover (vertical density and biomass; Redmond 1986). The tall, thick vegetation probably reduced small mammal vulnerability to raptor predation, and hindered the movements of Long-billed Curlew chicks, especially as they grew larger. If chicks then favored more open areas, they might have become more vulnerable to avian predators. We recorded no losses of radio-marked chicks to raptors before 14 June 1978, two days after most adults abandoned their broods (Redmond 1984). This emphasizes the importance of parental care to chick survival and suggests that the abnormally early departure of adults in 1978 facilitated a major shift in diet by local raptors to include Long-billed Curlew chicks. The cause of this adult departure remains unclear, but the tall, dense vegetation may have interfered with their ability to tend chicks or forage efficiently, or both.

Survivorship and demographic analysis.—An important assumption underlying estimates of adult survival is that all marked individuals alive in future years are equally likely to be resighted (Cormack 1964). Because no sex bias was detected in annual resightings of males and females (Redmond and Jenni 1982), we assumed approximately equal survival rates for both sexes. But females that were captured and subsequently lost their clutch were less likely to be resighted than females that nested successfully in their year of capture (Redmond and Jenni 1982). The same was not true of males. Resightings of females captured in 1978 were particularly low in 1979 (6/12; Redmond and Jenni 1982: table 1), but not because of poor hatching success. We suspect that females were discouraged from nesting in this area once they encountered the hostile vegetative conditions present during March and April of 1979. Thus, if female breeding dispersal rather than adult mortality produced the lower resightings in 1979, then the 64% survival estimate for that year was too low. Given the estimates of 84% and 89% for two separate years, and the likelihood that some breeding dispersal was undetected in 1979, we consider 85% to be a reasonable estimate of average annual adult survival. Comparative data, however, suggest that even this figure might be too low for such a large shorebird (Goss-Custard 1981, Evans and Pienkowski 1984).

The life-table analysis also assumes that both clutch size and adult mortality are age-constant. The former is reasonable for a species with a relatively fixed clutch size; the latter is widely accepted (Deevey 1947, Lack 1954, Ricklefs 1973) but difficult to evaluate (see Botkin and Miller 1974). Because annual resightings estimate minimum adult survival, calculations of net reproductive rate (R_0) based on such estimates are necessarily conservative.

The critical data missing from this analysis are annual survival rates for juveniles and subadults. For this population to be stable in size with females producing an average of 0.25 female fledglings per year (the mean observed for all years), survival from fledging to first breeding 33 months later must be 58%. This requires survival of about 84% of juveniles and subadults each year. Mortality is likely to be higher than this, however, at least for juvenile birds undertaking their first migration. Yearlings were never sighted on this breeding ground, and reports of Long-billed Curlews remaining on their winter range throughout the year (McCaskie 1970, Jurek 1974) suggest that yearlings, and perhaps some 2-year-olds, may not attempt a northward migration. In this case, subadult survival approaching 95% on the wintering grounds would be sufficient to offset mortality of up to 36% of juveniles during their first migration and still provide for 58% returning to attempt breeding as 3-year-olds. These figures are indeed plausible considering that in Britain 50% of Eurasian Curlews banded as chicks survived to 1 year of age when the species was legal quarry (Bainbridge and Minton 1978). Other limited data indicate that 2-year-old Eurasian Curlews survive better than adults, perhaps at a rate well over 90% (Evans and Pienkowski 1984).

Even if 58% represents a reasonable estimate of average subadult survival for Long-billed Curlews, a further complication remains. Males were more likely to return and breed in their natal area than were females (Table 7), suggesting that females disperse before first breeding (Redmond and Jenni 1982). The relative isolation of this breeding population suggests that females may disperse long distances. This has important ecological and management implications for Long-billed Curlews or any species with geographically isolated populations and sex differences in natal philopatry and dispersal (see Greenwood 1980). It means that adequate productivity, subadult survival, and adult survival in one population may not be sufficient to ensure its growth or stability. Clearly, the productivity of other populations that supply female recruits, as well as subadult survival of these recruits, also must be considered. In other words, the fates of geographically isolated populations may be interconnected by strong, sex-biased natal dispersal.

To conclude that this breeding population was stable, one must be relatively certain that local recruitment from marginal, surrounding areas was not responsible for the stable densities observed on the study plot. A method was devised to monitor numbers of breeding adults over about 70% of the entire study area, and no major declines were detected between 1977 and 1983 (Redmond et al. unpubl. data).

Productivity on the 1,600-ha study plot varied considerably among years. In 1977, a drought year, fledgling production was greatest and probably sufficient to offset the poor productivity associated with abnormally wet conditions the next year. But the abnormal rainfall in the spring of 1978 had an additional effect on Long-billed Curlew reproduction in 1979, mediated by the abundant, standing dead vegetation present during prelaying. Thus, the population faced unusual environmental conditions each year we monitored its productivity. If, in years with more normal rainfall and vegetative cover (see Redmond 1986), fledgling production varies between the values estimated for 1979 and 1977, and if our estimates of survival after fledging are realistic, then this population should remain stable within limits set by habitat quality and density-dependent mortality factors (Lack 1966).

The fact that population surveys in 1980 and 1981 did not reflect the poor fledgling production in 1978 is no doubt a function of the species' longevity. Populations of longer-lived organisms, because they are made up of individuals that vary widely in age, are less vulnerable to short-term fluctuations. Yet this numerical inertia makes population declines difficult to detect until they are well underway unless age structure can be determined.

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ROLE OF SIBLING AGGRESSION IN FOOD DISTRIBUTION TO NESTLING CATTLE EGRETS (*BUBULCUS IBIS*)

BONNIE J. PLOGER[1] AND DOUGLAS W. MOCK
Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019 USA

ABSTRACT.—Sibling aggression occurs in a wide variety of asynchronously hatching bird species. In some, fights among siblings lead inevitably to death, in which case the benefits of winning are clear. In species where sibling aggression is common but usually not fatal, the benefits gained by winning and the methods used to achieve them are less obvious. In a Texas colony of Cattle Egrets (*Bubulcus ibis*), sibling aggression was frequent but siblicide rare. Parents rarely interfered with fights. Last-hatched chicks lost more fights and received less food than their elder siblings. Fighting limited the losers' immediate access to food and contributed to the senior sib's ability to monopolize boluses. These results are consistent with the hypothesis that monopolizable food can act as both a proximate and ultimate cause of sibling aggression. The main effect of sibling aggression lay in depressing food supplies to last-hatched chicks. First- and second-hatched sibs accrued roughly equal feeding advantages. *Received 19 August 1985, accepted 11 April 1986.*

MANY raptors, cranes, herons, and various other birds lay their eggs at intervals of a day or more and commence incubation before laying is complete. This pattern produces an asynchronous hatch (Gibb 1950, Inoue 1985), wherein the youngest typically grow more slowly than their senior nest mates and consequently are more likely to die as nestlings (see reviews in Lack 1954, 1968; Howe 1978; O'Connor 1978; Hahn 1981; Mock 1984a, 1985). These deaths may be due to starvation or to physical abuse inflicted by siblings (reviews in O'Connor 1978, Stinson 1979, Mock 1984a).

As in other asynchronously hatching species, the youngest members of a Cattle Egret (*Bubulcus ibis*) brood typically grow more slowly than their nest mates and are more likely to die as nestlings (Blaker 1969, Siegfried 1972, Fujioka 1984, D. F. Werschkul unpubl. data). Although starvation appears to be the primary cause of death (Siegfried 1972), fights among siblings can result in mortality (Skead 1966; Blaker 1969; Siegfried 1972; Fujioka 1985a, b; Werschkul unpubl. data). The consequences of sibling fights may be direct (the victim dies from injuries) or indirect (the victim becomes too intimidated to feed). The indirect effects of sibling aggression on Cattle Egret nestling growth and mortality patterns remain unclear. We attempted to estimate the advantages and disadvantages of aggression among Cattle Egret siblings.

By creating asynchronous hatching, parents may facilitate adaptive brood reduction and thereby maximize their own reproductive output in the face of unpredictable food supplies (Lack 1947, 1954). If death of the youngest nestling enhances the survival chances of remaining brood members during food shortages, then the creation of competitive asymmetries among siblings can help maximize parental reproductive success. When food is abundant, all chicks are likely to survive, but if food is limited, the last-hatched siblings can be dispatched efficiently by nest mates. Parents thus may benefit because their surviving offspring gain food that might have gone to the doomed sibs.

In many avian species, sibling aggression is not required for brood reduction, size and age differences being sufficient to enforce the starvation of the smallest sibs (Lack 1954, 1968; Howe 1978; Werschkul 1979; Ryden and Bengsston 1980; Hahn 1981; Mock 1984a; Inoue 1985). Theoretically, chicks that rely on nonaggressive brood reduction could avoid the costs of time and energy associated with fighting (Hamilton 1964, Hahn 1981). Therefore, for fighting to be advantageous, victors must accrue compensatory benefits, such as enhanced access to limited food. Mock (1984b, 1985) proposed that when food is delivered in monop-

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[1] Present address: Department of Zoology, University of Florida, Gainesville, Florida 32611 USA.

olizably small units, selection can favor assault on junior sibs by senior nest mates.

Sibling aggression appears to be widespread among ardeids (see examples in Blaker 1969, Milstein et al. 1970, Werschkul 1979, Fujioka 1985b, Mock 1985), but little is known about its effects on the distribution of limited food. Detailed demonstrations of the advantages of nestling aggression have been presented only for Great Egrets (*Casmerodius albus;* Mock 1985) and for a Japanese population of Cattle Egrets (Fujioka 1984, 1985b). Great Egret senior nest mates obtain significantly larger shares of food than younger siblings by (1) gaining more frequent access to the food source (parent's bill), (2) obtaining larger bolus portions, and (3) monopolizing more boluses. Elder Great Egret chicks also intimidate junior sibs and cause them to miss many food offerings.

We studied intrabrood competition in Cattle Egrets. Our work parallels Fujioka's (1985b) descriptive study, which was complicated by variable brood sizes and small sample sizes. We used a single brood size, which allowed more robust statistical treatments. We provide new information on how aggression affects the relative feeding success among sibs by investigating the effects of aggression on the frequency of failed feeding attempts and the estimated amounts of food consumed by each chick.

We propose the hypothesis that fighting is most intense between the two youngest sibs. This idea is based on the two fundamental attributes of brood reduction in asynchronously hatching birds. First, mortality falls disproportionately on the last-hatched individual, and second, following initial brood reduction, mortality risks drop for the remaining individuals (both points well documented for Cattle Egrets by Blaker 1969, Siegfried 1972, Fujioka 1984, Werschkul unpubl. data; also shown in related species by Werschkul 1979, Mock and Parker 1986). Furthermore, occasional "dominance reversals," in which one of the senior sibs comes to occupy the lowest social position in the linear intrabrood hierarchy, have been observed in other ardeids (Mock unpubl. data). Because the penultimate chick may be most vulnerable to such potentially fatal reversals, it might be expected to invest extra effort in reinforcing its supremacy. Therefore, we predicted that a disproportionate amount of fighting would involve the two youngest sibs. We also predicted that if survival depends on avoiding the most subordinate position, then fights between the penultimate and last-hatched chicks should be more intense (longer, involving more blows) than those of the other two dyads.

METHODS

We studied natural 3-chick broods of Cattle Egrets on a Lavaca Bay dredge island (Calhoun Co., Texas; 28°39'N, 96°34'W) from May to July 1982. Newly hatched nestlings were marked on their heads with feather dye coded to hatch order: yellow (picric acid) on the first-hatched sib (hereafter, the *a*-chick), blackish brown (nyanzol-D) on the middle sib (the *b*-chick), and no marks on the last-hatched sib (*c*-chick). The dye marks did not appear to affect dominance rank among nestling Cattle Egrets (Mock and Ploger in press). The *a*- and *b*-chicks are referred to collectively as "senior siblings."

Detailed observations were made from two blinds within 10 m of observation nests. Activities of 7 broods were recorded on alternate days from the completion of hatching until all chicks had reached the age of at least 25 days. Only half the observation nests were watched each day (Ploger 1985), but the "off-watch" half were checked visually from the blind every hour on the hour for signs of imminent fatalities (such as intense harassment of the *c*-chick). Detailed behavioral observations were terminated when one or more brood members died or disappeared, but we continued to monitor the fates of surviving brood members.

Records were kept of all feeds and sibling fights. A "fight" by definition began with the first pecking blow and ended when (1) one sib conceded by crouching or fleeing; (2) combatants ceased exchanging blows for 10 s or more; or (3) the struggle was interrupted by parental activities (e.g. feeding). A chick was considered to have conceded if it (1) left the nest; (2) hung its head over the nest rim; (3) moved to the nest rim; (4) fled but remained in the nest; (5) crouched on the nest floor; (6) averted its head; or (7) failed to retaliate after being struck. Fights without a concession were scored as ties. Fighting rates were expressed as the number of fights per day. Blows were either simple pecks or forcible striking of a bill-grasped head against the nest structure. Fight duration was assessed by the number of blows per fight.

"Feeds" began with the regurgitation of the first bolus and ended when the parent failed to deliver boluses for at least 10 min. We counted the number of boluses delivered during each feed and estimated bolus sizes by comparing each bolus with known dimensions of the adult's skull (Mock 1985). In addition, a scale drawing of various-size boluses beside an adult's head was used to standardize bolus size estimates. These were later converted to cubic centimeters based on the volume of water displaced by clay bolus models.

We estimated actual food amounts as well as bolus counts because these two variables can differ. Boluses varied in size and seldom were shared equally among sibs. Chick feeding success was assessed by total amounts ingested.

The proportions of each bolus ingested by each sibling were estimated to the nearest 10%. A chick that gained an entire bolus was considered to have "monopolized" the bolus. We coded as "zero shares" (nothing ingested) cases where a chick (1) tried and failed to feed on a given bolus, (2) was absent from the nest, (3) appeared disinterested in the food, or (4) had recently been beaten by a sib until totally passive during a bolus presentation ("intimidated"; *sensu* Mock 1985). If a chick with food packed in its neck sat passively during a bolus presentation, the chick was coded as temporarily satiated.

When attempting to intercept boluses straight from the parent ("direct" feeding; Mock 1984b, 1985), chicks grasped the parent's mandibles with a scissoring grip, but often failed to elicit a bolus. The total number of scissorings performed by each chick during a feed provides a measure of a chick's level of solicitation during feeds and also relates to the chick's access to food. A scissoring chick by definition held the "pole" position if it grasped the topmost position on the parent's mandibles at the moment of bolus delivery. We recorded the number of scissors and poles held per feed, and the "pole-shares" (estimated bolus percentages obtained by the pole-holding chick).

To assess causes of natural mortality, we censused 40 3-chick egret nests (including the 7 observation broods) during brief (5-10 s) visits every second night. Injured and freshly dead chicks were examined quickly for the extent and type of external damages. To minimize the risk that highly mobile chicks would flee the nest and become lost (e.g. see Blaker 1969, Siegfried 1972, Fujioka 1984), all censuses after chicks reached 1 week of age were conducted well after dark (2200-0100). Chicks that were approached by flashlight nearly always remained in their nests and could be identified without handling. When handling was necessary (e.g. to renew dye marks after 2 weeks), the target brood and other broods in the vicinity were covered temporarily with nest cloths (Thomas 1977).

The causes of chick mortality were categorized as "brood reduction" or "other." As used here, brood reduction refers only to cases where the first mortality in a nest affected only one individual. In a few cases where causes of brood reduction could be determined in detail, brood reduction was further divided into categories of nonaggressive starvation or siblicide. Predation and all other deaths were categorized as "other." In the observation nests, we could exclude from the brood-reduction category cases of partial brood loss that probably were due to predation by Black-crowned Night-Herons (*Nycticorax nycticorax*). Many successful night-heron attacks in this colony were witnessed from blinds. We assumed that a disappearance between sunset and dawn of a single, healthy (nonemaciated) individual from an observation nest was due to such predation.

We determined chick survival to age 25 days, 5-10 days before fledging (Blaker 1969). Independence from at least partial parental support probably does not occur for some weeks after fledging. Brood reduction appears to be concentrated in the first month (Blaker 1969, Siegfried 1972).

Because the fates of some nestlings could not be determined, we analyzed brood fates twice, once for all fates (including all broods) and once for known fates (i.e. only those broods for which fates of all chicks were deduced). Similarly, chick fates were analyzed separately for known-fate and all-fate categories (this category might include chicks with unknown fates). In the known-fate category, the sizes of the brood- and chick-fate samples appear to disagree because inclusion of chicks in these samples is based on different criteria; although 58 chick fates were known and thus included in the chick-fate sample, only 15 broods were included in the brood-fate sample, for which all sibs' fates had to be known.

Statistical analyses were performed using SAS (1982 version) on an IBM 3081 computer. Details of the analyses performed, criteria for inclusion of data, and explanations for minor variations in sample sizes can be found in Ploger (1985).

RESULTS

Hatching intervals.—Cattle Egret siblings typically hatched on different days, with similar hatch intervals between *a*-*b*-chicks and *b*-*c*-chicks (Table 1; $t = 0.79$, df = 66, not significant; census $n = 34$ nests).

Nestling aggression.—Nestling Cattle Egrets fought frequently and quickly established stable linear dominance hierarchies according to hatch order. *C*-chicks lost 15 times more fights than *b*-chicks and 25 times more fights than *a*-chicks (181 *c*-chick losses, 28 *b* losses, 7 *a* losses; goodness-of-fit test, $G = 248.2$, df = 2, $P < 0.001$).

Despite considerable variability among nests, the mean fights per day differed among individual pairs of combatants (fight dyads; Table 2; $F_{2,117} = 7.76$ based on log-transformed data, $P < 0.001$), with *b*-*c* dyads fighting most often (Tukey-Kramer pairwise comparisons, $P < 0.05$, df = 117). *B*-*c* fights involved the fewest blows, but differences among dyads were not signifi-

TABLE 1. Frequency distribution of hatching intervals in 3-chick Cattle Egret broods. Data were drawn from census and observation (focal) broods in which the hatch intervals between all 3 chicks were known.

Interval (days)	Frequency					
	a-b-chicks			*b-c*-chicks		
	Total[a]	Census[b]	Focal	Total	Census	Focal
0	7	1	0	3	1	0
1	54	14	2	26	7	2
2	59	15	3	75	20	2
3	9	3	0	23	6	2
4	2	0	0	3	0	0
5	0	0	0	1	0	0
6	2	1	1	1	0	0
7	0	0	0	0	0	0
8	0	0	0	1	0	0
$\bar{x}$	1.6	1.7	2.3	2.1	1.9	2.0
SD	0.9	1.0	1.9	1.0	0.7	0.9
n	133	34	6	133	34	6

[a] Data include all census and focal broods, plus 99 broods censused for clutch sizes but not followed for fates sample.

[b] Includes observation (focal) broods.

TABLE 2. Dominance hierarchies, fighting rates, and blows per fight for 7 Cattle Egret broods.

	a vs. *b*	*b* vs. *c*	*a* vs. *c*
Elder wins[a]	79%	100%	99%
Fights per day[b,c]			
Mean	0.5	1.4	0.4
Upper 95% C.I.	0.7	2.2	0.7
Lower 95% C.I.	0.2	0.8	0.2
Blows per fight[c]			
Mean	2.2	1.6	2.3
Upper 95% C.I.	2.9	1.8	2.9
Lower 95% C.I.	1.8	1.5	1.8
No. of fights	38	137	46

[a] Ties ($n = 5$) were excluded in calculations of percentage of victories, but contributed to the other two categories.

[b] Fights per day were based on 138 observations (46 nest-days per dyad).

[c] Upper and lower 95% confidence intervals (95% C.I.) and means of fights per day and blows per fight were back transformed after log transformation.

cant (Table 2; $F_{2,205} = 2.86$, $0.05 < P < 0.06$; analysis based on log-transformed data).

Fighting rates were not obviously related to food supply. The daily fights per brood were not related linearly to the daily volume (in cubic centimeters) of food brought to the brood ($R^2 = 0.0008$, $n = 38$ nest-days). Fighting rates and amounts of food delivered to nests per day did not increase linearly with *c*-chick age ($R^2 = 0.021$, $n = 46$ nest-days and $R^2 = 0.08$, $n = 39$ nest-days for regressions of *c*-chick age on fights/day and food/day, respectively).

Feeding activities.—During the first few days after hatching, parents delivered food to their young by regurgitating boluses onto the nest floor, from which chicks pecked small pieces ("indirect feedings"; *sensu* Mock 1985). By the age of 2–4 days, the nestlings began to intercept boluses before their deposition on the nest floor. This was done by grasping the parent's mandibles in a scissor grip and catching the food as it fell from the adult's bill ("direct feeds"; *sensu* Mock 1985; Fujioka 1985b, Inoue 1985). The transition from indirect to direct feeds (the period when the proportion of direct boluses rises from 20% to 80%; see Mock 1985: fig. 3) occurred between the *c*-chick's second and eighth day. Thus, while *c*-chicks still had to get their food indirectly, much of the food was being intercepted directly by elder sibs.

Scissoring rates differed significantly among the chick ranks (Table 3; $F_{2,78} = 5.62$, $P < 0.01$). *A*-chicks scissored more often than did *c*-chicks (Tukey-Kramer pairwise comparisons, $P < 0.05$, df = 78; other two comparisons not significant).

The chick holding the pole position on the parent's bill obtained the most food, on average. The mean pole-share was 90%. Although seniors scissored more, they did not hold the pole position more often than *c*-chicks (Table 3; $F_{2,123} = 0.45$, not significant). However, *a*-chicks scissored more effectively. Consequently, when holding the pole position, they obtained significantly larger portions of boluses than did *c*-chicks (Table 3; $F_{2,220} = 3.81$, $P < 0.05$; pairwise comparisons, $P < 0.05$, df = 10). Other pairs did not differ significantly.

Parents fed broods an average of 5.2 boluses (±2.4 SD, $n = 85$ feeds) in each of the 3.0 feeds (±1.3 SD, $n = 47$ nest-days) delivered per day. Bolus volume averaged 6.7 cm^3 (±2.8 SD, $n = 320$ boluses).

Boluses were not shared equally among sibs. Throughout the first month, the amounts of food consumed by chicks per feed and per day differed significantly among sibling ranks (Table 4; $F_{2,237} = 14.97$, $P < 0.001$ and $F_{2,99} = 10.28$,

TABLE 3. Incidences of scissoring. Data are based on boluses delivered to 6 Cattle Egret nests. Values are means ± 1 SD.

Sibling rank	Scissors per feed[a]	Poles held per feed[b]	Pole-shares per feed[c]
a	4.4 ± 3.7	1.8 ± 0.8	96.8 ± 14.0%
b	3.8 ± 2.6	1.8 ± 1.0	92.5 ± 20.2%
c	2.2 ± 1.6	1.6 ± 1.1	80.9 ± 34.0%

[a] Scissors are based on 96 observations (32 feeds/sib rank).

[b] Poles held are based on 141 observations (53 *a*-chick poles, 58 *b* poles, 30 *c* poles).

[c] Pole-shares are based on 238 observations (92 boluses delivered when *a*-chicks held the pole, 100 boluses for *b*-chicks, 46 boluses for *c*-chicks).

$P < 0.001$, respectively). *A*- and *b*-chicks obtained an average of more than twice as much food, both per feed and per day, than did *c*-chicks (pairwise comparisons, $P < 0.05$, df = 12).

Chicks were often unsuccessful during attempts to feed, frequently because a sibling controlled access to the food by monopolizing entire boluses. Bolus monopolization differed significantly among sib ranks (Table 4; $F_{2,282} = 23.28$, $P < 0.001$). Senior siblings were more likely than *c*-chicks to obtain entire boluses (pairwise comparisons, $P < 0.05$, df = 12), but monopolization rates did not differ between *a*- and *b*-chicks. Sibling rank significantly affected the frequency of receiving no food (zero shares) from boluses (Table 4; $F_{2,282} = 17.99$, $P < 0.001$). In pairwise comparisons, *c*-chicks got zero shares during significantly more bolus deliveries than did *a*- and *b*-chicks ($P < 0.05$, df = 12). Again, differences between *a*- and *b*-chicks were nonsignificant.

Occasionally, repeated beatings intimidated a sib completely (see Mock 1985). Such intimidations differed significantly among sibling ranks (Table 4; $F_{2,282} = 3.69$, $P < 0.05$). *C*-chicks were intimidated significantly more often than *b*-chicks (pairwise comparisons, $P < 0.05$, df = 12), but intimidation rates between the other two sibling-rank pairs were similar.

Temporary satiation also differed significantly among chick ranks (Table 4; $F_{2,282} = 6.82$, $P < 0.01$). *A*-chicks were satiated significantly more often than were *c*-chicks (Table 4; $P < 0.05$, df = 282; other pairwise comparisons not significant).

Mortality.—The fates of all chicks were known in 15 broods. These broods produced an average of 1.4 survivors: 33% of the broods were totally successful, 20% were partially successful (1 or 2 chicks survived), and 47% failed completely. Twenty-seven percent of the known-fate broods had at least one brood reduction (20% of 40 broods in the all-fate sample). Of 58 chicks with known fates, 45% survived, 14% died during brood reductions, and 41% died of other causes.

Five *c*-chicks, 3 *a*-chicks, and no *b*-chicks were brood-reduction victims. The first brood reduction took place an average of 9.8 days after the *c*-chick hatched ($n = 8$ brood-reduction victims). Of these brood reductions, causes of death were determined in detail for two broods that were observed directly. In one of these broods, the *c*-chick starved; in the other, the *c*-chick was a siblicide victim. Deaths from causes other than brood reduction did not differ in frequency by chick rank (Table 5; $G = 0.58$ for known fates, $G = 0.31$ for all fates; both tests not significant with df = 2). Similarly, the overall probability of the *c*-chick surviving the study period was not significantly lower than that of seniors (Table 5; $G = 1.82$ for known fates, $G = 0.70$ for all fates; both tests not significant with df = 2).

DISCUSSION

Aggression among Cattle Egret nest mates plays an important, but circuitous, role in the brood-reduction process. Last-hatched chicks fight more, lose more, control the parent's bill less effectively, and eat less than senior siblings. They grow more slowly and are victims of brood reduction more often than elder nest mates (Fujioka 1984, Werschkul unpubl. data). Although complete intimidations were rarely observed in our study, they involved *c*-chicks disproportionately. More commonly, fights during feeds caused victims to hesitate momentarily at the critical moment of bolus delivery ("partial intimidations"; *sensu* Mock 1985). Thus, defeats of *c*-chicks apparently contributed to their being deprived of food. Senior sibs may have scissored more often in part because of such *c*-chick hesitation. Although all chicks held the pole position with similar frequency, seniors were more effective at it, monopolizing boluses more frequently and thus

TABLE 4. Comparisons of nestlings' abilities to control food. Means for food-control events per feed are based on 101 feeds per sibling rank, food amounts per feed are based on 86 feeds per sibling rank, and food amounts per day are based on 40 nest-days per sibling rank. Values are means ± 1 SD.

	Sibling rank		
	a	*b*	*c*
Events per feed			
Monopolizations	1.5 ± 1.2	1.5 ± 1.2	0.6 ± 0.8
Satiations	0.5 ± 0.8	0.3 ± 0.8	0.1 ± 0.4
Zero shares	1.9 ± 1.5	1.4 ± 0.9	3.2 ± 2.1
Intimidations[a]	0.1 ± 0.6	0.0 ± 0.0	0.2 ± 0.7
Food amounts (cm^3)			
Per feed	9.7 ± 8.8	8.9 ± 7.5	4.3 ± 5.1
Per day	21.0 ± 16.7	19.1 ± 14.6	9.2 ± 8.0

[a] "Complete" intimidations, *sensu* Mock 1985.

gaining more food. That *c*-chicks held pole positions as often as did seniors probably is because *c*-chicks seemed to hold the pole position during delivery of the final boluses of each feed, when seniors often were satiated. Similarly, in a Japanese colony of Cattle Egrets, first boluses usually were secured by senior nest mates, but all chicks were equally likely to obtain final boluses (Fujioka 1985b). The ability of seniors to gain priority access to food means last-hatched chicks may go without food if the number of boluses delivered is insufficient (see Inoue 1985 for Little Egrets, *Egretta garzetta,* and Mock 1985 for Great Egrets). We found that sibling competition led an average senior to gain twice as much food as the *c*-chick.

Sibling competition created and maintained feeding disadvantages for *c*-chicks and feeding advantages for senior sibs; feeding advantages accrued to *a*- and *b*-chicks equally, rather than to *a*-chicks disproportionately. Fujioka (1985b) showed a similar pattern across a variety of Cattle Egret brood sizes, as did Mock (1985) for Great Egrets. Senior sibs thus may achieve equivalent, high growth rates, sufficient for postfledging survival, by causing retarded growth of their last-hatched nest mate. Such last-hatch disadvantages may be common among asynchronously hatching species, where last-hatched chicks often exhibit markedly slower growth than their senior nest mates (Langham 1972, LeCroy and LeCroy 1974, Parsons 1975, Fujioka 1984, Inoue 1985, Mock 1985).

Growth retardation could increase the postfledging mortality of *c*-chicks. Starvation of *c*-chicks may contribute disproportionately to deaths in the first few months postfledging, when mortality is greater than at any other time in adult life (Siegfried 1970). Because hunting skills in Cattle Egrets probably improve with age (as in other ardeids; Recher and Recher 1969, Quinney and Smith 1980), fledglings probably face periods of food shortage caused by their less efficient foraging. Chicks with low reserves may be unable to survive such shortages.

Both parents and senior sibs may benefit from concentrating the competitive handicaps on a single nestling (O'Connor 1978). Cattle Egret parents almost never interfered with fights and made no obvious atempts to feed *c*-chicks preferentially. Rather than discouraging harassment of last-hatched offspring overtly, parents may influence *c*-chick prospects only through the initial hatch asynchrony; the resulting competitive disparities presumably enhance parental fitness by facilitating brood reduction when food is limiting (O'Connor 1978).

Assuming *b*-chicks face greater risks than *a*-chicks of becoming victims of dominance reversal, we predicted fighting would occur most intensely between *b*- and *c*-chicks. In this study, fighting rates differed significantly among sib dyads, with *b*-*c* dyads fighting most often. Data from Great Egret sibs suggest a similar pattern (Mock 1985). In our 7 nests, however, we observed no *b*-*c* dominance reversals, as have been seen in other Ardeidae (Mock unpubl. data).

The number of blows per fight did not differ significantly among sib dyads, although *b*-*c* dyads tended to deliver the fewest blows, a trend opposite to that predicted. This could result if the *c*-chick's situation is not yet desperate. If last-hatched chicks have a good chance of

TABLE 5. Fate summaries for 3-chick broods of Cattle Egrets censused in a Texas colony. Results are presented separately for chicks of all fates (including chicks with unknown fates) and for chicks with known fates only. Values are means ± 1 SD.

	All fates			Known fates		
	a	*b*	*c*	*a*	*b*	*c*
Total no. of chicks	40	40	40	20	17	21
Percentage of unknown fates	50%	58%	48%	—	—	—
Percentage of chicks surviving	25%	22%	18%	50%	53%	33%
Percentage of chicks dying from:						
Brood reductions	8%	0%	13%	15%	0%	24%
Other causes	18%	20%	23%	35%	47%	43%

obtaining uncontested food (e.g. when seniors are satiated), the best tactic may be to concede fights quickly, thereby reducing the risk of injury (Mock and Parker 1986).

The variability in fighting rates and blows per fight observed among nests (see Ploger 1985) could be due to differences in hatching intervals. Theoretically, small hatch intervals would promote fighting among food-stressed siblings because competitors are more evenly matched (Maynard Smith and Parker 1976). Experimental manipulations of hatch intervals based on larger sample sizes have demonstrated that reduction of hatching intervals enhances fighting among nestling Cattle Egrets (Fujioka 1985a, Mock and Ploger in press).

Food limitation is usually considered the ultimate cause of both avian brood reduction (Lack 1968) and sibling aggression (O'Connor 1978, Stinson 1979, Mock 1984a). Many workers have also assumed that food shortages and consequent chick hunger also act as proximate cues eliciting sibling aggression (Skutch 1967, Procter 1975, Brown et al. 1977, Gargett 1977, Stinson 1980, Braun 1981, Braun and Hunt 1983). A few studies have suggested that fighting increases with reduced food (Procter 1975; Stinson 1980; Poole 1982; Braun and Hunt 1983; H. Drummond, E. Gonzalez, and J. Osorno unpubl. data). Although Cattle Egret fighting rates in this study did not correlate inversely with food, differences in food supplies between nests may have been too small to create detectable changes in fighting rates.

Prey size also may act as a proximate cue for nestling aggression (Mock 1984b, 1985). The prey-size hypothesis predicts sibling aggression where nestlings are fed on a diet of small food that they can monopolize. Cattle Egret aggression is consistent with this hypothesis: the study broods were fed mainly on Orthoptera (with a few small vertebrates) packed in discrete boluses readily monopolized by scissor feeding.

Although overall mortality was high, brood reduction was rare in this study. The behavioral disadvantages of *c*-chicks did not lead clearly to *c*-chick biased mortality in this sample. Strongly *c*-chick biased mortality may be common in Africa, however: Blaker (1969) reported that for 12 brood reductions in 3-chick nests, 11 were *c*-chicks and only 1 was a senior sibling; similarly, Siegfried (1972) found that 85% of 32 partial brood failures involved *c*-chick deaths. Although brood reduction is common in many Cattle Egret populations (e.g. Skead 1966, Blaker 1969, Siegfried 1972, Werschkul unpubl. data), it is not common in all areas or seasons (Jenni 1969, Fujioka 1984, this study). Competitive asymmetries may facilitate brood reduction only when food is sharply limiting or predation is not sufficiently common to reduce the need for sibling competition and consequent mortality. The unbiased chick survival observed in our study may have resulted because either food was sufficiently abundant for *c*-chicks to survive despite frequent beatings (Mock 1985), or the causes of mortality independent of brood size (especially predation) occurred frequently before starvation thresholds were reached. Our data support the latter alternative more than the former.

The single siblicide case took a form not described previously for this species. After being deprived of food and beaten repeatedly by its siblings during its last three days in the nest, the victim entered a neighboring nest, where it may have been attempting to steal food (as was observed in numerous unmarked chicks). The chick was also evicted from that nest, however, and vanished shortly thereafter. Once evicted, the survival chances of a wandering chick are probably quite low (Mock 1984a). Unmarked chicks that we observed scavenging underneath nests and kleptoparasitizing observation broods typically appeared to be starving and dying of exposure. They were frequently attacked by adults and stalked by Black-crowned Night-Herons. However, scavenging and kleptoparasitism sometimes may enable wandering Cattle Egret chicks to survive, as do wanderers of other bird species (Mock 1984b, Pierotti unpubl. data). Because wandering Cattle Egret chicks frequently bore the bloody marks of sibling persecution, we speculate that these chicks were evicted subordinates. Survival of such wanderers could reduce the fitness costs to parents and sibs of evicting a subordinate chick.

We believe aggression among Cattle Egret nestlings helps seniors skew parental investment (here, food) toward senior sibs at the expense of the last-hatched sib. Because food may be insufficient for all sibs to thrive, the improved access to food gained by seniors through fighting may have lethal consequences for the last-hatched sib. We found that the penultimate chick was involved in a disproportionate share of the attacks on the youngest, which may be a tactic for the penultimate chick to ensure its own survival.

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FORAGING BEHAVIOR OF GENTOO AND CHINSTRAP PENGUINS AS DETERMINED BY NEW RADIOTELEMETRY TECHNIQUES

WAYNE Z. TRIVELPIECE, JOHN L. BENGTSON,[1] SUSAN G. TRIVELPIECE,
AND NICHOLAS J. VOLKMAN
Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 USA

ABSTRACT.—Analysis of radio signals from transmitters affixed to 7 Gentoo (*Pygoscelis papua*) and 6 Chinstrap (*P. antarctica*) penguins allowed us to track penguins at sea. Signal characteristics allowed us to distinguish among 5 foraging behaviors: porpoising, underwater swimming, horizontal diving, vertical diving, and resting or bathing. Gentoo Penguins spent a significantly greater portion of their foraging trips engaged in feeding behaviors than Chinstraps, which spent significantly more time traveling. Gentoos had significantly longer feeding dives than Chinstraps (128 s vs. 91 s) and significantly higher dive-pause ratios (3.4 vs. 2.6). These differences in foraging behavior suggest Gentoo and Chinstrap penguins may have different diving abilities and may forage at different depths. *Received 3 June 1985, accepted 24 April 1986.*

THE trophic relationships among *Pygoscelis* penguins, the Adélie (*P. adeliae*), Chinstrap (*P. antarctica*), and Gentoo (*P. papua*), have been a major focal point of research in recent years, particularly with respect to the ecology of their major prey species, krill (*Euphausia superba*). To date, however, our knowledge of the birds' feeding ecology is largely derived from stomach samples obtained ashore (Emison 1968; Croxall and Furse 1980; Croxall and Prince 1980a; Volkman et al. 1980, 1986; Lishman 1985).

Diving depth is one aspect of penguin foraging behavior that has been investigated in some detail. Multiple depth recorders, logging the number of dives within set depth ranges, have been deployed on King (*Aptenodytes patagonica*; Kooyman et al. 1982), Chinstrap (Lishman and Croxall 1983), and Gentoo (Costa pers. comm.) penguins. Maximum diving depths have been reported for Emperor (*A. forsteri*; Kooyman et al. 1971), Black-footed (*Spheniscus demersus*; Wilson and Bain 1984), and Gentoo (Adams and Brown 1983) penguins. Feeding range also has been investigated, but indirectly, using nest relief intervals (Williams and Siegfried 1980, Ainley et al. 1984, Croxall et al. 1984).

We report a new method of tracking penguins at sea that allowed us to differentiate among behaviors during foraging trips. This method improved our understanding of penguin feeding efficiencies, ranges, and traveling speeds, and permitted preliminary comparisons of Gentoo and Chinstrap penguin foraging behaviors.

METHODS

This study was conducted at a breeding rookery at Point Thomas, King George Island, South Shetland Islands, Antarctica (62°10'S, 58°30'W), between 26 January and 12 February 1984. We attached radio transmitters (1.5 cm in diameter, 5 cm long, 25 g) to the backs of 7 Gentoo and 6 Chinstrap penguins rearing chicks. We secured them to back feathers with Devcon epoxy and two plastic tie-wraps. A 30-cm long antenna curved upward from the penguin's back to assure it was well above the water when the penguin surfaced. We triangulated penguins' locations, at 15-min intervals, with radio receivers (164 MHz) from two huts, 200 m above sea level and approximately 3 km apart. We used a null-peak, 4-element double Yagi antenna receiving system. A third receiver was coupled to a strip-chart recorder and continuously monitored a single penguin during its foraging trip. Signals from foraging penguins were received only when the bird was on the surface and the antenna was not submerged. Thus, strip charts provided profiles of the surface vs. underwater time during penguins' foraging trips. Penguins were tracked between 0900 and 2300, and the two species were alternated over the study period. Krill was apparently plentiful in Admiralty Bay during this time as all penguins foraged exclusively in the bay, within 10 km of the rookery.

All data are expressed as means ± standard error.

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[1] Present address: National Marine Mammal Laboratory, NOAA/NMFS, 7600 San Point Way N.E., Seattle, Washington 98115 USA.

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Statistical analysis was done using the Mann-Whitney *U*-test or *G*-test with Yates correction.

RESULTS

Foraging behavior patterns.—The foraging track of Gentoo Penguin 3875 and sections from its chart recording are illustrated in Fig. 1. We were able to distinguish several types of diving patterns from the strip-chart records. We believe these indicate different behaviors such as resting at the surface, two modes of traveling (porpoising and underwater swimming), and two feeding behaviors (horizontal and vertical diving). Resting at the surface included time spent bathing.

Porpoising always was used by penguins leaving from or returning to the immediate vicinity of the beach. Outward-bound porpoising often was followed by bathing, and both behaviors were confirmed visually. Rapid porpoising, then bathing, is a constant feature of Adélie Penguin departure at Cape Crozier in the Ross Sea (Ainley 1972). Underwater swimming, the primary method of traveling used by penguins, accounted for 73% of all traveling time. It consisted of dives, averaging 50 s each, followed by surface pauses, averaging 12 s. Horizontal diving behavior followed underwater swimming and preceded vertical diving in 5 of the 6 penguins for which we have complete records. Penguins that exhibit this foraging pattern moved considerable distances by alternating periods of long dives with one or two short dives. The short dives were of approximately the same duration as the dives of underwater swimming. We hypothesize that horizontal diving may be the primary method of searching behavior used by penguins. The long dives of this behavior pattern may be to explore the deeper layers of the water column for krill. When no prey are located, the penguin moves to a new location by short "traveling dives" before diving again to search for prey. Vertical diving, like underwater swimming, was characterized by regular intervals of dive-to-surface pause times. The duration of dives and pauses were significantly longer, however, and the penguins remained in a localized area during vertical diving (Fig. 1).

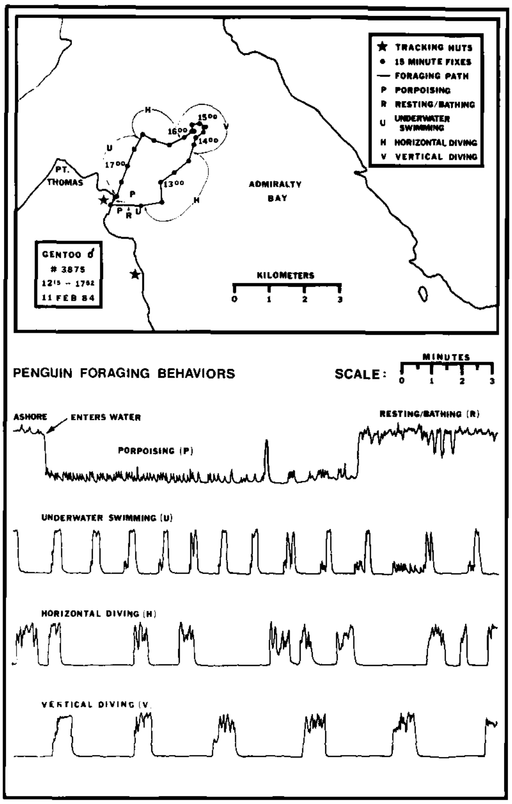

Fig. 1. The foraging trip of Gentoo male 3875 in Admiralty Bay. The penguin's path was plotted from compass bearings triangulated by radio and taken at 15-min intervals from the two tracking huts. Foraging behaviors were copied from a continuous strip chart. Whenever the penguin was submerged, the signal was lost and the strip-chart pen returned to baseline; upon surfacing, the radio signal caused the pen to deflect upward and remain there until the next dive. The ragged look of surface periods during horizontal and vertical diving was caused by changes in the orientation of the antenna because of bird movement and from waves washing over the bobbing penguin, which interfered with the signal's propagation. The paper speed of the strip chart was 16 mm/min. Data on surface times and dive times were taken directly from the charts by converting linear distance to time.

For analysis of the foraging behavior of the penguins, feeding dives were defined as all dives during vertical diving, plus the long dives during horizontal diving; traveling dives were all underwater swimming dives plus the short dives during horizontal diving behavior. Porpoising was not considered to be diving.

Comparisons of Gentoo and Chinstrap foraging behaviors.—Gentoo Penguins spent a significantly greater portion of foraging trips engaged in feeding behaviors (horizontal and vertical diving) than in traveling behaviors (porpoising and underwater swimming) than did Chinstrap Penguins ($G = 5.47$, $P < 0.025$; Table 1). Gentoos made significantly longer vertical dives than Chinstraps (128 ± 4.5 vs. 91 ± 4.9 s; $U = 42.00$, $P < 0.005$) and had significantly longer maximum dive times (189 ± 8.4 vs. 130 ± 4.3 s; $U = 12.00$, $P < 0.01$; Table 2). Gentoos also had significantly higher dive/pause ratios during vertical diving (3.4 ± 0.2 vs. 2.6 ± 0.2; $U = 36.50$, $P < 0.005$; Table 2). Gentoo Penguins made a mean 193 dives during 6.1 h of foraging, 90 of which (47%) were feeding dives; Chinstraps made 182 dives during 5.3 h, 74 of which (41%) were feeding dives (Table 2).

We calculated traveling speeds for penguins returning from feeding areas to the breeding rookeries. The mean (±SE) traveling speed for 3 Gentoo and 3 Chinstrap penguins was 4.5 ± 0.4 km/h (Table 2). Penguin return trips varied from 20 to 64 min. Strip-chart recordings assured us penguins were traveling (i.e. porpoising or underwater swimming) throughout their returns.

DISCUSSION

Using radiotelemetry to track penguins at sea and to distinguish among their behaviors provided detailed records of the activities of penguins during foraging trips and allowed two important general conclusions. First, a large percentage of dives recorded using multiple depth recorders (MDRs) in some other studies probably are not feeding dives. Therefore, MDRs could overestimate the number of feeding dives and underestimate the foraging efficiencies of penguins. Second, traveling speeds of penguins at sea may be considerably lower than the 7.2 km/h swimming speeds reported for Adélies (Kooyman 1975), and penguin foraging ranges based on these swimming speeds may have been overestimated (Croxall and Prince 1980b, Croxall et al. 1984).

Multiple depth recorders log the number of dives within preset depth ranges. Because Kooyman et al. (1982) deployed MDRs with minimum thresholds of 5 m, their estimates of King Penguin feeding dives probably do not include traveling dives and are likely to reflect feeding effort. Lishman and Croxall (1983), however, had no lower thresholds set on MDRs placed on Chinstrap Penguins, because Chinstraps forage at shallower depths. Our calculations from their histograms show that 445 of 1,110 dives made by Chinstrap Penguins were recorded in the shallowest depth range (0–7 or 0–10 m). This represents 40% of all dives, many of which may have been dives associated with traveling (i.e. porpoising and underwater swimming). Dives during underwater swimming accounted for 44% of all dives by the penguins we studied.

Penguins can swim 7.2 km/h (Kooyman et al. 1971); however, the sustained traveling we observed consisted of an underwater locomotory phase followed by a short pause at the surface (see Fig. 1). Analysis of the dive/pause ratios showed that penguins were swimming during only 76% of the time they were traveling; the remaining time was spent on the surface. Calculating an overall speed by taking 76% of 7.2 km/h results in an estimate of 5.5 km/h. The 4.5 km/h mean returning speeds observed were lower still, perhaps because calculations were based on straight-line distances between feeding and landing areas, whereas penguins swam more erratically.

Comparisons of Gentoo and Chinstrap foraging behaviors provided new insights into their feeding ecology. Gentoo and Chinstrap penguins ate predominantly krill during chick rearing; 3-year means were 86.5% and 99.4% by wet mass of all their food, respectively (Volk-

TABLE 1. The percentage of foraging time spent in different behaviors by Gentoo and Chinstrap penguins.[a]

		Foraging behaviors[b] (%)				
		Traveling		Feeding		
	Foraging trip (h)	P	U	H	V	R
Gentoo Penguins[c]						
3894 F	5.7	5	12	53	21	1
UB M	7.1	3	24	6	60	6
3875 M	5.5	6	15	34	44	1
Mean	6.1	5	17	31	44	3
Chinstrap Penguins[c]						
3896 M	4.8	9	18	11	57	4
3963 F	4.4	13	17	22	46	2
3893 F	6.8	10	47	7	32	4
Mean	5.3	11	27	14	45	3

[a] From analyses of strip-chart recordings of complete foraging trips.

[b] P = porpoising, U = underwater swimming, H = horizontal diving, V = vertical diving, R = resting or bathing on surface.

[c] M = male, F = female.

TABLE 2. Comparisons of Gentoo and Chinstrap penguin foraging behaviors.[a,b]

Bird[c]	Total foraging trip (h)	Total no. dives	Total feeding time (h)	No. feeding dives	Mean dive time (s)	Mean pause time (s)	Dive/pause ratio	Maximum dive time (s)	Travel speed (km/h)
Gentoo Penguins									
3894	5.7	192	4.6	85	131	38	3.5	203	4.2
UB	7.1	231	4.3	92	108	41	2.6	174	5.3
3875	5.5	157	4.3	93	119	34	3.6	190	3.1
2245	—	—	—	—	135	45	3.0	—	—
3895	—	—	—	—	132	30	4.3	—	—
UB	—	—	—	—	128	31	4.1	—	—
2219	—	—	—	—	145	50	2.9	—	—
Mean	6.1	193	4.4	90	128**	39	3.4**	189*	4.2
Chinstrap Penguins									
3896	4.8	139	3.0	86	97	31	3.2	126	4.7
3963	4.4	158	3.3	69	103	47	2.2	139	3.9
3893	6.8	249	3.6	68	99	34	2.9	126	5.7
3885	—	—	—	—	83	33	2.5	—	—
2573	—	—	—	—	71	40	1.8	—	—
2605	—	—	—	—	91	33	2.7	—	—
Mean	5.3	182	3.3	74	91	36	2.6	130	4.8

[a] Data for the first 3 Gentoo and Chinstrap penguins are from entire foraging trips and include a strip-chart record. Dive and pause time data for the remaining penguins were collected by timing a minimum of 10 consecutive dive/pause cycles during vertical feeding.

[b] * = Differs significantly from Chinstrap Penguin; Mann-Whitney *U*-test, $P < 0.01$. ** = $P < 0.005$.

[c] UB = unbanded penguin.

man et al. 1986). Gentoo Penguins require significantly more krill to rear their chicks to fledging than do Chinstrap chicks (118 kg vs. 73 kg per breeding pair; Trivelpiece et al. in press) and have significantly shorter nest relief intervals during chick rearing (12.5 h vs. 16.7 h; Volkman et al. 1986). Foraging ranges based on nest relief intervals, feeding times, and traveling speeds are estimated as within 17 km of the rookery for Gentoos and within 27 km for Chinstraps (Trivelpiece et al. in press). Thus, Gentoos require more krill per day for their chicks, and they acquire this food from a more restricted foraging range. We suggest that Gentoos can do this because of their greater diving abilities.

Gentoos dove significantly longer and had significantly higher dive/pause ratios than did Chinstraps (Table 2). Dive/pause ratios may indicate physiological diving abilities (Dow 1964), which in cormorants (*Phalacrocorax* spp.) are correlated with feeding depths (Stonehouse 1967a, Ainley et al. 1981). Gentoo Penguins have been caught in trammel nets at 100 m depth (Conroy and Twelves 1972) and are known to dive to at least 135 m (Costa pers. comm.); none of 1,110 dives by 4 Chinstrap Penguins exceeded 70 m and only 6% of the dives exceeded 45 m (Lishman and Croxall 1983). A direct relationship between body size and diving depth has been postulated for penguins (Stonehouse 1967b). Consistent with this idea, Gentoo Penguins are the largest of the pygoscelids, with mean adult masses during the chick phase of 5.3 kg, compared with 4.0 kg for adult Chinstraps (Volkman et al. 1980).

In the shallow-water regions of King George Island, krill aggregations occur in a broad layer from 10 to 80 m deep during the night, and descend to a daytime level between an upper 30–60 m limit and a lower 90–120 m limit (Kalinowski and Witek 1980). Thus, whereas the deeper-diving Gentoos can exploit any krill aggregations they locate, Chinstraps may be unable to feed effectively on deep krill swarms and therefore must spend more time traveling in search of available prey.

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FEMALE SITE FIDELITY AND POLYGYNY IN THE BLACKPOLL WARBLER (*DENDROICA STRIATA*)

BONITA C. ELIASON
James Ford Bell Museum of Natural History, Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA

ABSTRACT.—From 1980 to 1982, 8–30% of male Blackpoll Warblers (*Dendroica striata*) studied on Kent Island, New Brunswick, were bigamous each year ($\bar{x}$ = 16.8%). I tested whether differences in the quality of the breeding situation can give rise to polygynous matings. Five territory parameters and two male parameters were used as measures of quality. Male arrival times were correlated with male mating status and the reproductive success of monogamous females. Territories of bigamous males had more large conifers than did those of monogamous males. Territory parameters did not appear to influence female choices.

Strong site attachment by females may lead them to mate bigamously when few males are available early in the season near the females' former nest sites. The reproductive success of secondary females was not different from that of monogamous females. Any costs of mating bigamously may be offset by increased reproductive success associated with early nest initiation and competitive advantages conferred by site dominance.

Site attachment and return patterns can account for the incidence of polygyny in this population, but probably could not give rise to high levels of polygyny or large harems. More information is needed to evaluate the influence of site fidelity on mating decisions of females in other polygynous passerine species. *Received 5 November 1985, accepted 1 May 1986.*

RESEARCH on the evolution of polygyny in passerine birds has focused on species in which polygyny is common (see Wittenberger 1979, Vehrenkamp and Bradbury 1984 for reviews). Relatively little attention has been directed at understanding the occurrence of polygyny at low levels in primarily monogamous species (Ford 1983). I attempted to identify factors that cause low levels of polygyny in a population of the Blackpoll Warbler (*Dendroica striata*).

Early research on mating systems in territorial passerine birds demonstrated that the number of mates acquired by a male was correlated with the resources he defended. This led to the formulation of the polygyny threshold model, which explains how differences in territory quality can give rise to polygyny in territorial passerine birds (Verner 1964, Verner and Willson 1966, Orians 1969). The model was incorporated into a more general theory on the evolution of mating systems (Emlen and Oring 1977). In the model, female fitness is presumed to be a function of access to resources. Bigamy occurs when differences in territory quality are large enough that a female can have higher fitness if she shares resources on a high-quality territory of a mated male than if she mates monogamously on a low-quality territory.

In the original formulation of the polygyny threshold model, male quality and territory quality were assumed to be highly correlated (Orians 1969). Weatherhead and Robertson (1977, 1979) suggested that when male quality and territory quality are not highly correlated, females might choose mates based on male quality alone. Although the details of their theory have been disputed (Heisler 1981, Searcy and Yasukawa 1981, Wittenberger 1981), their ideas stimulated studies of the role of male characteristics as well as territory parameters in influencing female mate choice.

I evaluated the role of five territory-quality parameters and two male-quality parameters in determining mating status in a population of the Blackpoll Warbler. The mating status of males could be explained by male and territory parameters, but female settling dates could not. The reproductive success of monogamous females was correlated with male arrival dates.

The polygyny threshold model assumes that females are free to mate with any male. This implies that they survey all opportunities available at the time of settling before choosing. In reality, the tendency to return to a familiar site often constrains the choices of both males and females that have bred previously

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(Hinde 1956, Greenwood 1980, Oring 1982). Female Blackpoll Warblers tend to breed near their former nest sites. Local sex ratios are sometimes skewed by differential returns of males and females. Given these two factors, the benefits of early nest initiation may cause females to mate with mated males. I assess the costs and benefits to females of mating bigamously under these circumstances. Finally, I suggest that high nest success may make the island a favorable place to breed, enhancing the importance of site tenacity in maintaining a breeding spot there.

STUDY AREA AND METHODS

The study was conducted in a 35-ha spruce-fir forest on Kent Island, New Brunswick, during May–August 1979–1982. Kent is an 80-ha island located 20 km southeast of the Maine–New Brunswick border in the Bay of Fundy. The vegetation of the island has been described by McCain (1975). Blackpoll Warblers used only the forested parts of the island.

Birds were netted and marked with unique combinations of three plastic color bands and one numbered aluminum band. Blackpoll Warblers are sexually dichromatic, and therefore males and females were distinguished readily. During the 4 years of the study 41 adults and 173 nestlings were color-banded. For the purpose of analysis, "old" birds are those known to be 2 years old or older. Four males and 1 female that were banded before 1979 provided some known-age birds at the outset. Fourteen birds banded as nestlings returned in subsequent years, providing a group of known-age yearlings.

Arrival dates of both sexes were determined by patrolling the study area daily, looking and listening for birds. I use the term "settling date" for the first day a bird was seen on a territory on which it subsequently bred. Territory boundaries were determined by noting male singing posts and sites of interaction between males. Points were plotted on maps of the study area made from aerial photographs. Each week maps of all territories were drawn by connecting observation points accumulated during the week. After the territory establishment period, I visited each territory at least once every 2 days for a minimum of 1–2 h to determine mating relationships, monitor interactions between mates, and follow reproductive chronology.

A maximum of 15 males held territories on the island in any year. The first field season was devoted to a feasibility study during which the breeding biology of 5 males and their mates was studied. The breeding habitat is dense, and nesting females are secretive. To be reliable, I concentrated on the activities of 8–12 males per year in 1980–1982. A total of 35 male-years of data was obtained. These data represent 25 different males and 22 different females. To distinguish the mates of bigamous males, I term the first female to initiate her nest the "primary" female and the second the "secondary" female.

If differences in the quality of the breeding situation give rise to polygynous matings, variation in measures of quality should explain (1) the division of males into mating-status categories, (2) the settling patterns of the first females on all territories, and (3) the reproductive success of females within mating-status categories (Vehrenkamp and Bradbury 1984). To get sample sizes large enough to test these predictions, it was necessary to pool the information for 1980–1982.

Beginning in 1980, I used the following parameters as measures of territory quality: (1) territory size, (2) conifer density, (3) total conifers, (4) large conifer density, and (5) total large conifers. The birds forage at midcanopy in conifers up to 10 m tall. Microlepidoptera larvae that are inside needles and closed buds are an important part of the diet (Eliason unpubl. data). Because of these factors, direct assessment of food on each territory proved to be beyond the scope of this project. Male age and arrival dates were used as measures of male quality.

I determined territory size by tracing the outlines of the territories with a plane planimeter. For this analysis I used territory maps for the 2-week period when most females settled on territories. In this population, more than 90% of foraging by Blackpoll Warblers was done in conifers (Eliason unpubl. data), so conifer density on the territory was taken as a measure of available foraging space. Tree densities were determined by counting trees (by species and size class) in 10 × 10-m plots. The number of plots used to sample each territory was proportional to the size of the territory, so that sampling intensities were equal (about 6% of territory area). The third parameter, total number of conifers per territory, is the product of territory size and conifer density. Foraging observations also indicated that conifers smaller than 5 m tall and 8 cm in diameter at breast height were used infrequently by the birds. The large conifer parameters were calculated by including only trees above that minimum size.

Male mating-status categories were: bigamous, monogamous, or unmated. Logistic regression was used to construct the best possible model to explain variance in the mating status of males. The five territory-quality parameters and two male-quality parameters were used as potential explanatory variables.

An explanatory regression model was first sought for the response categories of mated vs. unmated. The analysis was then repeated within the mated category for bigamous vs. monogamous. The procedure was performed with the computer program LOGIT (K. Larntz and S. Weisberg, Dept. Applied Statistics, University of Minnesota). With this method, the statistic being minimized is the deviance (see equation below). The significance of various models is tested by calculating the difference between the deviance values associated with each model. This difference is distributed approximately as $\chi^2_{(k_1-k_2\,\mathrm{df})}$, where k_i = the number of explanatory variables in the models being compared (McCullagh and Nelder 1983).

A step-up method of analysis was used in which models with one explanatory variable were compared with the baseline deviance of a model with no variables {baseline deviance = $2n_1\log_e(n_1 + n_0)/n_1 + 2n_0\log_e[(n_1 + n_0)/n_0]$, where n_i = the number of individuals in a response category}. Additional variables then were added to the best single-variable model to see if a better fit could be obtained. Multiple-variable models were deemed better than single-variable models only if they produced significantly smaller deviance values than the best model with one fewer variable.

Nests were located by following females during building and incubation. Nests were checked daily to determine the date of first laying, number of eggs laid, hatching date, and number hatched. The day the first egg of a clutch hatched was designated day 1. Nestlings were weighed and measured daily from hatching through day 8. Young were banded at day 6. After day 8 nests were checked three times daily to determine the number of young fledged, which was used as a measure of female reproductive success. I did not anticipate second broods and did not seek them in 1979 and 1980. In 1981 and 1982 territories were monitored closely throughout the renesting period. Season-long reproductive success comparisons refer to 1981–1982 only.

Because females do not sing, they are less conspicuous than males. Female settling dates are thus more difficult to determine. I was confident of the accuracy of settling dates for females that were engaged in the early stages of courtship when first seen (n = 11). Eight of these 11 females were the first females to settle on their territories. I performed a correlation analysis on this sample to test the prediction that female settling dates are correlated with territory quality. I had a larger sample of females with known first-egg dates than of females with known settling dates, and settling dates and first-egg dates were positively correlated for the 11 females whose settling dates were known with confidence ($r = 0.58$, $t_9 = 2.15$, $P = 0.06$). I performed a multiple regression analysis using first-egg dates as the dependent variable and the five territory-quality parameters plus male arrival dates as potential explanatory variables. Male age was not included in this or the fitness analysis described below because too few yearling males were mated.

I also used multiple regression analysis to explore whether some combination of the territory- and male-quality parameters could explain the variance in female reproductive success (prediction 3). The polygyny threshold model allows one to make predictions about the relationship of territory quality and female fitness only within mating-status categories (Vehrenkamp and Bradbury 1984). I did this analysis for monogamous females only because sample sizes of nonmonogamous females were too small.

Multiple regression analyses were performed using the program MULTREG (Weisberg 1982). All other statistical analyses were performed using SPSS 6000, version 8.3 on the University of Minnesota computer system.

As part of the assessment of possible costs to females of their mating choices, the number of feeding trips of both sexes to the nest were counted during three 30-min periods each day throughout the nestling period. Means of feeding rates for days 5–8 post-hatching were used to compare the attentiveness of birds of different mating status.

RESULTS

MATING SYSTEM

Bigamy occurred in all years, ranging in frequency from 8 to 40% ($\bar{x}$ = 22.6%) of males of known mating status (Table 1). Territory parameters were not measured in 1979. The mean level of bigamy for the 3 years for which I have territory-quality information was 16.7%. Bigamy occurred in first broods only; no bigamous pair bonds lasted beyond the first brood. No monogamous females switched mates between broods. Two females switched after mating with bigamous males for their first broods to mate with previously unmated males for a second brood. The frequency of known unmated males at the time females were involved in their first broods ranged from 0 to 40% ($\bar{x}$ = 17%) over the 4 years. I saw no unmated females at the time females were involved in their first broods. This population exhibits "facultative polygyny" (Ford 1983) because polygyny occurs regularly, but less than 20% of males have more than one mate.

TERRITORY AND MALE QUALITY

Male mating status.—The best explanation of the fit of males into mated vs. unmated categories was provided by a regression model with arrival time as the only explanatory variable. The addition of territory-quality measures did not improve the fit (Table 2). A regression

TABLE 1. Male mating status. Percentages of males in each mating-status category in each year and the mean percentages for the 4 years are shown. The 35 male-years shown represent the histories of 25 different males.

Year	n	Monogamous	Bigamous	Unmated
1979	5	60	40	0
1980	8	75	12.5	12.5
1981	12	75	8	17
1982	10	30	30	40
Mean		60	22.6	17.4

model with total large conifers plus arrival time as explanatory variables provided the best explanation for the monogamous/bigamous dichotomy (Table 2).

Male arrival dates were correlated inversely with total large conifers ($r = -0.47$, $P = 0.01$), consistent with the idea that males that arrive first settle on the best territories. The mean values of all territory parameters were smallest for unmated males and largest for bigamous males, with the values for territories of monogamous males intermediate (Table 3). The mean values for large conifer density and total large conifers were significantly different among the territories of males of different mating status. Territories of bigamous males had significantly more total large conifers (Student-Newman-Keuls test, $P < 0.01$) than those of other males, but there was no difference between the territories of unmated and monogamous males. Thus, there appeared to be differences between the territories of bigamous males and other males.

TABLE 2. Deviance values from logistic regression analysis. Values for models containing each of the seven explanatory variables alone, plus the two best multiple-variable models, are shown, along with the baseline deviance values for the response categories of mated vs. unmated and bigamous vs. monogamous. Asterisks indicate best models.

	Response variables	
Explanatory variables	Mated vs. unmated	Bigamous vs. monogamous
Baseline	26.4	15.8
Territory size (TS)	24.2	15.1
Conifer density (CD)	24.0	15.5
Total conifers (TC)	23.0	10.8
Large conifer density (LCD)	22.7	13.8
Total large conifers (TLC)	21.8	5.1
Male arrival dates (ARR)	5.4*	13.8
Male age (AGE)	11.5	14.6
ARR + AGE	5.4	13.6
ARR + TLC	5.3	0.50×10^{-5}*

TABLE 3. Mean values of territory parameters for males in three mating-status categories: unmated (U), monogamous (M), and bigamous (B). Parameter abbreviations are defined in Table 2.

	Mating status			
Parameter	U	M	B	Mean
n	6	16	5	
TS (ha)	0.8	1.1	1.2	1.1
CD (trees/100 m^2)	23.9	37.3	48.2	36.3
LCD (trees/100 m^2)[a]	14.5	22.8	37.9	23.7
TC (trees/territory)	2,200	3,480	5,150	3,510
TLC (trees/territory)[b]	1,310	2,150	4,040	2,320

[a] One-way ANOVA, $F_{2,24} = 3.83$, $P = 0.04$.
[b] One-way ANOVA, $F_{2,24} = 9.46$, $P < 0.001$.

Female settling dates.—There was no significant correlation between female settling dates and any of the six breeding-quality parameters. No significant regression model could be constructed to explain the variance in first-egg dates using the six breeding-quality parameters as potential explanatory variables.

Female reproductive success.—The only significant regression model to explain the variance in the season-long reproductive success of monogamous females was one with male arrival dates alone ($r = 0.68$, $t_{10} = 2.91$, $P = 0.02$). The addition of the territory parameters did not improve the fit.

SITE FIDELITY AND ARRIVAL SCHEDULES

In all 12 cases where males with known breeding histories returned, the territories they defended in their second year included part of the territories they had defended in the previous year. In 11 of 12 cases where females with known breeding histories returned, they settled on or immediately adjacent to the territory on which they had nested the year before. In 4 cases the mate returned, but in 7 he did not.

Members of different age and sex classes re-

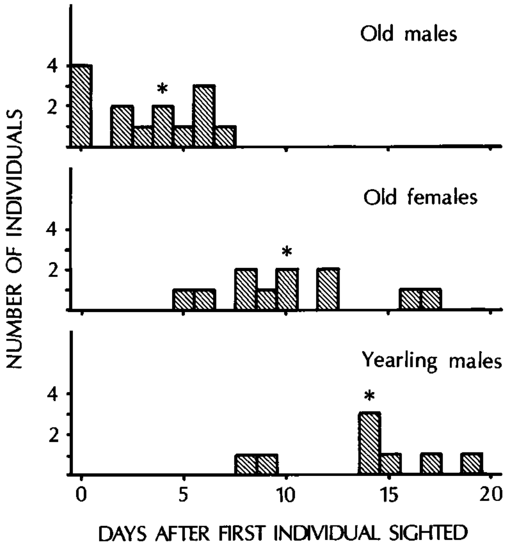

Fig. 1. First sighting dates of birds in three age and sex classes for 1981 and 1982. "Old" refers to birds 2 years old and older. Dates were ordered by using the date the first individual was sighted as day 0 and then numbering days consecutively. Asterisks indicate medians.

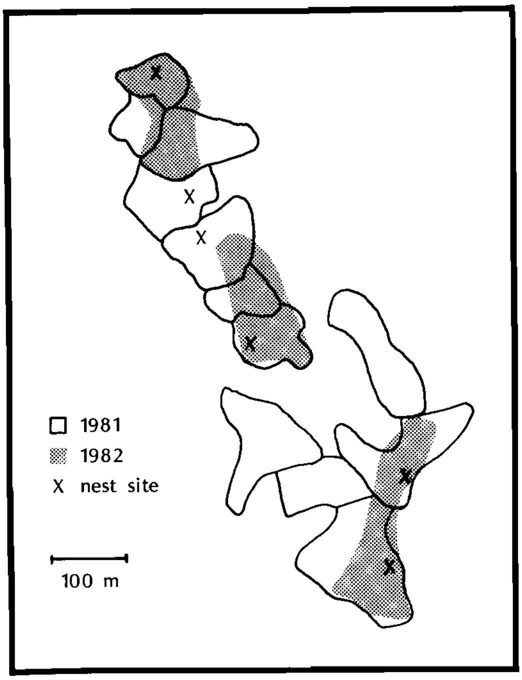

Fig. 2. Territories (stippled) of the first 3 males to settle in 1982 superimposed on 12 territories (solid lines) and 6 nest sites (X's) for 1981.

turned at different times (Fig. 1). Old males arrived first and yearling males latest, with no overlap in the dates they began advertising on territories. Females arrived over a longer period. Some old females arrived before any yearling males. The median date of old female arrival was earlier than that of yearling males (Fig. 1).

More old females than old males returned in some years, although the return rates of old birds were similar for males (48%) and females (49%) when averaged over the 4 years of the study. Depending on the settling patterns of early males, this could mean that no unmated males were available near the areas where returning females formerly nested.

This is evidently what happened in 1982 (Fig. 2), when 7 old females and only 3 old males returned. The territories of the 3 returning males contained portions of what had been multiple territories in 1981, but there were many unoccupied areas. All 6 females whose nest sites are shown in Fig. 2 returned in 1982. Each mated with the male that held the territory closest to her old nest site. This resulted in 3 bigamous matings.

Site fidelity appeared to influence mating choices in 1981 as well. There was one case of bigamy that involved a female (O/B) that had nested on the same territory in 1980, and a yearling female (M/Y). Although O/B arrived after M/Y, she initiated her nest first. The male made more feeding trips to her nest than to that of M/Y (3.2 vs. 2.7 trips$\cdot$nestling$^{-1}\cdot$h^{-1}), and the male fed her fledglings but not those of M/Y. In the bigamous mating described

TABLE 4. Reproductive output of females in relation to their mating status.[a] Values shown are means ± SD, with sample sizes in parentheses.

Mating status	Number fledged (first brood)** 1979–1982	Number fledged (season-long)* 1981–1982
Primary	4.8 ± 0.39 (6)	8.3 ± 0.96 (4)
Secondary	2.9 ± 1.30 (5)	4.8 ± 1.70 (4)
Monogamous	3.5 ± 1.05 (15)	4.8 ± 1.06 (10)

[a] * = $P < 0.05$, ** = $P < 0.01$; Kruskal-Wallis test.

TABLE 5. Male feeding rates on days 5–8 post-hatch.

Female status	n	Trips · nestling^{-1} · h^{-1} by male[a] ($\bar{x}$ ± SD)	Percentage of total trips made by male
Secondary	5	0.53 ± 0.53	16.1
Monogamous	14	1.89 ± 0.62	52.5

[a] $U = 2$, $P < 0.05$; two-tailed Mann-Whitney U-test.

above, only the primary female (O/B) returned to a site on which she had bred previously, but she settled there even though another female was already present.

COSTS AND BENEFITS OF SECONDARY STATUS

Costs of secondary over monogamous status.—I found no evidence of a significant cost to secondary females compared with monogamous females in terms of either number of young produced or adult survival. Primary females produced significantly more fledglings than did monogamous or secondary females, but there was no significant difference between the success of the monogamous and secondary females (Table 4). This was true for comparisons of first-brood and season-long success.

In terms of the number of young produced, secondary females were no worse off than the average monogamous female. However, secondary females received significantly less help from their mates in feeding nestlings relative to monogamous females (Table 5). Secondary females responded to reduced male aid by increasing nestling feeding rates compared with monogamous females. Secondary females made as many trips as were made by both members of 14 monogamous pairs (3.6 vs. 3.5 trips · nestling^{-1} · h^{-1}). There might be a cost to secondary females because of this extra effort. For example, secondary females might suffer higher overwinter mortality than monogamous females. I found no evidence for this, but the sample sizes were small. The average return rate for adult females was 49%, whereas 50% of secondary females ($n = 4$) from 1979–1981 returned in subsequent years.

Benefits: early nest initiation.—Females that had second broods initiated their first nests significantly earlier than those that did not have second broods (Table 6). In fact, no female that initiated her first brood more than 10 days after the first egg of the season was laid had a second brood. Females that attempted two broods fledged significantly more young than those that did not (Table 6).

TABLE 6. Laying dates and reproductive success of females in relation to the number of broods they produced. Egg 1 dates were recorded by making the date the first egg of the season was laid equal to 1 and numbering days sequentially.[a]

No. of broods	n	Date egg 1 laid* ($\bar{x}$ ± SD)	Fledglings produced** ($\bar{x}$ ± SD)
1	6	9.8 ± 5.3	3.7 ± 0.82
2	13	4.7 ± 2.46	6.6 ± 1.76

[a] *$U = 14.5$, $P = 0.03$; **$U = 6.5$, $P < 0.01$; two-tailed Mann-Whitney U-test.

Early nest initiation allows, but does not guarantee, an opportunity for a second brood. Only secondary females that switched mates after their first broods and mated with previously unmated males had second broods. These previously unmated males were not present when the females initiated their first nests.

DISCUSSION

One measure of territory quality, the number of large conifers on the territory, was correlated with male mating status. Female settlement choices were better explained by site fidelity than by variations in territory quality. Bigamous matings resulted when no unmated males were available near the former nest sites of returning females. The cost of bigamous matings appeared to be low. Secondary females did not have lower reproductive success or survival than did monogamous females. Mating with already-mated males allowed females to initiate their nests early enough to have second broods.

The correlation of male arrival time with male mating status and female reproductive success is consistent with the idea that the mating choices of female Blackpoll Warblers on Kent Island are influenced by the benefits of early nest initiation. I found the influence of territory quality to be equivocal in female settlement choices. In particular, territories of bigamous and monogamous males differed in the numbers of total large conifers (TLC), but TLC was not correlated with female settling patterns, nor did it explain the variance in reproductive success among monogamous females.

The difference in the number of large conifers between the territories of bigamous males and other males may be an artifact of small sample sizes and differences in male return patterns due to chance alone. Four of the 5 instances of bigamy occurred in the part of the study area with the highest tree density. The low return rates of males in that area resulted in reduced competition among the males. As a result, males claimed territories with large numbers of conifers. If bigamy arose as I have suggested, however, females mated with those males, not because the males' territories had large numbers of conifers, but because the females preferred to nest near where they had nested formerly.

Territory quality may limit the number of females that can breed on a territory. No male had more than two mates. In one case 5 females returned that had bred on adjacent territories in the previous year. Two males returned and established territories that included the territories on which the 5 females had bred. Two bigamous matings resulted that involved 4 females. The fifth female mated monogamously on a territory more than 3 territories away from her former breeding spot. This was the only one of 12 returning females that did not settle near her former breeding spot.

Several factors may have obscured relationships between the quality of the breeding situation and female settling patterns and reproductive success. First, females may have chosen where to settle based on characteristics that I did not measure. Second, pooling among years may have obscured the actual relationship between the number of large conifers on the territory and female settling patterns or reproductive success. Third, the number of young fledged annually may not be a reliable indicator of lifetime reproductive success. There may be differential postfledging or overwinter mortality, or a lack of congruence between seasonal and lifetime reproductive success. Finally, even if females base their choices of where to settle on territory quality, unpredictable nestling mortality factors such as weather may obscure relationships in a small sample.

Site fidelity by males has been recognized as a complicating factor in determining the relationship among male quality, territory quality, and mating status in other species (Searcy 1979, Oring 1982). There have been few studies of the effects of female site fidelity on female mate choices in polygynous species. Although the role of territory quality in mate choice by females in this population remains equivocal, site fidelity was a sufficient explanation for the occurrence of polygyny.

Kent Island may be a favorable place to breed for reasons independent of territory quality. Ricklefs (1969) found that predation was the most important mortality factor of eggs and young for most birds. Predation on eggs and nestlings was very low on Kent Island because there are no mammalian and few avian predators. The minimum number of fledglings produced by any female in a season was 2 ($n = 34$). Ninety-eight percent of clutches ($n = 48$) produced at least one fledgling (Eliason 1986). This compares with 52.5% for 35 altricial passerine species (Nice 1957). A female Blackpoll Warbler breeding on Kent Island has a high probability of producing some young no matter what her mating status.

High nest success may explain the tendency of females to breed near where they formerly bred. Birds that nest successfully have been shown to disperse shorter distances between breeding attempts than those that are unsuccessful (Catchpole 1972, Harvey et al. 1979, Blockstein 1986). If female Blackpoll Warblers use the simple rule of returning to a site where they were successful, then 98% of them should return to their former sites (92% of them did so).

A female Blackpoll Warbler has several options if she returns to her former territory and finds no unmated males nearby. If she pairs with a mated male and initiates her nest immediately, she almost certainly can raise some young, and may be able to have a second brood. Also, a female that maintains her position on a site by becoming a secondary female may have an advantage in competing for breeding opportunities on the site in subsequent years. In fact, two secondary females that returned to the same site the next year became primary females. Primary females had significantly higher annual reproductive success than either secondary or monogamous females (Table 4), received as much male aid as monogamous females, and received significantly more aid than secondary females (Eliason 1986). A female that does not mate with a mated male when no unmated males are present near where she formerly nested faces the possibilities of not mating or not having a second brood. If she decides to leave the island, the same uncertainties exist, plus the likelihood of higher predation rates.

Assuming the sample of birds I studied was typical of the population as a whole, the overall sex ratio once all birds had arrived was slightly biased toward males in years when it deviated from equality (Table 1). Female-biased sex ratios existed early in the season because yearling males returned later than older males. Yearlings return later in a number of species (e.g. Martin 1970, Nolan 1978, Oring and Lank 1982). Oring and Lank (1982) suggested that because yearlings could not compete successfully with more experienced birds for territories, they delayed their arrival until older males were involved in breeding activities and less committed to territory defense. An alternative explanation for the later arrival of yearlings is that yearlings are less successful in competing for resources in wintering areas, take longer to build up reserves for migration, and are not ready to migrate as soon as older birds are (Rohwer and Butler unpubl. ms.).

Site attachment and return patterns can account for the incidence of polygyny in this population, but data are not available to evaluate the role of these factors in determining mating status in other populations of Blackpoll Warblers. The combination of site fidelity and return patterns that led to polygyny in this population probably could not give rise to high levels of polygyny or large harems. Long-term data on breeding locations and mating relationships of marked individuals are needed to determine the influence of site fidelity in other species that exhibit low levels of polygyny.

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DENSITY TRENDS AND RANGE BOUNDARY CONSTRAINTS OF FOREST BIRDS ALONG A LATITUDINAL GRADIENT

JOHN T. EMLEN,[1] MICHAEL J. DEJONG,[1,3] MICHAEL JOHN JAEGER,[1,4]
TIMOTHY C. MOERMOND,[1] KURT A. RUSTERHOLZ,[1,5] AND ROBIN P. WHITE[2]
[1]Department of Zoology and [2]Department of Geography, University of Wisconsin,
Madison, Wisconsin 53706 USA

ABSTRACT.—We plotted the density distributions of 41 land-bird species along a 1,200-km transect spanning 7°28′ (865 km) of latitude through relatively uniform bottomland deciduous forest in middle North America. Standardized counts and observations at 12 survey stations, closely matched in habitat structure and widely distributed along the route, provided population data for all species and indices of total avian foraging pressure (consuming biomass) on each of six major foraging substrates.

Density curves for species fluctuated considerably from station to station but tended to be level across range centers and slope peripherally to north and south boundaries at rates of 3–30% per degree of latitude. Substrate foraging pressures declined northward on the aerial and midfoliage substrates and southward on the low-foliage substrate. Summed community densities showed no significant latitudinal trends.

We used the distinctive distribution patterns of climate (smooth latitudinal gradients), habitat structure (irregular mosaics of vegetation patches), and competition (reciprocally sloping density gradients) to identify and evaluate the role of these three constraints along the transect. Progressive latitudinal trends in species abundance thus were attributed to climatic factors, irregular station-to-station fluctuations to habitat factors, and inversely sloping density trends in paired profiles to competition. On this basis all species apparently responded to both climatic and habitat factors, and about half of the species showed suggestions of competition. In a correlation analysis across the 12 stations, latitude per se most closely matched density distribution in 12 species, one or another of the habitat parameters in 25 species. We proposed that season length (days available for breeding activity) was the principal constraining attribute of latitude at northern range boundaries, day length (hours available for feeding and provisioning young) at southern boundaries.

Boundaries have been essentially stable during the past 50–100 yr in most species, but the northern boundary expanded northward in one species following human-induced habitat enhancement, and temporarily receded southward in another following a winter of severe stress. We attribute this general stability of range boundaries over time to within-population gene flow and the associated peripherally declining mean fitness of phenotypes adapted to central range conditions along radially diverging environmental gradients.

We suggest that two boundary lines should be recognized for each species, an inner functional boundary at the line where birth rates drop below death rates, and an outer empirical boundary at the limit of recorded occurrences. *Received 21 June 1985, accepted 20 April 1986.*

RECENT developments in estimating bird densities (Ralph and Scott 1981) have made it possible to plot species distributions quantitatively on maps showing contours of relative abundance as well as the locations of range boundaries (Bystrak 1981). These developments have also created opportunities to evaluate the effects of habitat structure (primarily vegetation), climate (ambient physical conditions), and competition on population growth and dispersion. Habitat factors, often changing extensively over short distances, have been examined intensively with relation to bird den-

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[3] Present address: Department of Biology, College of St. Thomas, St. Paul, Minnesota 55105 USA.

[4] Present address: Wisconsin Public Service Commission, P.O. Box 7854, Madison, Wisconsin 53707 USA.

[5] Present address: Department of Biology, University of Minnesota-Duluth, Duluth, Minnesota 55804 USA.

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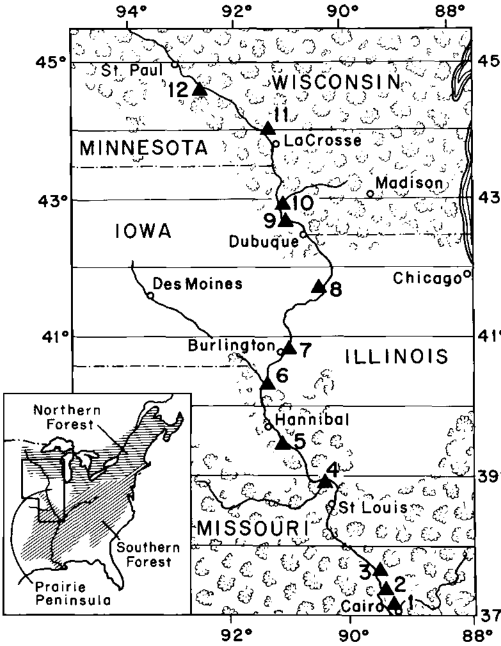

Fig. 1. Location of the 12 survey stations along the Mississippi bottomland transect. Inset shows setting in relation to northern and southern forests and the intervening "prairie peninsula."

sity distributions in many regional community studies. But climatic factors (where conditions change gradually over long distances) and competition (where distributional responses reflect direct or indirect interactions between taxa in the community) present problems that can be approached only on a broad geographic scale.

The direct effects of climate on bird distributions and densities can be separated from the effects of habitat structure by recognizing the distinctive distributional patterns of the two categories: smooth latitudinal (or altitudinal) gradients for climate, patchy mosaics for habitat structure. We attempted to separate climatic and habitat effects empirically by collecting population density data at a series of survey sites selected to minimize habitat variance (stations were similar in vegetation structure) and maximize climatic variance (stations were widely spaced along an extended latitudinal transect). Competition, the third constraint category, could, we suggest, be revealed along the transect by reciprocally sloping density gradients in ecologically similar species pairs.

STUDY AREA AND METHODS

We studied the elm-ash-maple bottomland forest of the central Mississippi River Valley, an area supporting one of the longest north-south stretches of relatively uniform vegetation on the North American continent. We laid out a transect of 12 survey stations between Cairo, Illinois, and St. Paul, Minnesota, a distance of 1,200 km covering 7°28′ (865 km) of latitude (Fig. 1). The southern third of this transect lies in the southern deciduous forest biome of eastern North America, the central third forms a narrow habitat corridor bridging the 9,000-yr-old (Webb 1981) prairie peninsula of the central plains, and the northern third lies in the northern deciduous forest biome.

Although continuously wooded until 150 yr ago, this strip is now fragmented into a series of forest patches. Many of the bird species that occupy these patches as breeding residents appear to have originated in the south, others in the north. Their present distributions presumably reflect varying range expansions along the extended strip between the Gulf of Mexico and Hudson Bay.

The Mississippi River flows southward (Fig. 1) through the middle of a broad and gently sloping basin bounded by steep bluffs. The floodplain averages 2-4 km in width at the northern end of our transect, gradually widens to 5-10 km at midpoint, and spreads to 10-20 km as the bluffs become lower at the southern end. The river itself, varying from 300 to 2,000 m in width, meanders through the floodplain between scattered sloughs and oxbows, interrupted every 15-40 km by long artificial lakes created by navigation dams built in the 1930's.

The climate of the area is midtemperate continental. Mean annual precipitation ranges from 1,000 mm in the south to 700 mm in the north. Actual evapotranspiration (AE) rates, indicators of local primary productivity (Rosenzweig 1968), also decline northward (Table 1). Mean daily temperatures at the northern end of the transect average about 5°C colder in summer and 9°C colder in winter. Stressful summer heat is slightly less frequent in the north than in the south, but stressful winter cold is considerably more frequent in the north. Summer season length, a measure of the period of insect availability, is two months shorter in the north; day length, a measure of hours available for foraging and provisioning young, is 1.2 h longer (Table 1).

The high, closed-canopy, mesic forest of elm, ash, silver maple, and oak that originally covered this floodplain has been cleared extensively for agriculture, industry, and urban development and persists only as a broken chain of forest patches, connected along river and slough banks by narrow strips of willow and cottonwood. Vegetation structure varied only slightly from station to station and showed no significant latitudinal trends in any of our measured dimensions (Table 2). Forest composition and extent

Table 1. Locations of and climatic data for survey stations along the Mississippi bottomland transect.

Survey station		Location		Temperature (1975–1979)						
				Mean daily[a]		No. stress days		Productivity (AE)[b]	Breeding season length[c]	Day length (June)[d]
Station	Nearest city	Lat. (°N)	Long. (°W)	Summer	Winter	Summer (No. >35°)	Winter (No. <−20°)			
1 Cache	Cairo, Illinois	37°07′	89°17′	26.7°	−1.7°	7.0	0	805	237	14.4
2 Jonesboro	Cape Girardeau, Missouri	37°25′	89°22′	25.4°	0°	4.6	1.2		234	14.5
3 Oakwood	Carbondale, Illlinois	37°40′	89°26′	24.2°	−1.3°	2.8	4.0		230	14.5
4 Grafton	St. Louis, Missouri	38°56′	90°25′	25.1°	−1.8°	5.0	2.8	756	219	14.7
5 Ashburn	Hannibal, Missouri	39°30′	91°05′	23.9°	−4.2°	4.0	8.6	713	210	14.8
6 Warsaw	Keokuk, Iowa	40°22′	91°25′	24.3°	−3.6°	2.6	6.8		204	14.9
7 Burlington	Burlington, Iowa	40°51′	91°03′	22.4°	−5.5°	2.2	10.2	716	200	15.0
8 Wapsipinicon	Clinton, Iowa	41°44′	90°20′	22.4°	−6.2°	1.6	14.0		193	15.1
9 Cassville	Dubuque, Iowa	42°44′	91°03′	22.0°	−6.8°	0.6	15.8	656	185	15.1
10 Wyalusing	Prairie du Chien, Wisconsin	43°00′	91°20′	21.7°	−7.6°	3.0	22.2		182	15.2
11 Black River	LaCrosse, Wisconsin	43°59′	91°20′	21.1°	−8.9°	0.6	25.4	640	173	15.4
12 Cannon River	St. Paul, Minnesota	44°35′	92°38′	21.6°	−9.9°	1.4	26.8	621	164	15.6

[a] Mean daily temperature (°C) for June–July (summer) and December–February (winter) at nearest city (U.S. Environ. Data and Info. Serv. 1975–1979). The deviations from a smooth latitudinal gradient are attributed largely to differences in altitude and exposure of the nearest meteorological stations, which are located up to 25 km from the survey station sites.

[b] Actual evapotranspiration rates in millimeters (Thornthwaite Assocs. 1964).

[c] Number of days in which the daytime mean temperature was above 10°C (computed from Smithsonian Meteorol. Tables 1964).

[d] Number of hours between sunrise and sunset during June.

were less uniform because of the patchy and uneven distribution of soil types and human disturbance areas, but again we found no consistent latitudinal trends.

Along its margins the floodplain changes abruptly at the foot of the bordering bluffs to strips or blocks of upland forest dominated by oak. Beyond the bluff tops lie broad expanses of farmland with scattered woodlots on terrain that formerly was covered with hardwood forests in the north and south, and open prairie in the central portion (Fig. 1, inset).

The 43 bird species (15 permanent residents and 28 summer migrants) that we recorded along this transect (Table 3) are midlatitude representatives of a breeding fauna that extends from the Gulf of Mexico at 29°N to Hudson Bay at 57°N (Fig. 2). All of the species are found beyond the 7° span of our transect, but the southern boundaries of 6 northern species and the northern boundaries of 12 southern species fall within this area.

Observations were made at 12 survey stations along the transect in areas with extensive and minimally disturbed natural stands of large trees. To obtain phenologically comparable data we (1) restricted all observations to a 30-day period at the height of the breeding season (June) in a single year (1979), (2) made two 10–12-day traverses of the route, one in early June (odd-numbered stations), the other in late June (even-numbered stations), and (3) traversed the route from south to north both times, roughly keeping pace with the advancing season of ca. 120 km per day. One observer (JE) participated in and coordinated both traverses; three additional observers participated on each traverse, each of them experienced

TABLE 2. Habitat measurements and assessments at the 12 transect stations.

Habitat parameter	Transect station 1	2	3	4	5	6	7	8	9	10	11	12	CV	Slope[a]	r^2
Canopy quality[b]	36	41	32	35	35	35	30	35	39	34	35	37	8.13	N 1.32	0.000
Forest extent[c]	50	30	70	20	40	20	20	50	40	50	60	40	39.70	S 2.03	0.009
Forest profile[d]															
Upper trees (>15 m)	8.0	8.3	6.7	7.1	6.9	6.7	5.4	7.2	8.4	7.6	7.4	7.6	11.29	S 0.20	0.002
Lower trees (7–15 m)	5.8	8.0	6.6	6.7	6.9	7.3	6.8	6.6	6.7	5.6	6.9	7.0	9.22	N 0.39	0.012
Upper shrubs (2–7 m)	4.0	6.3	5.8	6.2	4.7	4.0	5.4	5.2	3.3	3.0	4.9	3.6	23.87	N 4.45	0.326
Lower shrubs (0.8–2 m)	2.6	3.8	4.7	4.8	4.3	2.5	3.9	3.1	1.4	1.1	4.3	1.2	43.51	N 6.84	0.289
Herbs (0.1–0.8 m)	6.2	6.6	6.5	8.3	5.8	7.6	6.6	9.4	4.1	7.0	8.8	8.3	20.67	S 2.13	0.085
Ground cover (<0.1 m)	7.0	9.9	5.8	10.0	9.5	9.9	7.7	9.4	6.6	7.9	8.0	8.3	8.33	N 0.37	0.003
Forest structure															
Mean DBH (cm)	24.3	35.3	23.7	36.3	24.5	32.7	26.6	30.6	25.4	32.1	27.1	23.7	16.27	N 1.03	0.029
Density (trees/ha)	635	417	613	403	650	531	739	514	860	613	714	578	21.62	S 3.01	0.168
Basal area (m^2/ha)	32.6	40.7	27.0	41.5	30.3	44.7	41.0	37.8	43.6	49.5	41.1	26.0	19.45	S 1.55	0.048
Dead trees (no./ha)	56.1	36.5	72.6	49.6	109.1	23.2	71.4	66.2	78.6	142.2	132.2	49.6	49.71	S 6.37	0.196
Saplings (no./100 m^2)	7.9	5.4	13.1	4.6	3.9	3.6	12.5	7.3	4.3	2.5	4.0	4.3	56.70	N 7.10	0.188
Lianas (no./100 m^2)	0.5	1.3	0.5	0.2	0.1	0.7	1.0	1.0	0.1	0.2	0.3	1.8	83.65	S 3.42	0.015

[a] Regression slope in percentage decrease northward (N) or southward (S) per degree of latitude.

[b] A relative evaluation of tree canopy volume derived by summing 3× the canopy cover estimate of large trees (>15 m), and 2× the canopy cover estimate of small trees (7–15 m).

[c] Proportion of a 28-km^2 (3-km radius) area surrounding each station that was forested.

[d] Direct subjective evaluations of vegetative cover in tenths of complete cover for six forest levels from treetop to ground. Values are the means of observations at the 60 bird counting points at each survey station.

field ornithologists familiar with the census procedure and with all species resident in the area.

Census methods.—At each station we selected the four least disturbed and most extensive forest stands and assigned one observer to each. Each observer plotted his own course, following essentially straight segments through the forest, staying at least 100 m from edges, avoiding slashed, grazed, and otherwise disturbed areas, and making counts only where the tree canopy was closed (estimated >70% cover).

Because of the difficulty of following straight courses through the trackless and sometimes difficult understory, we adopted a point-count census method similar to that of Reynolds et al. (1980), in which the observer stopped every 100 m or more along a transect to stand and listen for 7 min. All birds detected by sight or sound (>90% were by sound) were recorded at each point. Fifteen points were sampled by each observer on nonrainy, nonwindy mornings within 3 h of sunrise. We thus collected data at $15 \times 4 = 60$ points at each of the 12 stations.

All diurnal land birds, except raptors and nonforest species passing overhead, were tallied as detected, and the records of each observer totaled for each station. Tallies based on song detections were doubled to give a total population estimate (assuming equal numbers of males and females). Tallies based on call notes and visual detections were not doubled, and juvenile birds (recorded in only a few late June surveys) were omitted. For each species we adjusted the count for changes in total detection frequency between the early and late June traverses on the assumption that such differences reflected seasonal changes in vocal activity and hence conspicuousness rather than changes in actual population density. Counts were higher in the late traverse for some species and in the early traverse for others, and, again assuming that the lower of the two reflected seasonally depressed song activity, we applied the adjustment to the lower of the two values in each case.

We summed the densities for the entire community and for each of six trophic categories (Table 3) after converting the adjusted counts for each species at each station to absolute density estimates. For this conversion we applied species-specific areal denominators derived from field measurements of detection threshold distances (Emlen and DeJong 1981, DeJong and Emlen 1985) (Table 3). Threshold values not available from the Emlen and DeJong studies were estimated by subjective interpolation from values for species with similar vocal and behavioral characteristics.

Foraging observations.—We made foraging observations for all species at all stations as opportunity permitted. For each observed or apparent prey capture we recorded the bird's position in the vegetation, height above the ground, foraging substrate, and foraging method. To minimize sampling bias we recorded no more than five observations on any single bird. Our first objective was to quantify the distribution of foraging activity for each species across the six primary substrates of the forest (air, bark, ground, upper tree foliage, lower tree foliage, and shrub foliage). Our second objective was to estimate the total avian activity and foraging pressure on each substrate (F_s) in terms of summed density and consuming biomass (all species) per unit of forest area [$F_s = \Sigma\, Psi(D_i M_i^{0.74})$, where *Psi* is the proportion of total foraging activity on substrate *s* by species *i*, D_i is the density, and $M_i^{0.74}$ is the mean body mass of the species adjusted for metabolic efficiency related to body size (Lasiewski and Dawson 1967)].

Habitat assessment.—We used two procedures to assess the forest structure and composition at each of the 12 survey stations along the transect: (1) a quick visual appraisal of the forest profile within approximately 30 m of the observer at each of the 60 census points at each station, and (2) a partially randomized sampling of major vegetation parameters at points located by random numbers in 30 successive 100-m intervals through representative portions of the forest.

The profile analyses were made on the census route immediately following each 7-min bird count and before moving to the next census points. We scored cover density from 0 (no cover) to 10 (full cover) at each of six levels in the forest: upper tree canopy (>15 m), lower tree canopy (7–15 m), upper shrub canopy (2–7 m), lower shrub canopy (0.8–2.0 m), herb cover (0.1–0.8 m), and ground cover (<0.1 m).

The partially randomized vegetation sampling was done by two members of the party experienced in habitat measurement. Circular plots of 0.01 ha were located at each of the 30 sampling sites at each station, and within each plot each tree (>10 cm diameter at breast height) was identified and measured (basal area). Saplings and lianas (2.5–10 cm DBH) within each plot also were identified and counted.

RESULTS

Species density pattern and profiles.—Densities decreased northward in all of the 12 southern species at rates between 2.6% and 29.8% per degree of latitude (Fig. 3A). They decreased southward in all 6 northern species at rates between 2.5% and 27.7% per degree of latitude (Fig. 3B). Profiles for the 23 wide-ranging species in which our transect spanned only a middle segment of the total latitudinal range (Fig. 3C) sloped variously from 14.1% south to 13.3% north and averaged essentially level (0.06% south).

Community density patterns.—Significant latitudinal gradients were found in 3 of the 6 foraging substrate categories. Aerial sallying and midfoliage gleaning declined northward at rates

TABLE 3. Bird species recorded along the Mississippi bottomland transect with pertinent distributional, seasonal, foraging, and census data.

Species[a]	Region of origin[b]	No. of subspecies[c]	Seasonal status[d]	Foraging distribution[e]						Detection distance[f]	Body mass[g]
				Gd	Tr	A	Fl	Fm	Fh		
Yellow-billed Cuckoo (*Coccyzus americanus*)[h] Black-billed Cuckoo (*C. erythropthalmus*)[h]		(1)	S						10	190	58
Northern Flicker (*Colaptes auratus*)	?	3	P	4	6					160	133
Red-bellied Woodpecker (*Melanerpes carolinus*)	S	1	P		9			1		130	64
Red-headed Woodpecker (*M. erythrocephalus*)	?	1	P		8	2				130	67
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	N	1	S		9			1		100	50
Hairy Woodpecker (*Picoides villosus*)	?	3	P		10					120	66
Downy Woodpecker (*P. pubescens*)	?	3	P		8			2		110	27
Pileated Woodpecker (*Dryocopus pileatus*)	?	2	P		10					190	314
Eastern Wood-Pewee (*Contopus virens*)	?	1	S			9			1	120	14
Acadian Flycatcher (*Empidonax virescens*)	S	1	S			6		2	2	90	13
Great Crested Flycatcher (*Myiarchus crinitus*)	?	1	S			6			4	130	34
Blue Jay (*Cyanocitta cristata*)	?	2	P	6	2				2	130	87
Black-capped Chickadee (*Parus atricapillus*)	N	1	P		1			9		80	10.8
Carolina Chickadee (*P. carolinensis*)	S	2	P		1			9		80	9.2
Tufted Titmouse (*P. bicolor*)	S	1	P		2			8		150	22
White-breasted Nuthatch (*Sitta carolinensis*)	?	2	P		9			1		110	21
Brown Creeper (*Certhia americana*)	N	1	P		10					80	8.4
Carolina Wren (*Thryothorus ludovicianus*)	S	1	P	2	3		5			150	21
House Wren (*Troglodytes aedon*)	N	1	S	2	3		5			140	11
Blue-gray Gnatcatcher (*Polioptila caerulea*)	S	1	S		1	1		8		70	6.0
Wood Thrush (*Hylocichla mustelina*)	S	1	S	8			1	1		180	47
American Robin (*Turdus migratorius*)	?	2	S	7	1		1		1	150	77
Gray Catbird (*Dumetella carolinensis*)	?	1	S	2	3		5			110	37
White-eyed Vireo (*Vireo griseus*)	S	1	S				10			110	11
Yellow-throated Vireo (*V. flavifrons*)	?	1	S						10	130	19
Warbling Vireo (*V. gilvus*)	?	1	S						10	110	12
Red-eyed Vireo (*V. olivaceus*)	?	1	S						10	130	17
Northern Parula (*Parula americana*)	S	1	S						10	90	9
Cerulean Warbler (*Dendroica caerulea*)	?	1	S						10	90	9
Yellow-throated Warbler (*D. dominica*)	S	1	S		2				8	100	9
American Redstart (*Setophaga ruticilla*)	N	2	S		1	2		5	2	100	8
Prothonotary Warbler (*Protonotaria citrea*)	S	1	S		4		1	3	2	130	17
Kentucky Warbler (*Oporornis formosus*)	S	1	S	4			6			130	14
Common Yellowthroat (*Geothlypis trichas*)	?	2	S	8			2			120	10
Summer Tanager (*Piranga rubra*)	S	1	S						10	140	30
Scarlet Tanager (*P. olivacea*)	N	1	S						10	140	29
Northern Cardinal (*Cardinalis cardinalis*)	S	1	P	7			2	1		180	45
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	N	1	S					8	2	140	46
Indigo Bunting (*Passerina cyanea*)	?	1	S	6			4			140	15
Song Sparrow (*Melospiza melodia*)	N	1	P	5			5			120	21
Brown-headed Cowbird (*Molothrus ater*)	?	1	S	8				1	1	100	39
Northern Oriole (*Icterus galbula*)	?	1	S	1					9	140	34

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[a] Nomenclature follows A.O.U. 1983. Waterbirds, birds of prey, nocturnal birds, and land birds recorded fewer than 5 times in the study are not included in this list.

[b] Presumed derivation of the bottomland corridor populations from southern deciduous forests (S) or northern mixed conifer-hardwood forests (N). A question mark indicates indeterminate origin.

[c] Number of subspecies (A.O.U. 1957) along the extended north-south axis of the Mississippi River Valley between the Gulf of Mexico and Hudson Bay.

of 12.79% and 7.73% per degree of latitude, respectively, while low-foliage gleaning declined southward at rates of 12.4% per degree of latitude (Fig. 4). Thus, total avian foraging pressures on the air and midfoliage substrates were less than half as high at the northern as at the southern end of the transect, while in the low foliage they were twice as high. Whole communities (the sum of all species populations) showed no significant density trends along the transect (Fig. 3C, block 24).

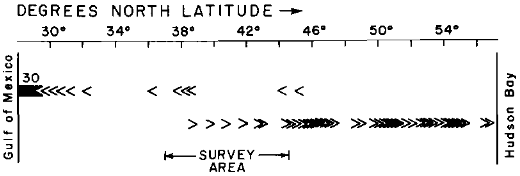

Fig. 2. Distribution of the southern and northern range boundaries of the 41 forest bird species of this study along the 90°W meridian of longitude between the Gulf of Mexico (at left) and Hudson Bay (at right). (Thirty species extend south to within 2° of the Gulf coast.) Data from Peterson (1980).

BOUNDARY CONSTRAINTS

We recognize three primary environmental factors potentially restricting range dispersal along our transect: climate, habitat structure, and interspecies competition. Climate and habitat structure are both direct functions of latitude, but while the relationship of latitude with climate is essentially uncomplicated in our topographically uniform study area, its relationship with habitat structure is strongly complicated by irregular edaphic patterns and human-created mosaics of agriculture and urbanization along the route. On this basis we interpret the underlying directional trends in most of the distributional profiles (Fig. 3) as reflecting climatic factors, and the irregular, station-to-station fluctuations superimposed on the profile slopes as reflecting the complex patterns of habitat distribution along the transect. Competition is not related directly to latitude but may be revealed in reciprocally sloping latitudinal slopes where species ranges overlap.

Climatic factors.—We recognize three climate-related factors as constraints on latitudinal range expansion: temperature, season length, and day length. While range boundaries often coincide neatly with isotherms, little progress has been made in distinguishing whether temperature acts on avian distributions directly or secondarily through its effects on vegetation and resources. Although the close correlation of periodic advances and retreats of northern range boundaries with temperature cycles (e.g. von Haartman 1973, Järvinen and Väisänen 1979) suggests direct temperature responses, the proximal factors in these cases may be food and substrate changes rather than temperature per se.

While the direct effects of temperature are difficult to demonstrate under stable or relatively stable conditions, episodes of climatic extremes, such as floods, storms, and droughts, may decimate local populations of vulnerable species, periodically producing temporary boundary retractions or population extirpations. The Carolina Wren (*Thryothorus ludovicianus*), a nonmigratory terrestrial insectivore, is such a species. Normally an abundant member of southeastern hardwood forest communities as far north as 42° (transect station 8), we never detected this species along our transect in 1979. This scarcity was attributed to a two-week period of extreme cold and deep snow in the winter of 1976–1977 when the species was essentially extirpated from the northern third of its geographic range (Graber and Graber 1979).

Food availability, commonly invoked as the prime determiner of a species' presence and abundance in an area (Lack 1954, Newton 1980),

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←

[d] P = permanent resident, S = summer resident (migrant).

[e] Proportion of foraging activity (in tenths) on six forest substrates: ground, tree trunks, air, low foliage (shrub level), medium-height foliage (subcanopy level), and high foliage (upper canopy). (Data from on-site observations supplemented as necessary by literature.)

[f] Threshold distance (m) for detecting songs of each species as described in text. Used as the radius of detection areas for density calculations.

[g] Body mass in grams (from tabulations of Dunning 1984).

[h] The difficulty of distinguishing these species by call necessitated a pooling of all cuckoo records. Detection distances and body masses here are means for the two species.

depends on the time available for foraging as well as on prey abundance (see Austin 1978, Zammuto et al. 1981). Thus, in species adapted for the long summers of southern latitudes, a northward range expansion may be suppressed by progressive northerly reductions in the number of days in which vegetation, food, and foraging conditions are favorable for breeding and raising young. Similarly, species adapted for the long summer days of northern latitudes may be constrained from southward range expansion by the shorter daylight hours available for foraging and provisioning their young.

The season of favorable conditions for breeding is determined by many factors and cannot be measured definitively. We arbitrarily selected 10°C as a temperature threshold for high insect activity and used the number of days when the mean daily temperature curve for each locality was above threshold level as our indicator of breeding season length. The constraints of season length on northward range expansion are obvious and well documented for subarctic species where the potential season in these terms is less than 50 days (cf. Morton 1976, Järvinen 1980). Constraints are less obvious but potentially considerable in the middle latitudes where differences in season length between southern and northern range boundaries ranged between about 100 and 180 days

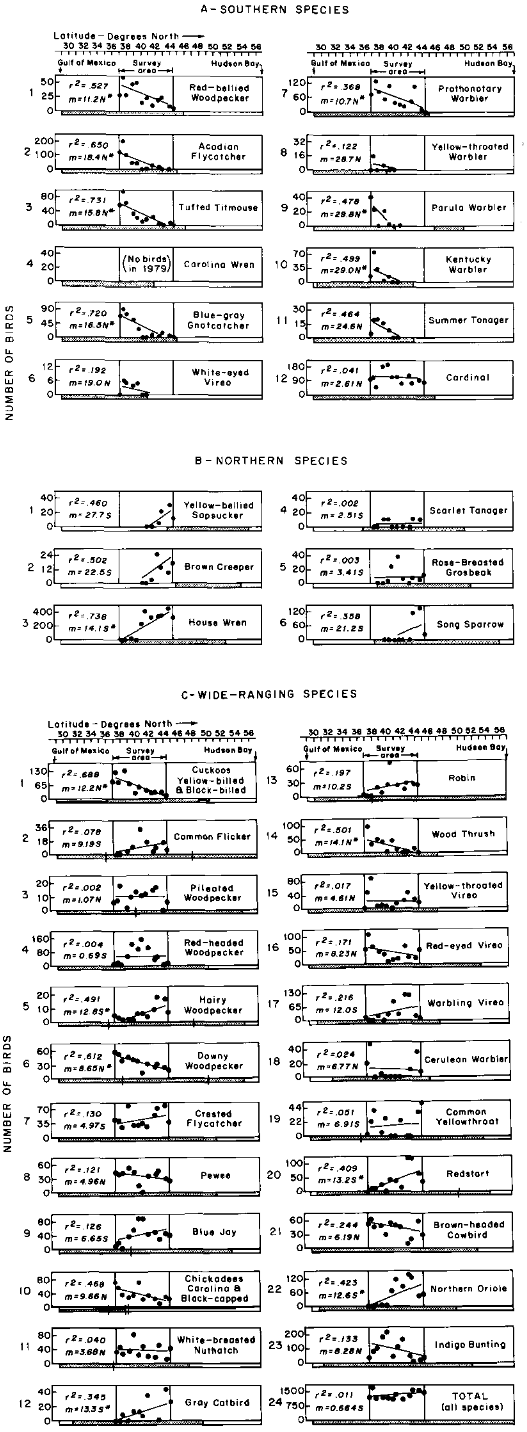

Fig. 3. Abundance profiles for 41 forest bird species along the Mississippi bottomland transect; (A) southern species, (B) northern species, and (C) species with extensive north-south ranges. Shaded bars at the base of each block indicate the extent of the range of each species along a north-south axis between the Gulf of Mexico and Hudson Bay (data from Peterson 1980). Dots and sloping lines in the middle sections indicate the number of birds detected at 60 observation points at each of the 12 stations, and the calculated linear slope of population trends [*m* = percentage decrease per degree of latitude northward (N) or southward (S) within the transect area]. An asterisk indicates significance at the 0.05 level. Short vertical bars along the baseline (e.g. C-2) indicate the boundaries between recognized subspecies; the double bar on graph C-10 indicates a species boundary.

Three species recorded fewer than 10 times are omitted because of small sample sizes. One species, the Carolina Wren, is included although none were recorded (see text). Records for the two cuckoos were combined and the pair treated as a single species because of our inability to consistently distinguish between their vocalizations in the field. Records for the two chickadees are profiled together to show their distributional relationship.

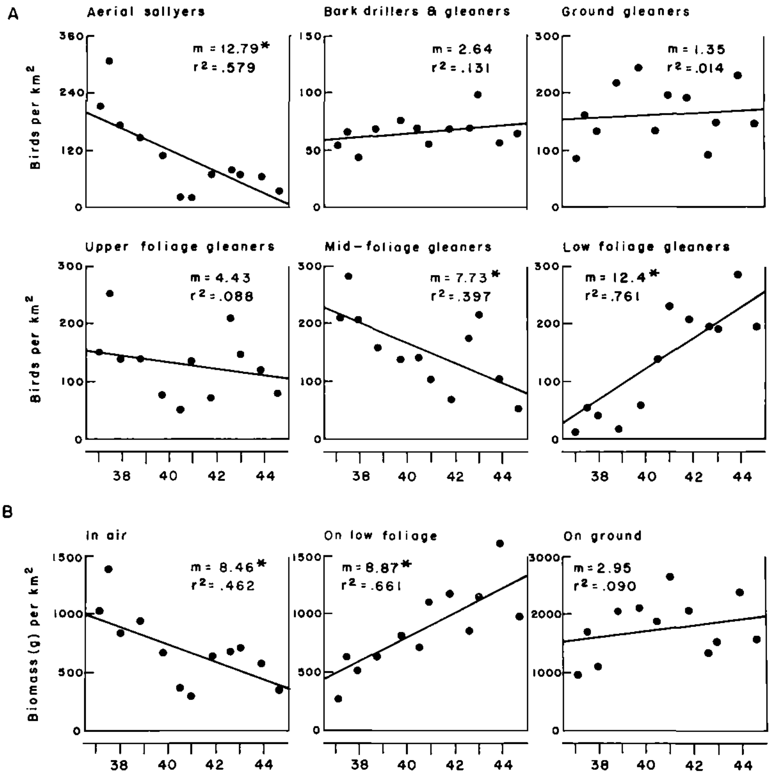

Fig. 4. (A) Latitudinal density trends for 6 trophic categories along the transect, and (B) latitudinal trends of summed foraging pressure (total foraging activity) on the air, low-foliage, and ground substrates. Density and biomass values (ordinate) are reduced to a common areal denominator to permit the grouping of species with different detectability values. Slope values (m) represent percentage decrease northward (to right) or southward (to left) per degree of latitude. Asterisks indicate significance at the 0.05 level.

for the various species (see Fig. 3 baselines for species range boundaries and Table 1, column 8 for season length indicators).

The number of daylight hours available for foraging and provisioning nestlings or fledglings (defined here as the time between sunrise and sunset at summer solstice) decreases southward from about 18 h at Hudson Bay to 14 h at the Gulf of Mexico. We know very little about the effect of available foraging time on reproductive success, but where small variations in reproductive output are critical for the survival of a population, even a slight reduction in parental provisioning time could constitute a barrier to southward range expansion.

Habitat factors.—Although ostensibly minimized in our study, considerable latitude-unrelated density variation was evident in the station-to-station fluctuations in the density profiles (Fig. 3). We attributed many of these fluctuations to variations in vegetation structure and composition associated particularly with patchy soil distribution and human interference.

While habitats and their associated food supplies have changed extensively over the past century, range boundaries apparently have been relatively stable in most species. A conspicuous exception is the Northern Cardinal (*Cardinalis cardinalis*), whose populations have increased and expanded in the past century, particularly in the northern portions of the transect area. This expansion has coincided with a recent increase in winter feeding and ornamental shrub planting around human habitations (Mayfield 1962). Food offered at suburban feeding stations also may have affected population densities in the Tufted Titmouse (*Parus bicolor*) in New England (Kricher 1981). Direct evidence for the role of food abundance in bird

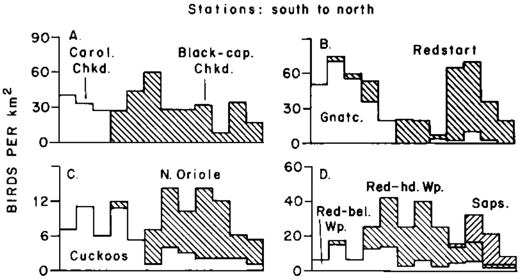

Fig. 5. Density distribution patterns along the latitudinal gradient for selected pairs of phylogenetically or ecologically related species.

abundance and distribution is difficult to obtain except in such unplanned natural experiments.

Evidence for a direct link between population density and nest substrate abundance can be seen in the Prothonotary Warbler (*Protonotaria citrea*), a species closely associated with hollow tree stubs over standing or running water (Bent 1953). Prothonotaries were more numerous where these conditions prevailed at our southern stations, and at station 10 in the north (Fig. 3A, block 7). House Wrens (*Troglodytes aedon*) have increased markedly in southern Illinois with the provision of artificial nest boxes around human habitations, but this numerical increase apparently has not been reflected in a southward range expansion in the species' natural bottomland habitat (R. Graber pers. comm.).

Increases in summed foraging activity northward on the air and midfoliage substrates and southward on low-foliage substrates (Fig. 4) suggest corresponding latitudinal trends in insect prey densities. Time constraints did not allow us to test these possibilities.

Competition.—Prevailing theory predicts that the joint exploitation of a limiting resource by two or more sympatric species will lead to a reduction in the available supply and precipitate either a behavioral or a population adjustment in one or the other population. If there is no behavioral adjustment, a geographic adjustment would be expected, with one of the species disappearing from the zone of overlap. Thus, disjunct ranges in congeneric pairs or broken strings of segregated ranges in congeneric groups have been interpreted as evidence of competition (Terborgh 1971, Diamond 1973). We adopt this rationale, but found no reason to restrict this search procedure to congenerics or to expect complete withdrawal of either competing species from the area of range overlap (Pielou 1975).

Among the 29 species in the Mississippi bottomland bird community for which we have sufficient data on density slopes, 14 faced potential or real competitors as identified by congeneric status or appreciable overlap in food requirements and foraging substrate preferences. Geographic displacement was complete and abrupt in two of these (one pair), partial and graduated in the others. The two segregated species, the Black-capped (*Parus atricapillus*) and Carolina chickadees (*P. carolinensis*) (Figs. 3C, block 10; and 5A), resemble each other closely in morphology, behavior, and ecology. Boundaries overlap slightly in winter, but the two populations withdraw to the appropriate side of the line each spring before the onset of breeding (Tanner 1952, Merritt 1981). A third member of the genus, the Tufted Titmouse, is a considerably larger bird with little ecological overlap with the two chickadees and no evidence of distributional interaction (Fig. 3A, block 3).

The remaining congeneric pairs in the community showed various degrees of overlap. The Downy (*Picoides pubescens*) and Hairy woodpeckers (*P. villosus*) had broadly overlapping distributions with densities sloping reciprocally in the surveyed middle section of their ranges (Fig. 3C, blocks 5 and 6). The two tanagers (genus *Piranga*), apparently very similar in foraging and nesting requirements, overlapped over about half of their respective geographic ranges (Fig. 3A, block 11, and 3B, block 4); the Summer Tanager (*P. rubra*) decreased northward rather steeply to its northern boundary; the Scarlet Tanager's (*P. olivacea*) sample was small and showed no clear density trend. Opposing density slopes in 2 of the 3 arboreal vireos (genus *Vireo*), although not significantly different from zero in this small sample, suggest a possible competitive interaction in their broad area of range overlap (Fig. 3C, blocks 15–17). The midtransect increase of the Warbling Vireo (*V. gilvus*), however, may simply reflect a response of a characteristically open woodland species to subtle habitat variations in the area of the prairie peninsula at stations 6–10. The fourth vireo in the community, the shrub-foraging White-eyed Vireo (*V. griseus*), showed no evidence of geographic interaction with its arboreal congeners (Fig. 3A, block 6). The northward slopes of warblers of the genus *Dendroica* showed no suggestions of geographical displacement; the Cerulean Warbler (*D. caerulea*) (Fig. 3C, block 18) reached its highest densities in the area of overlap with the southern Yellow-throated Warbler (*D. dominica*) (Fig. 3A, block 8).

The most striking examples of reciprocal density trends along our transect occurred between noncongeneric species. Reciprocal trends were predicted in these cases on the basis of strong trophic and ecological similarities in each of the matched pairs. Blue-gray Gnatcatchers (*Polioptila caerulea*) (Sylviidae) decreased in density northward as Redstarts (*Setophaga ruticilla*) (Parulidae) increased (Fig. 5B); both are arboreal insect gleaners of the middle canopy that indulge in considerable aerial sallying (Table 3). Cuckoos (*Coccyzus* spp.) (Cuciliformes) decreased northward as Northern Orioles (*Icterus galbula*) (Passeriformes) increased (Fig. 5C); both are large arboreal insect gleaners of the upper canopy that specialize on hairy lepidopteran larvae, prey items avoided by most birds (Bent 1958). The Yellow-bellied Sapsucker (*Sphyrapicus varius*) occurred only in the northern third of the transect where Red-bellied Woodpeckers (*Melanerpes carolinus*) were scarce (Fig. 5D). These two woodpeckers are similar in size and overlap considerably in their trophic specializations, but belong to remotely related genera. A third species, the Red-headed Woodpecker (*M. erythrocephalus*), which frequents taller trees in more open situations, reached its highest densities in the central stations, suggesting a possible compensatory interaction between these three middle-size woodpeckers. The reason for the steep density attenuation of House Wrens south of latitude 40° (Fig. 3B, block 3) is unclear, but the boundary roughly coincides with the northern range boundary of the normally common Carolina Wren (Fig. 3A, block 4), another insect gleaner of the forest understory. This could reflect a compensatory interaction prior to the abrupt disappearance of Carolina Wrens two years before our survey.

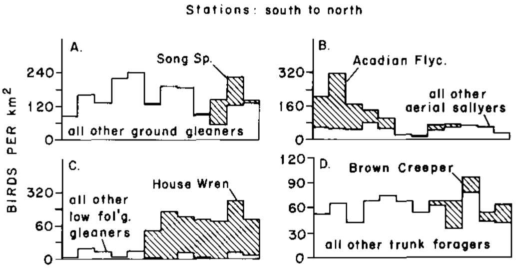

Fig. 6. Density distribution patterns for dominant guild members and their guild associates.

For situations in which more than two species may be competing for a common resource (i.e. diffuse competition), we compared the density distribution of single, abundant species with the summed density of the other (secondary) members of the same trophic guild (Fig. 6). Evidence for the predicted suppression of the secondary species by the numerically dominant species is lacking in two of these tests (Fig. 6B, C) and equivocal in the other two (Fig. 6A, D). In the air sallyers a sharp reduction in the abundant Acadian Flycatcher (*Empidonax virescens*) north of station 5 was not matched with a compensatory increase in the numbers of other flycatchers (Fig. 6B). A similar absence of competitive replacement was seen in the low-foliage gleaners, where the sudden appearance of abundant House Wrens north of station 6 had no apparent suppressive effect on the other low-foliage gleaners (Fig. 6C). The previously noted scarcity of Carolina Wrens in the southern forests in the year of our survey may have contributed to the striking summed density contrast. The pattern of species replacement predicted by competition theory was potentially detectable in the ground-gleaner guild (Fig. 6A) and the bark-gleaner guild (Fig. 6D), but in neither case was it adequate to be considered evidence for competitive displacement.

Relative importance of the constraining factors.—The factors discussed above may combine in various ways to suppress a population along a species' latitudinal range. Certain factors undoubtedly dominate in each species, and we have attempted to identify through correlation analyses the single environmental factor or category that most closely paralleled the density changes of each species across the 12 stations. Latitude, interpreted as operating through season length or day length, was most closely correlated in 12 species; one or another dimension of habitat structure was most closely correlated in 25 (Table 4). Competition, not accessible for this analysis, presumably played a prominent

TABLE 4. Principal environmental constraints on range expansion for Mississippi bottomland birds as indicated by correlations of density patterns with habitat factors (Table 2) and latitude across the survey stations of the transect. A question mark indicates that no environmental factors were significantly correlated.

Species[a]	Principal constraint	r^2
Cuckoos (2 spp.)	Latitude	0.688
Northern Flicker	Sparse tall trees	0.529
Red-bellied Woodpecker	Latitude	0.527
Red-headed Woodpecker	Sparse tall trees	0.492
Yellow-bellied Sapsucker	Many dead trees	0.666
Hairy Woodpecker	Many dead trees	0.494
Downy Woodpecker	Latitude	0.612
Pileated Woodpecker	?	
Eastern Wood-Pewee	Dense tall trees	0.319
Acadian Flycatcher	Latitude	0.650
Great Crested Flycatcher	?	
Blue Jay	Small forest extent	0.420
Chickadees (2 spp.)	Latitude	0.468
Tufted Titmouse	Latitude	0.731
White-breasted Nuthatch	?	
Brown Creeper	Dense tall trees	0.732
Carolina Wren	?	
House Wren	Latitude	0.738
Blue-gray Gnatcatcher	Latitude	0.720
Wood Thrush	Dense low trees	0.656
American Robin	Sparse tall trees	0.486
Gray Catbird	Dense herbs	0.410
White-eyed Vireo	Dense low shrubs	0.519
Yellow-throated Vireo	Large forest extent	0.384
Warbling Vireo	Large basal area	0.475
Red-eyed Vireo	Good canopy quality	0.475
Northern Parula	Dense tall trees	0.590
Cerulean Warbler	?	
Yellow-throated Warbler	Good canopy quality	0.722
American Redstart	Large basal area	0.418
Prothonotary Warbler	Latitude	0.368
Kentucky Warbler	Latitude	0.499
Common Yellowthroat	Small basal area	0.515
Summer Tanager	Dense high shrubs	0.569
Scarlet Tanager	Many dead trees	0.418
Northern Cardinal	Small forest extent	0.446
Rose-breasted Grosbeak	Sparse tall trees	0.527
Indigo Bunting	Dense low shrubs	0.375
Song Sparrow	Many dead trees	0.592
Brown-headed Cowbird	Many high shrubs	0.485
Northern Oriole	Latitude	0.423

[a] For scientific names and other data on species, see Table 2.

role in the 2 species (1 pair) that showed abrupt geographic replacement, and may have featured in 12 others (6 pairs) where densities declined reciprocally over the zones of range overlap.

BOUNDARY DYNAMICS

In our study we concentrated on ecological constraint systems and did not consider why many populations in the peripheral zones of their geographic ranges do not, over evolutionary time, adapt to peripheral constraining factors and expand their ranges until they encounter a physical or steep environmental barrier. To explain this phenomenon we favor the model that visualizes species populations as constrained adaptationally and hence geographically by the neutralizing effects of within-range gene flow on adaptive selection in peripheral zones (Miller 1947, Haldane 1956, Mayr 1970). On this basis we attribute the observed centrifugally declining densities to declining fitness of relatively uniform phenotypes along radially diverging environmental gradients.

Peripherally attenuating densities complicate the problem of designating range boundary lines. Two lines should be recognized for most continental land-bird ranges: a functional boundary beyond which reproduction, on average, falls below mortality, and an empirical boundary enclosing an outer submarginal zone within which the species occurs and may occasionally breed though, on average, unsuccessfully. The boundaries that appear in most current field reference books and distribution maps are empirically determined outer boundaries.

ACKNOWLEDGMENTS

We are grateful to Chandler Robbins and Danny Bystrak of the U.S. Fish and Wildlife Service and to Julie Sloan Denslow of the University of Wisconsin Botany Department for helpful ideas on the organization of this study, to Richard Toltzmann and field officers of the U.S. Fish and Wildlife Service for advice and cooperation in arranging visits to Department of Interior lands, to Mary Landin and personnel of the U.S. Army Corps of Engineers, and to state conservation officers in Illinois, Missouri, Iowa, Wisconsin, and Minnesota for facilitating fieldwork on other federal and state lands along the Mississippi. The Western Illinois University and the Hager Hinge Co. of St. Louis provided much appreciated logistic assistance in the field. David H. Thompson assisted importantly in the field operations. Helpful suggestions for revising early drafts of the manuscript were contributed by J. H. Brown, G. Cox, J. M. Emlen, P. Landres, E. Mayr, J. Terborgh, and several anonymous reviewers.

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REIDENTIFICATION OF "*PHALACROCORAX*" *SUBVOLANS* BRODKORB AS THE EARLIEST RECORD OF ANHINGIDAE

JONATHAN J. BECKER[1]

Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

ABSTRACT.—The putative cormorant *Phalacrocorax subvolans* Brodkorb 1956, from the early Miocene of Florida, is moved from the Phalacrocoracidae to the Anhingidae and should be known as *Anhinga subvolans* (Brodkorb 1956). This species is the earliest known anhinga and demonstrates that the family Anhingidae has been present in North America for at least 18 million years. It has been at least 30 million years since the Anhingidae and the Phalacrocoracidae shared a common ancestor. *Received 18 December 1985, accepted 17 March 1986.*

IN a study of fossil birds from the Hawthorn Formation, Brodkorb (1956) described a new species of cormorant, *Phalacrocorax subvolans*, from the Thomas Farm local fauna, Gilchrist Co., Florida. This species, known only from the holotypical proximal end of a humerus (Brodkorb 1956), "agrees with *Phalacrocorax wetmorei* Brodkorb (1955) in conformation of caput humeri and bicipital crest, but differs as follows: proximal width less; width of shaft less; ligamental furrow [sulcus ligamentosus transversus] shorter and less deep; deltoid crest [crista pectoralis] longer; internal tuberosity [tuberculum ventrale] sharper and capital groove [incisura capitis] correspondingly deeper; bicipital furrow [impressio m. coracobrachialis cranialis] wider." Brodkorb noted that the greater width of the bicipital furrow in *P. subvolans* leaves a larger surface for the attachment of M. coracobrachialis anterior (= M. coracobrachialis cranialis) and suggested that this indicates that *P. subvolans* was a better soarer than living or fossil cormorants. Brodkorb also noted that this condition of the humerus in *P. subvolans* approached that of anhingas, birds that customarily soar for long intervals.

Reexamination of the holotype indicates that *Phalacrocorax subvolans* should be moved to the genus *Anhinga* in the family Anhingidae.

MATERIALS AND METHODS

Fossil specimens included in this study are housed in the Vertebrate Paleontology collections of the Florida State Museum (UF). Comparative material of living species is in the collections of P. Brodkorb; Florida State Museum; National Museum of Natural History, Smithsonian Institution; American Museum of Natural History; University of Michigan; and Royal Ontario Museum. Anatomical terminology follows Baumel et al. (1979). Measurements are described in Table 1.

SYSTEMATICS

Family Anhingidae Ridgway 1887

The proximal ends of humeri of the Anhingidae may be distinguished from those of the Phalacrocoracidae using two characters (Miller 1966). In cormorants the crus dorsale fossae overhangs the fossa pneumotricipitalis (see Fig. 1) and fully covers its proximal end, whereas in anhingas the less extensive fossa is well exposed. The sulcus ligamentosus transversus on the cranial surface is longer, deeper, and extends transversely to, but is narrowly separated from, the impressio M. coracobrachialis cranialis in cormorants; the sulcus is shorter and deep only ventrally in anhingas. In addition, anhingas have a strong sulcus on the cranial face of the humerus paralleling the distal portion of the crista pectoralis. In cormorants this sulcus is absent, causing the crista pectoralis to merge more smoothly with the shaft. Also, anhingas tend to have a proportionally longer crista pectoralis than do cormorants.

Genus *Anhinga* Brisson 1760

Anhinga subvolans (Brodkorb 1956)

Holotype.—UF 4500, proximal half of right humerus. Florida State Museum, Vertebrate Paleontology collection. From the Thomas Farm

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[1] Present address: Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA.

TABLE 1. Measurements of humeri of living and fossil *Anhinga* species. Data are means ± SD and observed ranges. Number of specimens for *A. anhinga* and *A. rufa* = 10, all other *n* = 1. Measurements of the humerus are as follows: W-SHAFT = transverse width of midshaft; D-SHAFT = depth of midshaft; W-PROX = transverse width of proximal end from the external tuberosity (tuberculum dorsale) to the most ventral face of the bicipital crest (crista bicipitalis); D-PROX = depth of proximal end, from the bicipital surface (facies bicipitalis) to the internal tuberosity (tuberculum ventrale), measured at right angles to the long axis of the shaft; D-HEAD = depth of head, measured parallel to the axis of the head; L-DELTOID = length of deltoid crest (crista pectoralis), measured from the external tuberosity to the most distal extension of the deltoid crest.

Measurement	*anhinga*	*rufa*	*novaehollandiae*	*melanogaster*	*grandis*	*subvolans*
W-SHAFT	6.66 ± 0.39	6.81 ± 0.55	7.0	6.4	8.7	7.6
	5.7–7.1	6.2–7.9	—	—	—	—
D-SHAFT	5.76 ± 0.38	6.06 ± 0.54	5.8	6.2	7.7	6.7
	5.1–6.2	5.4–7.1	—	—	—	—
W-PROX	18.02 ± 0.80	19.85 ± 1.11	20.0	18.5	23.1	21.4
	17.2–19.8	18.1–21.6	—	—	—	—
D-PROX	8.62 ± 0.35	9.85 ± 0.54	9.8	8.9	—	9.7
	8.0–9.1	8.8–10.5	—	—	—	—
D-HEAD	6.71 ± 0.25	7.22 ± 0.49	7.7	6.8	8.0	7.4
	6.1–7.1	6.5–7.9	—	—	—	—
L-DELTOID	35.19 ± 1.88	37.86 ± 2.61	40.7	38.5	42.3	37.5
	31.7–37.8	35.0–43.3	—	—	—	—

locality, early Miocene (early Hemingfordian; approximately 18 million years before present), Gilchrist Co., Florida. Collected by R. Bader in the spring of 1955. Webb (1981) reviewed this local fauna. The Thomas Farm locality represents a high-sided sinkhole that was at least partially water filled (A. E. Pratt pers. comm.). The fossil birds of Thomas Farm local fauna were studied by Wetmore (1943, 1958), Brodkorb (1954, 1956, 1963a), Cracraft (1971), Olson and Farrand (1974), and Steadman (1980).

Emended diagnosis.—Referable to the family Anhingidae by the characters listed above. The type of *Anhinga subvolans* differs from the proximal ends of the humeri of all species of *Anhinga* examined (*A. grandis*; UF 25739, Love Bone Bed locality, Alachua Co., Florida; *A. rufa*; *A. melanogaster*; *A. anhinga*) in having a deeper fossa pneumotricipitalis and impressio M. coracobrachialis cranialis, a more prominent crus dorsale fossae, and a better-developed and sharper ridge that extends distally down the shaft from the crus dorsale fossae. The proximal end of the humerus of *A. subvolans* is similar in size to that of *A. rufa* (*A. anhinga* smaller, *A. grandis* larger; Table 1).

DISCUSSION

The two implied generic characters (configuration of caput humeri and bicipital crest) originally used by Brodkorb (1956) are found in both the Anhingidae and the Phalacrocoracidae. Two of the original specific characters of *A. subvolans* (sulcus lig. transversus and length of the crista pectoralis) are actually diagnostic of the family Anhingidae. All other characters in the original description are either size dependent or serve only to distinguish *Anhinga subvolans* from *Phalacrocorax wetmorei.*

Olson (1985) reviewed the fossil history of this family. I can add that *Anhinga grandis* Martin and Mengel (1975) is now known from three additional localities in the late Miocene of Florida (Becker 1985). Ballman (MS) reported a species of *Anhinga* from the Pliocene Sahabi Formation of Libya. It is about the size of *Anhinga grandis* and therefore can be distinguished from *Anhinga subvolans* on the basis of size. There is also a large, indeterminate species of anhinga from the earliest Pliocene (early Hemphillian) Bone Valley Mining District (Becker 1985) and from the early Pleistocene (Irvingtonian) Coleman III locality (Ritchie 1980). Based on only a few ulnae, this species does not appear to be referable either to the living *Anhinga anhinga* or to *Anhinga grandis* (contra Ritchie 1980). Fossils representing the living species, *Anhinga anhinga,* are known from numerous localities in the late Pleistocene (Rancholabrean) of Florida (Brodkorb 1963b).

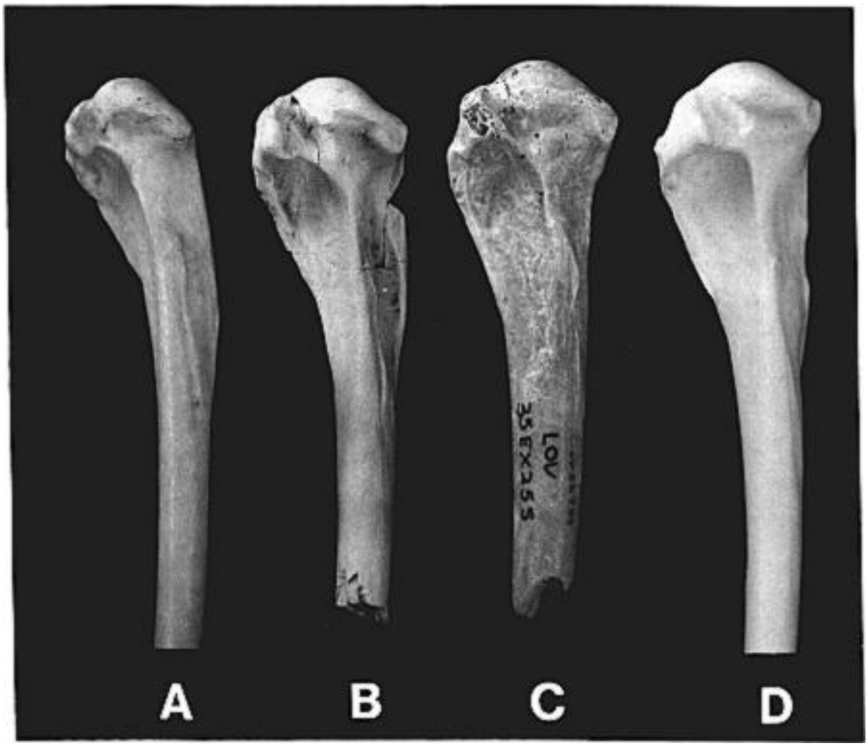

Fig. 1. Caudal view of the proximal end of humeri of anhingas. (A) *Anhinga anhinga,* USNM 500870. (B) *A. subvolans,* UF 4500, holotype. (C) *A. grandis,* UF 25739. (D) *Phalacrocorax auritus,* USNM 500819. All photos are 1×.

Protoplotus beauforti Lambrecht from the middle Eocene of Sumatra is probably not referable to the Anhingidae (Rich in litt., cited in Olson 1985). *Protoplotus beauforti* is smaller and has different limb proportions than any anhinga. Regardless of its familial affinities, little detail can be seen on the humerus of this species (Lambrecht 1931). The humerus is not known in the fossil species *Anhinga pannonica* Lambrecht from the late Miocene of Hungary, *A. hadarensis* Brodkorb and Mourer-Chauviré from the Plio-Pleistocene of Ethiopia and Tanzania, and *A. laticeps* Devis from the Pleistocene of Australia. Considering their geographic and geologic provenances, none of these species is likely to be conspecific with *Anhinga subvolans.*

Olson (1985), citing cranial and tarsometatarsal characters, showed that the New World *Anhinga anhinga* is distinct from the Old World species of *Anhinga* and that all members of this genus should not be viewed as a single superspecies. A number of additional characters support Olson's view. The Old World species share a similar structure of the proventriculus (glandular tissue in two separate patches; proventricular glands collected in a diverticulum in *A. anhinga;* Garrod 1876, 1878; Forbes 1882), pyloric lobe (conical and retractile pyloric plug present; absent in *A. anhinga;* Garrod 1876, 1878; Forbes 1882), structure of temporal fossa (fossae boundaries distinct; indistinct in *A. anhinga;* Beddard 1892), development of the postorbital process (smaller; well developed in *A. anhinga;* Beddard 1892), and structure of the bridge of Dönitz (ossified; not ossified in *A. anhinga;* Garrod 1876; pers. obs., $n = 10+$). Additionally, the sexes are dimorphic in *Anhinga novaehollandiae* and in *A. anhinga* but are similar in *A. rufa* and *A. melanogaster* (Vaurie 1965).

Fossil evidence shows the Anhingidae to be present in the early Miocene and the Phalacrocoracidae to exist in the Eo-Oligocene (Phosphorites du Quercy; Mourer-Chauviré 1982). Therefore, these two groups have not shared a common ancestor for at least 30 million years (see Savage and Russell 1983 for information and references on the age of the Phosphorites du Quercy), and probably much longer.

Some authors (Dorst and Mougin 1979, Cracraft 1985) have reduced the Anhingidae to a subfamily of the Phalacrocoracidae without comment. Anhingas have a feeding behavior and a straight, laterally compressed rostrum with serrated tomia that is unique in the Pelecaniformes. Other studies have shown that cormorants and anhingas differ significantly in their habitat preference, locomotion, ecology, and arrangement of the carotid arteries (Garrod 1876, 1978; Beddard 1892; Owre 1967). Given that anhingas and cormorants have had a long fossil history, that the magnitude of morphological difference between cormorants and anhingas is comparable to that found among other pelecaniform families, and that the ranking of anhingas at the family level is consistent with the taxonomy of the order as a whole, it seems more reasonable to maintain the Anhingidae and the Phalacrocoracidae at their traditional family ranks, as recently suggested by Brodkorb and Mourer-Chauviré (1982) and Olson (1985).

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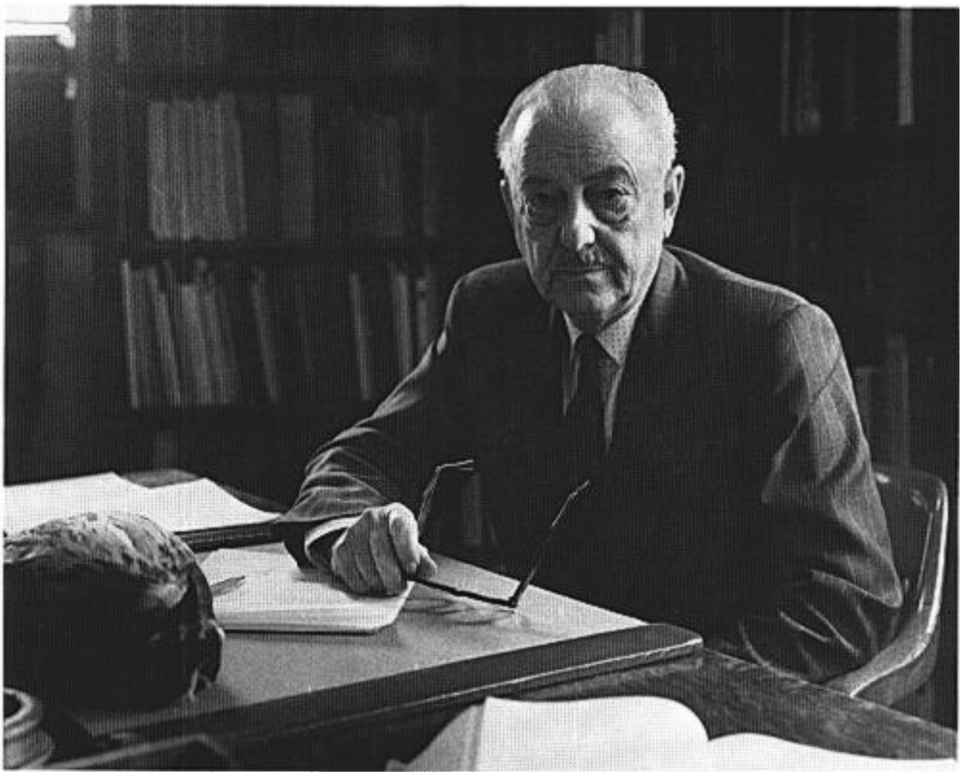

LESTER L. SNYDER, 1894–1968
(From a photograph taken about 1961)

IN MEMORIAM: LESTER L. SNYDER

R. CHARLES LONG AND JON C. BARLOW
Department of Ornithology, Royal Ontario Museum, 100 Queen's Park Crescent,
Toronto, Ontario M5S 2C6, Canada

Lester Lynne Snyder, the youngest child of John Theodore and Dora B. Snyder (née Miller), was born at Panora, Gutherie Co., Iowa, on 11 July 1894. A Life Fellow of the American Ornithologists' Union, Snyder died, age 74, of a stroke on 26 December 1968, in York Co. Hospital, Newmarket, Ontario.

He attended public school in Panora, then spent 3 years (1909–1912) at Gutherie High School. In his senior year Lester transferred to Mason City High School, and lived with his older sister Aimee. In September 1913 he enrolled in a 4-year liberal arts program at the State University of Iowa in Iowa City. He came under the influence of Professor H. R. Dill and enrolled in the University's museum training course. He received training in basic museum techniques, ornithology, general zoology, and entomology. He also completed courses in graphic and plastic arts (from the Fine Arts College), technical English (from the College of Engineering), and harmony (from the School of Music), all of which were to prove useful in his professional work in ornithology.

In September 1917, with sufficient course credits for a B.A., he successfully competed for a position as technologist at the Royal Ontario Museum (ROM) of Zoology in Toronto, Ontario, and thus never officially completed his undergraduate degree. Snyder went to Toronto on 17 September to join the curatorial staff of three other persons in the Zoology Museum. Thus was initiated his career of 46 years at the ROM, first as technologist in gallery work and then as technologist in ornithology. In September 1935 he was appointed curator of birds, serving in that capacity until his retirement on 30 June 1963. Concurrent with his curatorship, he was assistant director (1938–1949) and associate director (1949–1955) of ROM Zoology, one of five curatorial divisions within the Museum complex.

He married Florence Ethyl Steece of Mason City, Iowa, in Toronto on 2 January 1918. Their one son, Richard Lynne, born 18 February 1927, is at present science librarian at Drexel University, Philadelphia.

Snyder's major contributions to ornithology in Ontario and concomitantly in Canada lay in three areas: (1) He initiated a faunal survey of Ontario that was conducted during most summers until 1952. (2) He developed a magnificent ornithological library as well as the research collections of bird specimens (and in part those of mammals) at the ROM. During his tenure the collection increased from 5,000 to approximately 100,000 skins, eggs, and nests. (3) He actively encouraged the study of birds by individuals and groups.

He had special insight concerning the responsibilities of the museum ornithologist for exhibition, teaching, and scientific investigations. He led numerous field expeditions to diverse parts of Ontario, from Point Pelee and Long Point on Lake Erie north to Fort Severn on Hudson Bay. These field ventures produced data and specimens for exhibits, especially habitat groups, and representative samples of bird species such as Ruffed Grouse (*Bonasa umbellus*), Sharp-tailed Grouse (*Tympanuchus phasianellus*), Great Horned Owl (*Bubo virginianus*), and Common Nighthawk (*Chordeiles minor*) for taxonomic and biogeographic studies.

Snyder was responsible for the first dioramas in ROM history, and played the central conceptional as well as an artistic role. Today none of these displays survives in the much altered and expanded museum, but the guiding principles enshrined by Snyder still have currency.

The thousands of research specimens acquired during the surveys provided material for two important books: "Ontario Birds" (1951), chosen as the book of the year by the *Toronto Daily Star*, and "Arctic Birds of Canada" (1957). One substantial disappointment was his inability to complete the 1,000-page typescript account of the distributional and taxonomic aspects of Ontario avifauna. Tentatively titled "Ontario ornithological manual," he began this work in 1956 and continued it in the bird department for two years after retirement.

In addition to faunal surveys in Ontario, Snyder was instrumental in enlarging the Museum's holdings in other ways. Through his encouragement the private collections of J. H. Fleming (32,267 specimens of worldwide origin), J. A. Munro (8,461), and Hoyes Lloyd (4,726) were donated to the ROM. The Fleming material included 80% of the world's species as recognized in 1940 and representatives of all families of birds except Atrichornithidae. The collections of Munro and Lloyd greatly enriched species representation from across Canada and selected parts of the United States.

Snyder published 183 papers, including species lists from his many field surveys, records of unusual birds, taxonomic reviews of bird species, popular papers for naturalists, and 23 about mammals. He chronicled the history of the two recognized song types of the *Empidonax alnorum/traillii* complex, noting the arrival of "*fitzbew*" near Toronto in 1950 with its trenchant differences in nest construction, habitat, plumage, and mensural characters and paving the way for R. C. Stein's subsequent studies.

In founding the Brodie Club in 1921, which continues as the senior natural science organization in Ontario, Snyder noted that the meetings were ". . . for the purpose of studying natural history, and at the same time to have a sociable evening together." He had a hand in establishing the Toronto Field Naturalists (1923) and the Federation of Ontario Naturalists (1931), which he served as a director until 1947.

L. L. Snyder joined the A.O.U. in 1919 but did not attend an annual meeting until 1924. He was elected a Member in 1929, the year he gave his first paper in Philadelphia. Snyder became a part of the Canadian inner circle of the A.O.U., known as the Appleton Club, with Hoyes Lloyd, J. H. Fleming, P. A. Taverner, and W. E. Saunders. Association with these men facilitated his appointment to a number of committees and his election to Council in 1951–1953 and 1959–1961. He served on the local committee for the three Toronto A.O.U. meetings in 1935, 1947, and 1967. He was chairman of the Snowy Owl committee from its inception in 1938, reporting in the *Wilson Bulletin* in 1943, 1947, and 1949 on the periodic southern invasions. In 1947, in recognition of his contributions to Ontario ornithology and his seminal role in the development of the ROM bird collection, he was elected a Fellow.

He was active in the Ontario Research Council's Wildlife Advisory Committee, the committee of 100 of the International Ornithological Congress, and the General Committee of Toronto City Council for the establishment of zoological, botanical, and horticultural facilities in that city.

Snyder retired in 1963. Apart from participation in the local committee for the 1967 A.O.U. meeting, he ceased all formal scientific activity in 1965. Repairing to his rural home near Pottageville, Ontario, he contented himself with his lovely wife and a home-based chickadee study until the end.

EDITOR'S NOTE

R. Charles Long died on 1 April 1986.

IN MEMORIAM: FINN SALOMONSEN, 1909–1983

F. G. COOCH
Migratory Birds Branch, Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0E7, Canada

Finn Salomonsen, Corresponding Fellow of the American Ornithologists' Union, died suddenly on 23 April 1983. He was best known in North America for his contributions to Greenland ornithology. His association with the people and birds of that vast island began when Finn was 16 years old when he accompanied Lehn Schioler to the Upernavik District.

Finn Salomonsen's ornithological interests resulted in over 200 scientific publications, and authorship or co-authorship of 19 books. Besides Greenland and the Arctic, he made expeditions to the Philippines (1951–1952) and to the Bismarck Archipelago, New Guinea (1962).

Finn played an active role in affairs of the International Committee for Bird Preservation, the World Wildlife Fund, and the International Ornithological Congresses. He was an honorary member of half a dozen foreign ornithological societies. He was President of the Danish Ornithological Society for 12 years (1959–1971) and Editor of its journal from 1942 to 1961. He joined the Zoological Museum in Copenhagen in 1943 as an assistant responsible for the bird collections, in 1952 he became curator, and in 1958 chief curator, a position he held until his retirement in 1978.

Finn's greatest contribution may have been as a result of his dedication to the well-being of the people and avifauna of Greenland, his unique banding scheme, and in 1977 the passage of a bird hunting law to help control excessive hunting in a traditional hunting culture.

A more complete statement of Finn Salomonsen appeared in *Ibis* 127: 391–393 (1985). This brief statement does not do justice to the man or his contributions.

IN MEMORIAM: FRANK RICHARDSON, 1913–1985

TONY ANGELL
18237 40th Avenue NE, Seattle, Washington 98155 USA

Twenty years ago, the Curator of Birds in the Burke Museum at the University of Washington welcomed a young graduate student/artist who was eager to study the patterns of color and forms of birds. The fact that the young man had majored in English rather than zoology made no difference, and the needed reference material was quickly made available. A look at the aspiring artist's watercolors was followed by thoughtful comment and bubbling enthusiasm. For the student, an important door had suddenly been opened and a relationship was being forged that would influence his life's work.

I was that student, and Frank Richardson was the Curator of Birds. How often I remember that day and the many to follow as Frank and later his wife Dorothy became my dearest of friends, friends who held deep-felt hope and expectation for a young man making his way in the world. Here were kindred spirits who shared not only in the adventures of scientific inquiry, but in the pleasures of creative expression in the arts.

Over time, I discovered that Frank gave much of his time and counsel not only to students and friends, but to the important environmental affairs of the Pacific Northwest. He was instrumental in forming the Washington Environmental Council and chaired the first wildlife committee. He was a principal force in bringing scientific attention to the significant wintering populations of Bald Eagles on the Skagit River. By persistently speaking in support of a preserve for these birds, Frank induced The Nature Conservancy to begin efforts that later culminated in the Skagit River Bald Eagle Natural Area.

In more recent years, following his retirement from the University, Frank focused his scientific surveys and inventory work on unique habitats and avian populations in northern Puget Sound, and he worked aggressively for the successful preservation of these locations. During the period of his work, more than a half dozen islands in the Puget Sound archipelago were acquired by The Nature Conservancy. Because of these singular efforts, a preserve in these islands is to be established and named in his honor.

Frank earned his doctorate at the University of California at Berkeley and taught at the University of Nevada before coming to Washington in 1955. He was among the first of our contemporary scientists to carefully study segments of the Hawaiian avifauna, with a focus on honeycreepers. Island seabird populations along Washington's outer coast and within the Strait of Juan de Fuca also were given attention in his research. Breeding and foraging strategies described by Frank provided the foundation for a series of research papers.

Frank surely fit the description of the "curious naturalist," as there seemed to be little in the out-of-doors that escaped his interest. He understood the here and now, but looked to the future as well and applied his knowledge vigorously so that we might fashion a better tomorrow. With quiet dignity he gave more than most of his time, wisdom, and energy and inspired those who knew him well.

The Auk 103: 812. October 1986

SHORT COMMUNICATIONS

Dynamics of Nest Parasitism in Wood Ducks

Brad Semel[1] and Paul W. Sherman[2]
[1]*Max McGraw Wildlife Foundation, P.O. Box 194, Dundee, Illinois 60118 USA, and*
[2]*Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853 USA*

Intraspecific brood parasitism is widespread among waterfowl (Weller 1959, Yom-Tov 1980, Andersson 1984). Often referred to as "dump nesting," the phenomenon is particularly prevalent in Wood Ducks (*Aix sponsa*). In this species more than 50% of the nests may be parasitized, and clutches of 20–40 eggs, far exceeding a female's normal 11–15-egg capacity, are commonly observed (e.g. Grice and Rogers 1965, Morse and Wight 1969, Hansen 1971, Clawson et al. 1979). Although it is clear that supernormal clutches are produced by multiple females, the number of individuals contributing to each nest is unknown. We studied a population of Wood Ducks in southeast Missouri during the spring of 1985 to determine (1) the rate of egg deposition, (2) the minimum number of females laying in each clutch, and (3) behaviors associated with nest searching and laying.

The study was conducted on a reservoir ("Pool 1") located in the Duck Creek Wildlife Management Area in Stoddard and Bollinger counties, Missouri. Pool 1 was created in 1954 when a 718-ha tract of lowland hardwood forest was flooded. Today only scattered bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) trees and stumps remain. In 1955, 55 Wood Duck nest boxes were erected on the area. Since then nesting structures have been added and the Wood Duck population has increased (see Hartman 1972, Clawson 1975). By 1985 there were 103 wood or metal nesting structures on Pool 1; these were attached to living trees, snags, or metal poles, 1–3 m above the water, and 0 m (double boxes) to 500 m apart. The wooden boxes were similar in dimensions and construction (see Webster and Uhler 1964).

The nesting activities of female Wood Ducks were observed from 14 March to 5 April, coincident with the peak of clutch initiations at Duck Creek (see Clawson et al. 1979: fig. 1). To determine rates of egg deposition, a sample of 50 wooden nest boxes was chosen randomly and checked daily between 1000 and 1500, after each day's laying activity had ceased. All eggs were marked individually and dated; increases in egg number and egg disappearances were recorded. To minimize disturbance, we stopped checking a box 2 days after incubation commenced. The first day on which warm, down-covered, symmetrically arranged eggs were observed in the nest bowl was considered the onset of incubation. The accuracy of these criteria was verified by subsequent candling of all the eggs in 5 clutches (Weller 1956). A clutch was considered abandoned if it was never incubated; the date of abandonment was defined as the day after the last egg was laid.

Detailed observations of Wood Duck behavior in the vicinity of 12 of the 50 wooden nest boxes were conducted on 19 days, from first light until all birds had departed (ca. 0900). The boxes under observation were erected during the winter of 1985 in an area of Pool 1 that previously had contained a dense concentration of nesting structures (Hartman 1972: 18). Existing boxes were removed and new ones placed in a semicircle, 5–6 m apart and 10–30 m from a blind; the 12 focal boxes and the blind were connected by a catwalk. Traps consisting of a spring-loaded sliding door and an electrically triggered release mechanism were installed in each box (trap specifications are available from the authors). Twenty-six female Wood Ducks were captured and marked with individually numbered nasal saddles and U.S. Fish and Wildlife Service leg bands. Trapping occurred only after a day's observations had ended.

Nest-box checks.—Of the 50 boxes that were examined daily, 25 (50%) were used by Wood Ducks, 2 (4%) contained mixed clutches of Wood Ducks and Hooded Mergansers (*Lophodytes cucullatus*), and 23 (46%) were unused. Detailed chronologies were obtained for 21 of the 25 Wood Duck nests, in which 361 eggs were laid; egg deposition in the other 4 nests was well advanced at the start of our study. Of the 21 clutches whose development we witnessed, 20 increased by ≥ 2 eggs/day at least once, implying a parasitism rate of 95%. Nine of the 21 nests (43%) were abandoned before incubation (including 2 nests in the 12 observation boxes). For the remainder, the mean interval between clutch initiation and incubation was 12.8 ± 1.4 (SD) days.

Within each box, rates of egg deposition were erratic (Fig. 1). Clutches could increase by 7–8 eggs in a single day (Fig. 1b, e), or fail to increase on one or more days (Fig. 1a, b). Most nests (76%) were initiated by one female (i.e. only one egg appeared on the first day of laying in 13 of the 17 nests in which the first egg was recorded), and the heaviest parasitism occurred during the latter half of the laying period (Fig. 1a–f). Eggs were laid parasitically at all stages, however, from clutch initiation (Fig. 1f, h) through incubation (Fig. 1a–g). Most nests had one or two days of peak parasitism when the rate of egg deposition increased 2- to 4-fold (Fig. 1b–f). The variances in the daily rates at which eggs appeared were homogeneous among nests ($\chi^2 = 19.7$, df $= 17$, $P = 0.4$, Bart-

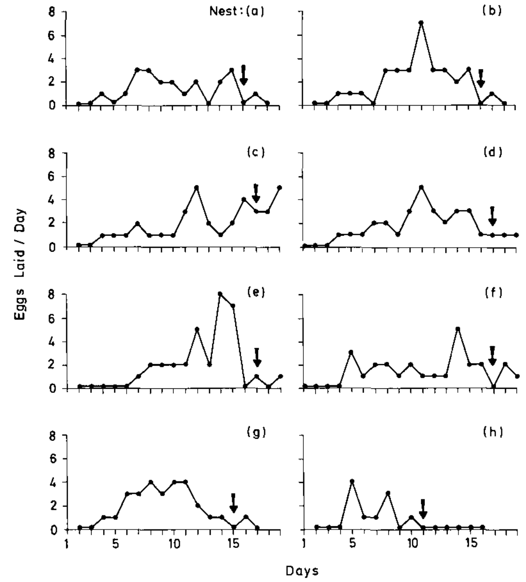

Fig. 1. Daily clutch-size increases (new eggs laid/day) in 8 boxes used by Wood Ducks during the spring of 1985 at Duck Creek, Missouri. The 8 nests depicted are among those with the most complete chronologies, beginning before clutch initiation and continuing to incubation or abandonment. For all panels, day 1 = 16 March; arrows indicate the start of incubation (a–g) or the date of abandonment (h).

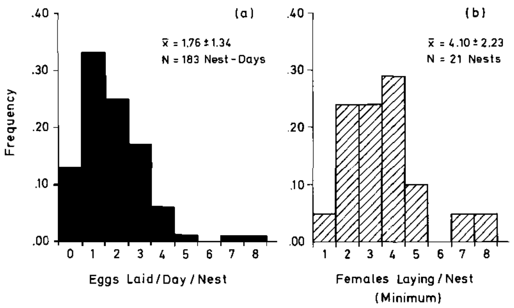

Fig. 2. (a) Rates of egg laying in 21 Wood Duck nests during the spring of 1985 at Duck Creek. Nests were examined daily until 2 days after incubation started or until abandonment (see text); data from all 183 checks of the focal nests are presented. The "0" category indicates a skip: a nest containing eggs and to which eggs subsequently were added failed to increase on a given day (e.g. days 5 and 13 in Fig. 1a). (b) Minimum number of hens that contributed eggs to each of the 21 focal nests, based on the maximum daily egg accumulation in each box (e.g. day 11 in Fig. 1b, or day 12 in Fig. 1c).

lett's test; Sokal and Rohlf 1981: 403), suggesting that irregular egg deposition rates were the norm rather than the exception.

Among the sampled nests, the largest clutch contained 37 eggs and the two smallest contained 1 egg apiece (all three eventually were abandoned). On average, nests increased by 1.76 eggs/day (Fig. 2a), and the number of eggs added per nest each day was random (i.e. the distribution of egg deposition rates did not differ significantly from a Poisson: $\chi^2 = 4.8$, df = 7, $P = 0.5$). Because each female lays no more than 1 egg/day (Leopold 1951, Drobney 1980), the maximum daily egg accumulation in a nest yields a minimum estimate of the number of females that laid in it. In our sample, at least 4 different females typically contributed to each clutch (range: 1–8; Fig. 2b). These estimates, however, are unquestionably conservative. For example, direct observations revealed that a minimum of 6 different females (5 marked, ≥ 1 unmarked) laid in one nest to which no more than 3 new eggs were added on any one day (see Fig. 1a). Furthermore, three times when a closely observed nest increased by only 1 egg/day, the egg was laid by a female other than the one that eventually incubated the clutch (i.e. at least 2 females laid in each of these 3 nests).

Occasionally, eggs disappeared from nests. In 18 of 20 cases (90%) a missing egg was known to have been damaged before its disappearance. Eggs were sometimes cracked by the ducks themselves ($n = 6$), especially on days of peak parasitism when many females entered and exited a box in quick succession. More frequently ($n = 12$), Red-bellied Woodpeckers (*Melanerpes carolinus*) entered unattended boxes, pecked a hole in an egg, and ate some of the contents. We directly observed the fate of damaged eggs five times. In every case a female Wood Duck carried the damaged egg from a box to the water in her bill, broke it open, and quickly ate the contents.

Behavioral observations.—During our unobtrusive observations ($n = 62$ h) we saw how rapid clutch development occurred. Soon after sunrise each day, pairs of Wood Ducks began appearing near boxes. Pairs arrived singly, usually from different directions, and remained apart. If one female entered or left a box, however, a group of pairs quickly coalesced and more females sought to enter that nest. Pairs often flew considerable distances (e.g. 0.5–1.0 km) from vantage points high in trees to boxes where such activity was occurring. Soon the chosen box was surrounded by many birds (e.g. in one case 8 pairs), either on the water or perched on stumps or adjacent boxes.

Groups of paired birds changed frequently in size and composition as females entered and exited the chosen box, then departed the area followed by their mates. Investigations of nest boxes by females typically occurred rapidly, and because many of the birds laid eggs, clutches could develop quickly. For example, 5 different females entered and left one box in 21 min; 4 of them laid eggs. Intense activity around recently occupied boxes contrasted with the birds' relative lack of interest in nearby nests (regardless of whether they contained eggs) and suggests that the mechanism underlying parasitism involves following and observing conspecifics entering or leaving nest sites. Similar observations were made by Heusmann et al. (1980) for Wood Ducks and by Andersson and Eriksson (1982) for Common Goldeneyes (*Bucephala clangula*).

Female Wood Ducks attempted to evade nest parasitism in two ways. First, they behaved surreptitiously in the vicinity of their box and avoided approaching or entering it when conspecifics were nearby. For example, we observed the arrival of marked female Gr-4 to the nest she eventually incubated on 8 mornings (0630–0730). On 4 days no other females were visible to us when she arrived, and Gr-4 entered the box 12.4 ± 5.7 min after we first sighted her. In contrast, on the 4 days when at least one other female was visible to us, Gr-4's latency to enter the box was 68.5 ± 18.4 min ($P < 0.01$, t-test). Second, females attempted to thwart parasitism by aggressively excluding intruders from their nests. On 9 occasions we saw a female try to enter a box when it was occupied; in 7 of these cases, involving 4 different nest "owners," there was a struggle and the intruder was repelled (similar aggressive defense of nests was reported by Clawson et al. 1979).

There was a striking lack of box fidelity among laying females. For example, one marked bird laid 4 eggs in one box (over a 6-day period), then disappeared, and a different female laid 8 eggs and incubated the entire clutch. Another female laid 3 eggs in one box (over 5 days) and 1 in a second box, and two females laid 1 egg in each of two different boxes before disappearing. Twice, females that we saw repulsed by nest owners entered a nearby empty box, laid an egg, and abandoned it. In addition, freshly laid eggs were found on the catwalk ($n = 1$), on top of a box ($n = 1$), and on the shore near boxes ($n = 4$).

Effects of nest boxes on parasitism.—Our data (Figs. 1 and 2) reveal that (1) clutch sizes increased erratically and sometimes explosively, (2) daily egg deposition rates were random among nests, and (3) many different females contributed to each clutch. Although similar phenomena have been described previously in Wood Ducks (e.g. Grice and Rogers 1965, Hartman 1972, Heusmann et al. 1980), this is the first time they have been quantified. Interestingly, nearly every nest we studied (95%) was parasitized despite an abundance (46%) of empty boxes that had been used in previous years (J. Ware unpubl. data). This supports the contention that brood parasitism in *A. sponsa* is not caused solely by a scarcity of suitable nest sites (Morse and Wight 1969, Haramis 1975, Andersson 1984).

Naturally occurring tree cavities in which Wood Ducks nest are typically widely spaced and difficult for humans, and perhaps potentially parasitic females, to locate (Weier 1966, Prince 1968). Although nest parasitism can occur under natural conditions (e.g. Sampson 1901, Bellrose et al. 1964), its frequency is apparently lower and the size of clutches is smaller than in man-made nesting situations. For example, we located clutch-size data in the literature from 28 nests in natural cavities (Bent 1923, Dixon 1924, Prince 1965, Bolen and Cottam 1967). Of these, 71% ($n = 20$) contained ≤16 eggs (range: 7–16), likely laid by one female, while 29% (8) clearly were parasitized (range: 19–31 eggs). In contrast, 76% ($n = 19$) of our 25 occupied nest boxes contained ≥19 eggs, and clutch sizes ranged as high as 37. Furthermore, dump nests containing 45–50 eggs have been observed at Duck Creek (Clawson et al. 1979, L. H. Fredrickson pers. comm.) and elsewhere (e.g. Oregon: Morse and Wight 1969).

We hypothesize that proximity and visibility of nest boxes facilitates the development of supernormal clutches (i.e. dump nesting). The grouping of artificial structures forces Wood Ducks, which normally nest solitarily, into semicoloniality. This causes the surreptitious behavior of females, which probably helps conceal nest-site locations in natural situations (and so reduces parasitism), to become ineffectual. In other words, the placement of boxes at high densities and in obvious places (a standard management practice) makes it difficult for females to visit their nests undetected. If the local population density rises due to successful reproduction and female philopatry (Bellrose et al. 1964, Doty and Kruse 1972), the effect is exacerbated (e.g. Jones and Leopold 1967, Haramis and Thompson 1985), making it nearly impossible for females to hide their nest sites or to repel increasing numbers of potentially parasitic conspecifics.

Female birds that lay eggs in others' nests potentially achieve reproductive success without incurring the physiological costs or the dangers associated with incubation and parental care (Payne 1977, Andersson 1984). However, extreme parasitism rates, explosive increases in clutch size, frequent nest abandonment, and parasitic egg laying at inappropriate times (e.g. during incubation) and places (atop boxes, on the ground, or in the water; see Clawson et al. 1979) together suggest that nesting interference may have reached a pathologically high level in *A. sponsa* at Duck Creek and perhaps elsewhere (e.g. Massachusetts: Heusmann et al. 1980). If so, dump nesting may have become reproductively disadvantageous for females laying parasitically as well as for birds incubating clutches, due to drastically reduced hatchability (e.g. Haramis and Thompson 1985). Under these artificial ecological and social conditions, it is impossible to quantify either the "normal" frequency of brood parasitism or its costs and benefits for individual females (e.g. Emlen and Wrege 1986). Evaluating hypotheses concerning the evolution or adaptive significance of brood parasitism in *A. sponsa* (e.g. the kinship component: Andersson 1984), as well as the implications of dump nesting for Wood Duck population biology and its management, will require detailed comparisons under more natural nesting situations.

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Songbird Carcasses Disappear Rapidly from Agricultural Fields

RICHARD BALCOMB[1]
Office of Pesticide Programs (TS-769), U.S. Environmental Protection Agency,
Washington, D.C. 20460 USA

In field studies of the effects of pesticides on birds, attempts often are made to estimate mortality by searching pesticide-treated areas for dead or moribund animals (Finley 1965, Mills 1973, Flickinger et al. 1980, Bunyan et al. 1981, DeWeese et al. 1983, Overgaard et al. 1983, Balcomb et al. 1984). Similar procedures have been used to study mortality resulting from collisions with motor vehicles and flight obstructions such as television towers (Avery et al. 1980). Body-count estimates of mortality may be biased by scavenging, failure to find carcasses, movement of affected animals outside of study areas, and other factors.

Field researchers cannot continually monitor their study sites. Birds rarely will be found at the onset of paralysis or death after exposure to pesticides. Instead, time is likely to elapse between the death or immobilization of birds and a search. Meanwhile, predators and scavengers can be expected to find and remove a portion of the available prey. I report an attempt to measure the rate of loss of small dead birds from agricultural fields by monitoring carcasses placed to simulate mortality after pesticide application.

I conducted fieldwork in two successive spring plantings (April and May 1981-1982) at the Agricultural Research Center (U.S. Department of Agriculture) in Beltsville, Maryland. This site is a restricted-access preserve that consists of 1,074 ha of agricultural fields and other undeveloped open areas, 340 ha of forest, 499 ha of woodlots (wooded areas ≤40 ha), 2 ponds with a total surface area of 23 ha, and 199 ha in buildings and grounds (V. Miller pers. comm.).

Seventy-eight intact carcasses were placed in corn fields 0-7 days after planting (Table 1). Field surfaces varied in amounts of corn stubble and scattered weeds but were generally clear, and birds were never directly concealed by vegetation or field litter. Twenty-eight birds were monitored in 3 trials in 1981, and 50 birds in 4 trials in 1982. Birds were banded for identification, and the distal wing tips and tail feathers were squared off with scissors to provide a means for identifying feather remains for birds that were eaten. All birds were placed between 0530 and 0630 EST and were revisited at 24-h intervals until carcasses disappeared or for at least 5 days. In trials 6 and 7 in 1982, sites were visited twice during the first 24 h after placement (sunset and sunrise) to determine diurnal and nocturnal disappearance rates.

I used 23 roughly rectangular corn fields (1.7-13.2 ha) as placement sites. Some fields were used twice each year. One to 3 birds were placed randomly in each field, and their locations were marked with small (15 cm) metal stakes and noted on the field map. Carcass density (birds/ha) in corn fields was 0.27 (SD = 0.14) in 1981 and 0.23 (SD = 0.13) in 1982.

Fresh predator or scavenger butcher sites of small birds, mainly passerines, consisting of various amounts of feathers and body parts, are found frequently in some newly planted and insecticide-treated corn fields (Balcomb 1983, Balcomb et al. 1984).

TABLE 1. Description of field trials.

Year	Trial no.	Start date	No. of fields	Mean field size[a] (SD)	No. of birds	Species (no. of birds)
1981	1	26 April	4	7.1 (2.0)	8	*Melospiza melodia* (3)[b] *Passer domesticus* (5)[b]
	2	28 April	4	5.6 (1.6)	8	*P. domesticus*[b]
	3	5 May	9	6.2 (2.7)	12	*Agelaius phoeniceus*[c]
1982	4	14 April	9	6.7 (3.0)	12	*A. phoeniceus*[d]
	5	25 April	9	6.5 (2.6)	13	*A. phoeniceus*[d]
	6	12 May	10	6.8 (2.5)	13	*A. phoeniceus* (7)[d] *Quiscalus quiscula* (6)[b]
	7	25 May	10	6.8 (4.0)	12	*A. phoeniceus* (4)[d] *Q. quiscula* (8)[b]

[a] Hectares.
[b] Males and females.
[c] Females only.
[d] Males only.

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[1] Present address: Environmental Investigations Staff, Agricultural Division, CIBA-GEIGY Corporation, P.O. Box 18300, Greensboro, North Carolina 27419 USA.

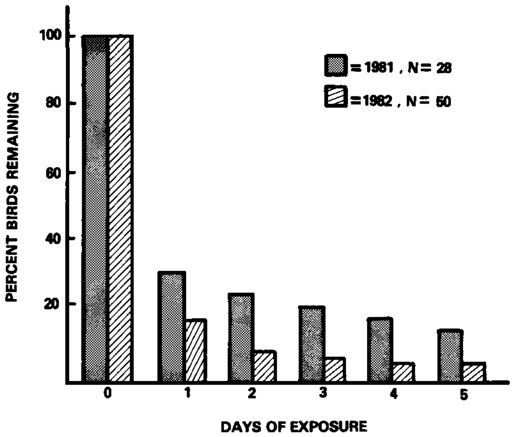

Fig. 1. Disappearance of songbird carcasses from Maryland corn fields, April and May 1981–1982.

Bird remains found in this study were characterized after carcass removal (or after 5 days exposure) as (1) removed with no apparent trace, (2) less than 10 feathers remaining, (3) 10 or more feathers remaining or fewer than 10 feathers plus body tissue or limbs, or (4) slightly eaten or intact. Category 3 was established to identify sites that might suggest to an observer that a mortality had occurred. I was particularly interested in the proportion of carcasses removed with no trace, as this would be a major source of error in estimates of the extent of bird mortality that are based on field-found carcasses and butcher sites.

The time to carcass disappearance may be viewed as a survival period. Survival times, therefore, were analyzed as survival curves using the BMDP-77 Life Table computer program (Brown 1977). This program tests the equality of survival distributions for experimental groups (Mantel 1966, Breslow 1970). The tests are analogues of nonparametric rank tests (Brown 1977). Differences in carcass survival were tested between trials within years and between years (with trials within years pooled). In addition, the program

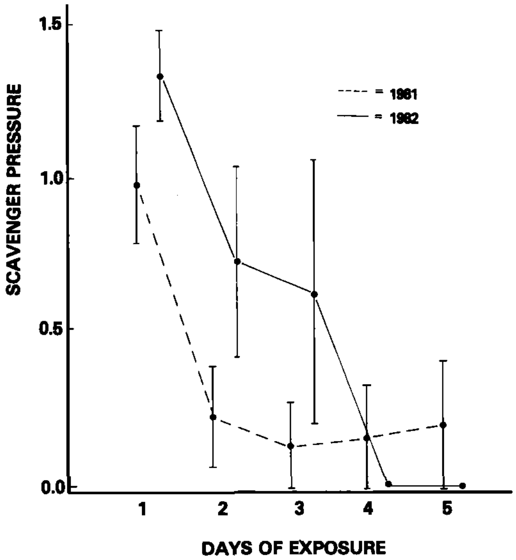

Fig. 2. Scavenger pressure (SP) over a 5-day exposure period. SP values (λ_i) are shown with their standard errors and are based on pooled results of 1981 (n = 28) and 1982 (n = 50).

TABLE 2. Results of carcass disappearance trials. Trials 1–3 were run in 1981 and 4–7 in 1982.

Trial no.	No. of carcasses monitored	No. remaining at daily checks after placement				
		Day 1	Day 2	Day 3	Day 4	Day 5
1	8	3 (37.5%)	2 (25%)	2	1 (12.5%)	0
2	8	3 (37.5%)	3	2 (25%)	2	2
3	12	3 (25%)	0	0	0	0
4	12	3 (25%)	2 (16.7%)	2	2	2
5	13	1 (7.7%)	1	0	0	0
6	13	4 (30.8%)	2 (15.4%)	2	1 (7.7%)	1
7	12	1 (8.3%)	1	1	1	1
Total	78	18 (23.1%)	11 (14.1%)	9 (11.5%)	7 (9.0%)	6 (7.7%)

TABLE 3. Results of BMDP (Brown 1977) statistical comparisons of carcass survival curves within and between years.

Comparison	Breslow test	df	P	Mantel test	df	P
1981 (between trials, $n = 3$)	0.42	2	0.81	0.72	2	0.70
1982 (between trials, $n = 4$)	3.06	3	0.38	1.76	3	0.62
1981 vs. 1982	2.66	1	0.10	3.76	1	0.05

calculates a hazard function "also called the failure rate, instantaneous death rate or force of mortality" (Brown 1977). In the context of this study, this function is the instantaneous carcass removal rate or scavenger pressure (SP). I used the SP function to analyze the uniformity of carcass loss rates over the 5-day monitoring periods. This function is calculated at the midpoint of each interval (i.e. day in my analysis) of the life table by the formula:

$$\lambda_i = 2q_i/h_i(1 + p_i),$$

with an approximate standard error of

$$\mathrm{SE}\,(\lambda_i) \simeq \lambda_i[1 - (h_i\lambda_i/2)^2/r_iq_i]^{1/2},$$

where q_i (the number removed divided by the number exposed in each interval) is the probability of a carcass disappearing in the ith interval, p_i is the probability of surviving the ith interval (calculated as $1 - q_i$), h_i is the width of the time interval, and r_i is the number of birds exposed during the interval (also see Gross and Clark 1975).

The initial disappearance of songbird carcasses was rapid (Fig. 1). In the 7 trials, losses 24 h after placement ranged from 62 to 92%; the mean loss at 24 h was 75% (SD = 12.4) (Table 2). In trial 3, all birds were gone 48 h after placement, and in trial 5 all birds had disappeared by 72 h. Overall, by the end of the 5-day monitoring period, 72 of 78 carcasses (92.3%) had been removed by scavengers. Mean survival time was 1.6 (SD = 1.9) days in 1981 and 0.9 (SD = 1.1) days in 1982.

The rate of carcass disappearance, as indicated by the scavenger-pressure function, was not uniform during the 5-day exposure period (Fig. 2). Carcass losses were markedly greater during the first 24-h period (1981: SP = 1.03; 1982: SP = 1.39) than on subsequent days (Fig. 2).

In trials 6 and 7 birds were monitored just before sunset and just after sunrise during the first day of exposure to determine differences in diurnal and nocturnal losses. In trial 6, 38% (5/13) of the birds were gone at sunset and 4 of the remaining 8 (50%) had disappeared by sunrise. For trial 7, 67% (8/12) were gone at sunset with 3 of the 4 (75%) remaining missing at sunrise. In pooled trials 6 and 7, 52% (13/25) had disappeared by sunset and 58% (7/12) of those remaining were gone at sunrise; this difference was not statistically significant ($\chi^2 = 1.00$, df = 1, $0.3 < P < 0.4$). These data suggest that diurnal and nocturnal scavenging at the study site was of similar intensity. Scavenger pressures (±SE) calculated for day and night removal likewise did not indicate significant differences (trial 6: SP day = 1.0 ± 0.31, SP night = 0.67 ± 0.31; trial 7: SP day = 1.0 ± 0.31, SP night = 1.2 ± 0.55; trials 6 and 7 pooled: SP day = 0.70 ± 0.18, SP night = 0.82 ± 0.28).

Evaluation of all residual evidence indicated that the majority of birds were scavenged without leaving readily observable remains. Over the 7 trials, a mean of 58.2% (SD = 20.6) were removed without a trace, 27.3% (SD = 20.7) showed remains of 10 feathers or more, and 8.2% (SD = 9.6) were untouched or were only slightly eaten. Most (15/21) of those carcass sites categorized as having more than 10 feathers (or <10 feathers plus body parts) consisted of extensive "feather piles" that indicated clear scavenger or predator activity. Searches following carcass disappearance showed that feathers and other body parts were always found within approximately 5 m of the original placement sites; in no instance were there indications that carcasses were moved to other locations in the fields. Rather, they appeared to be removed entirely from the general field area when they were not consumed at the placement site.

Carcass loss rates (scavenging pressure; Fig. 2) were greatest during the first 24 h of exposure, and most birds disappeared during this interval (Table 2). This pattern might occur if scavengers maintained regular hunting territories or search routes that covered most of the field areas studied. Carcasses located outside of predator/scavenger territories probably disappear at slower rates than those within.

I found that carcass survival was not different between successive trials within years, suggesting that scavenger pressure was relatively uniform during the spring monitoring period (Table 3). The rates of disappearance were different between years. The larger size and greater color contrast (with soil colors) of the birds used in 1982 (Table 1) may have made them more conspicuous. This would account for their more rapid disappearance, but these factors were not compared simultaneously in the trials and, hence, the hypothesis cannot be tested. Alternatively, there may have been more scavengers present in 1982.

Clearly, songbird carcasses may disappear rapidly from agricultural fields at the time of spring planting. Other studies have reported both faster (Crawford 1971) and much slower (Fowle 1965) removal rates in other habitats than I found in corn fields. Quantitative studies of avian mortality that depend on recovery of dead birds should monitor scavenger activity. Searches should follow immediately mortality events if a large proportion of the affected birds are to be detected.

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Changes in Plasma Prolactin Associated With Laying and Hatch in the Spotted Sandpiper

LEWIS W. ORING,[1] ALBERT J. FIVIZZANI,[1] AND MOHAMED E. EL HALAWANI[2]
[1]*Department of Biology, University of North Dakota, Grand Forks, North Dakota 58202 USA, and*
[2]*Department of Animal Science, University of Minnesota, St. Paul, Minnesota 55118 USA*

Among captive galliform and anseriform birds, plasma prolactin (Prl) levels tend to rise during laying, peak during incubation, and decline rapidly at hatch (Etches et al. 1979, Burke and Dennison 1980, Bedrak et al. 1981, Dittami 1981, Lea et al. 1981, Proudman and Opel 1981, Goldsmith 1982, Hall and Goldsmith 1983, Wentworth et al. 1983). While the role of Prl as a regulator of avian incubation has been discussed widely, it is not clear whether Prl induces incubation, incubation behavior causes a rise in Prl, both, or neither (reviewed in Goldsmith 1983). In Spotted Sandpipers (*Actitis macularia*), where incubation is biparental but males perform the greater share, Prl levels increase significantly in both sexes

TABLE 1. Plasma prolactin levels (ng/ml) in male Spotted Sandpipers ($\bar{x}$ ± SE).

Prelaying	1-egg	2-egg	3-egg	Midincubation	2-3 days post-hatch
87.8 ±9.3 (n = 8)	149.4 ±16.6 (n = 4)	130.2 ±13.0 (n = 4)	178.0 ±14.5 (n = 3)	182.5 ±11.3 (n = 14)	156.5 ±15.6 (n = 9)

during incubation, but the rise is larger in males (Oring et al. 1986). Our earlier analyses, however, lacked information on Prl levels at two critical life history stages: egg laying and post-hatch.

Spotted Sandpipers were studied at Leech Lake, Minnesota (47°07′N, 94°22′W). All birds were marked individually, and the precise breeding history of each was known. For details relative to the population, see Maxson and Oring (1980), Oring and Lank (1982, in press), and Oring et al. (1983). All birds were captured in mist nets and handled for a maximum of 10 min. Previously, we established that differences in Prl levels between individuals were not due to daily variation or to time of year independent of breeding cycle stage (Oring et al. 1986, unpubl. data). The limited number of birds in this study made assessment of the rhythmicity of hormone secretion impossible; hence, samples were taken between 0600 and 1000 whenever possible. Blood sampling procedures were as reported in Oring et al. (1986). Analyses were performed with the homologous turkey assay described by Burke and Papkoff (1980) and Burke and Dennison (1980), as validated for use with Spotted Sandpipers through comparison of serum dilution curves and molecular size (Oring et al. 1986).

In 1985, we obtained samples from males at the following stages: prelaying, 1-egg, 2-egg, 3-egg, midincubation (days 8-14 of 21-day incubation period), and 2-3 days post-hatch. There was a significant increase in plasma Prl from prelaying to the 1-egg stage ($P < 0.05$, Duncan's multiple range test). No further significant increases in Prl levels occurred; Prl remained high at least through the third day post-hatch. These data differ from the typical pattern of Prl levels in precocial birds in two ways: (1) Prl rose sharply with the laying of the first egg, 2 days before a high incubation constancy, and (2) Prl did not drop sharply at hatch.

Spotted Sandpiper males incubate sporadically after the laying of the first egg. The total incubation effort in any portion of the day involves less than 5% of the time. Once the third egg is laid, however, incubation constancy is high—63-86% at various times during daylight, and 100% at night (Maxson and Oring 1980). Here we have shown that Prl levels rise significantly an average of 2 days before full incubation. Previously, we showed that plasma Prl levels in males, but not females, continued to rise slightly, but significantly, from week 1 to week 3 of incubation (Oring et al. 1986). Thus, in Spotted Sandpipers, Prl may induce incubation, but incubation may result in further increases in Prl. These results suggest experiments in which eggs are added to fresh 1-egg nests to determine whether Prl must, in fact, prime birds for the normal incubation response to be expressed, or, alternatively, whether incubation is initiated solely through perception of 3 eggs.

Prl levels drop precipitously shortly before or within 2 days of hatch in turkeys (*Meleagris gallopavo;* Wentworth et al. 1983), Mallards (*Anas platyrhynchos;* Goldsmith and Williams 1980), and Black Swans (*Cygnus atratus;* Goldsmith 1982). This hatch-related decline in Prl may be characteristic of most precocial birds (Goldsmith 1983). By contrast, in Spotted Sandpipers, Prl remained high through at least 3 days post-hatch (Table 1). Because in central Minnesota Spotted Sandpiper males brood 1-3-day-old chicks an average of 36% of the time from 0500 to 2100, and nearly 100% of the time from 2100 to 0500, the high post-hatch levels of plasma Prl may be associated with brooding, as is the case in altricial birds. The percentage of time male Spotted Sandpipers spend brooding drops steadily from hatch to 10 days post-hatch, but we have no data on post-hatch Prl levels beyond 3 days. Alternatively, the continued high Prl levels witnessed in Spotted Sandpipers may be due to phylogenetic factors. As with the incubation period, our post-hatch data suggest the need for experiments aimed at teasing apart cause and effect in behavioral-physiological interactions underlying parental behavior.

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Composition and Quantity of Feather Sheaths Produced by White-crowned Sparrows During the Postnuptial Molt

Mary E. Murphy and James R. King

Department of Zoology, Washington State University, Pullman, Washington 99164-4220 USA

Measures of nitrogen balance and sulfur balance in molting White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) revealed that the new plumage mass accounted for only about 50% of the nitrogen, and only about 80% of the sulfur, retained above the maintenance level during the molt (Murphy and King 1984a, b; corrected to a regenerated plumage mass of 2.1 g). These discrepancies result from undetected sites of nitrogen and sulfur deposition during molt or from nonquantified losses from the body. Included among the potential routes of deposition and undetected loss of nitrogen and sulfur are the sheaths that temporarily encase the growing feathers (Murphy and King 1984a). A sheath is a keratinized epithelial tube (Lucas and Jamroz 1961) that protects the pulp and growing feather from desiccation. It may help initially to retain the feather in its follicle, and function in the elongation of feather barbs (Lillie 1940). Sheaths are ephemeral. They rupture when the growing feather reaches about 20% of its final length, and soon thereafter begin to disintegrate from the tip into small flakes. Probably because they are short-lived and difficult to collect, sheaths have been essentially disregarded in analyses of the nutritional requirements of molt. To help remedy this lapse, we analyzed sheath chemical composition and attempted to estimate the mass of sheaths produced during the complete postnuptial molt of White-crowned Sparrows.

We captured White-crowned Sparrows during their spring migration through eastern Washington and kept them in an outdoor aviary where chick-starter mash and fresh water were freely available. During the postnuptial (late summer) molt, we plucked samples of growing feathers from the alar (primaries, secondaries, greater coverts), caudal (rectrices), and

TABLE 1. Feather masses, sheath masses, and derivation of factors to estimate the mass of intact sheaths (mean ± SD).

	Feather type			
Quantity	Primaries	Secondaries	Greater wing coverts	Spinal tract contours
Sheath mass (mg/feather)	1.60 ± 0.22 (*n* = 75)	0.94 ± 0.22 (*n* = 94)	0.34 ± 0.03 (*n* = 9 × 20)	0.14 ± 0.01 (*n* = 9 × 100)
Feather mass (mg/feather)	10.56 ± 1.69 (*n* = 5 × 9)	6.96 ± 0.85 (*n* = 5 × 7)	1.77 ± 0.16 (*n* = 5 × 10)	1.09 ± 0.06 (*n* = 5 × 10)
Uncorrected sheath/feather	0.151	0.135	0.192	0.128
Intact sheath length[a] (mm)	18.7 ± 1.02 (*n* = 30)	19.25 ± 1.81 (*n* = 94)	nd[b] —	nd —
Separated sheath length (mm)	15.0 ± 2.15 (*n* = 75)	12.98 ± 2.42 (*n* = 94)	nd —	nd —
Correction factor[c]	1.25	1.48	1.36[d]	1.36[d]
Corrected mass, sheath/feather	0.189	0.200	0.261	0.175

[a] Including an estimated 1 mm lost during natural rupturing of the sheath.

[b] Not determined.

[c] Intact length/separated length.

[d] Average of remigial factors.

spinal tracts. The length of the feather and its intact sheath were recorded in the case of flight feathers, and the length of the separated sheath was measured later. An "intact" sheath is one that is still encasing its feather, although it may be ruptured at the tip, and a "separated" sheath is one that has been dissected from the feather and washed. We separated the pulp and growing feather from the sheath by first tugging exposed parts of the feather vane out of the sheath. Then we inserted a hypodermic needle of appropriate gauge into the emptied sheath and cut it lengthwise with the sharpened edge of a second needle. We could then open the sheath and scrape its inner surface clean. Sheaths were washed (Harrap and Woods 1964), air-dried, and weighed individually to the nearest 0.05 mg. We likewise weighed mature remiges (primaries and secondaries), spinal contour feathers, and greater wing coverts collected from recently molted White-crowned Sparrows. Coverts and spinal contours were weighed in batches of 10 of each, and the separated sheaths were weighed in batches of 20 and 100, respectively. Later, we analyzed samples of finely cut sheaths for nitrogen content (micro-Kjeldahl method according to Horwitz 1980) and amino-acid composition (Beckman model 121 MB, Bioanalytical Laboratory, Washington State Univ.). For details, see Murphy and King (1982).

To estimate the total mass of sheaths produced during the molt, we determined the ratio of sheath mass to feather mass in four feather groups (primaries, secondaries, wing coverts, and spinal contours). To account for small bits of sheath that flaked off during the normal eruption of the feather, and other bits that were unavoidably lost during cleaning of the sheaths, we generated a correction factor equal to the mean intact sheath length divided by the mean separated sheath length. We multiplied the measured sheath mass by this correction factor to obtain a sheath mass corrected for losses.

We estimated that White-crowned Sparrows during their postnuptial molt generate a total mass of feather sheaths (ca. 380–420 mg) equivalent to at least 18–20% of the mass of the new plumage (ca. 2.0 g; Murphy and King 1984b). This is a conservative estimate because the correction factor for loss of sheath material was based on the larger and sturdier remigial sheaths (Table 1). Our dissection of the smaller, more delicate sheaths of the spinal contour feathers probably entailed a slightly greater proportional loss than in the remiges, and use of the correction factor probably underestimates the amount of sheath produced. Nevertheless, the estimate of sheath mass as 18–20% of the new plumage mass is accurate enough to show that the synthesis of feather sheaths requires a quantity of nutrients that should not be overlooked in assessing the nutritional requirements of molting birds.

Chemical analysis of sheaths showed that they, like feathers, are largely proteinaceous. Their mean (±SD, $n = 3$) nitrogen content was 15.16 ± 0.09% by mass, which is essentially indistinguishable from the 15.22% nitrogen content of White-crowned Sparrow feathers (Murphy and King 1982). The amino acid composition of sheaths (Table 2) differed, however, from that of homogenized plumage and of feather calamus (Fig. 1). This is consistent with the observation by Rudall (1947) that x-ray diffraction analysis of thin sheath material from the calamus of a domestic goose yields the "α-pattern" of keratin, while all other parts of the feather yield the "feather-pattern." Avian epi-

TABLE 2. Mean amino acid composition of feather sheaths.

	μmoles/g		mg/g		
Amino acid[a]	Remiges	Contours	Remiges	Contours	cv[b]
Essential					
Arginine	371	390	58.0	61.0	4.3
Histidine	54	58	7.4	8.0	4.7
Isoleucine	264	232	29.8	26.3	6.4
Leucine	702	658	79.4	74.4	8.1
Lysine	259	275	33.2	35.2	7.3
Methionine	54	66	7.1	8.7	5.5
Cystine/2	577	605	58.9	61.8	6.0
Phenylalanine	284	297	41.8	43.7	8.1
Tyrosine	264	280	43.0	45.6	7.5
Threonine	264	272	26.7	27.5	6.8
Tryptophan	nd[c]	nd	nd	nd	—
Valine	464	480	46.0	47.6	7.3
Nonessential					
Alanine	832	834	59.1	59.2	6.6
Aspartic acid	424	457	48.8	52.6	4.2
Glutamic acid	838	813	108.2	105.0	8.8
Glycine	1,160	1,259	66.2	74.1	9.8
Proline	902	910	87.5	88.3	4.5
Serine	493	463	42.9	40.3	5.1
NH_3 released	1,174	1,263	20.0	21.5	15.6
Percentage accounted for:					
Nitrogen	99.9	103.0			
Mass	86.4	88.1			

[a] Uncorrected for destruction during hydrolysis; n = 6 birds for remiges, n = 1 bird for contour feathers. Amino acid concentrations in contour sheaths are within the range of concentrations measured in remigial sheaths.

[b] Coefficient of variation for remiges.

[c] Not determined.

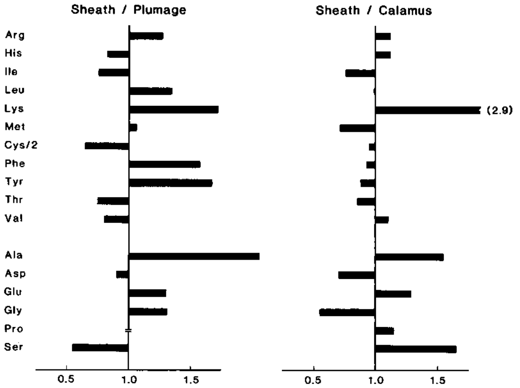

Fig. 1. Relative amino acid composition of feather sheaths and of whole plumage and calamus, shown as the ratio of molar concentration in sheath to molar concentration in plumage or calamus. Concentrations were equal (ratio = 1.0) only in proline in sheath and plumage. All other amino acids were either less concentrated (ratio <1.0) or more concentrated (>1.0) in sheaths than in other feather parts. Analyses of all samples were uncorrected for destruction of amino acids during hydrolysis (about 3% threonine and about 6% serine; Rattenbury 1981: 129). Direct comparisons were considered justified by the less than 5% variability in total μmoles of amino acid per gram of the various materials. Likewise, masses of amino acids per gram of plumage, calamus, and sheath were similar (832, 850, and 864 mg/g, respectively). Differences in percentage mass accounted for by constituent amino acids is largely attributable to variabilities in the molecular weights of constituent amino acids. All calculations were based on dehydrated molecular masses.

dermis likewise yields the α-keratin pattern (Fraser et al. 1972), as would be expected in view of the similar histological origin of epidermis and sheath (Lucas and Stettenheim 1972). The disparities of amino acid composition among sheaths, calamus, and whole plumage were greatest in lysine, phenylalanine, tyrosine, alanine, glycine, and serine. There do not appear to be trends of difference in essential vs. nonessential amino acids. Cyst(e)ine concentrations in sheaths and calamus were similar, but were only about two-thirds of the concentration found in homogenized whole plumage. This is attributable to the typically higher concentration of cyst(e)ine in barbs than in other feather parts (Murphy unpubl. data). We surmise that the differentiation of feather parts in respect to the type or types of keratin [and hence the amount of cyst(e)ine] that they contain reflects the demands of their mechanical functions. The sheaths, fated to split at an appropriate stage and then be preened away, are constructed from relatively lower cyst(e)ine keratins.

The production of sheaths during molt entails the deposition of about 1.13 mg of nitrogen (N) (about 7 mg protein) per day [(380 mg sheath/54 days) × 0.1516 N], but can approach twice this amount at peak molt. Nitrogen deposition as sheaths during molt therefore is equivalent to 19–38% of the daily endogenous nitrogen loss of a nonmolting White-crowned Sparrow (6 mg N/day, calculated from Robbins 1981). When nutrition is adequate (high-quality protein), and assuming ca. 100% metabolic efficiency, sheath synthesis would increase maintenance protein requirement (27 mg N/day, calculated from Robbins 1981) by *at least* 4–8% per day.

The *net* nitrogen retention of molt averages about

11.5 mg N/day, which is 43% above maintenance retention. Feather synthesis accounts for the retention of roughly 6.0 mg N/day [(2.0 g of new plumage plus a correction factor of 105 mg for replacement of rectrices damaged and lost during growth) multiplied by 0.1522 N; Murphy and King 1984a, b]. Synthesis of sheaths adds appreciably to this quantity and accounts for at least an additional 10% of the nitrogen retained during molt. About 4 mg N/day retained during molt is still not accounted for quantitatively. Some of it undoubtedly is deposited in other integumentary structures that are renewed during the molt, and in accessory structures such as pulp, increasing numbers of erythrocytes, increases in peptide stores (Murphy and King 1985), and perhaps in accretion of other body proteins.

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Analysis of feather parts completed after this report was in press suggested larger losses of serine during hydrolysis than reported by Rattenbury (1981). By analyzing the amino acid composition of samples of rachis hydrolyzed from 12 to 24 h, we found that as much as 35% of serine and 14% of threonine was destroyed between 12 and 24 h. The other amino acids were stable. We used 24-h hydrolysates in the analysis reported in Table 2.

Estimating Nest Detection Probabilities for White-winged Dove Nest Transects in Tamaulipas, Mexico

JAMES D. NICHOLS,[1] ROY E. TOMLINSON,[2] AND GARY WAGGERMAN[3]
[1]*U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center,*
Laurel, Maryland 20708 USA,
[2]*U.S. Fish and Wildlife Service, Office of Migratory Bird Management,*
Albuquerque, New Mexico 87103 USA, and
[3]*Texas Parks and Wildlife Department, Wildlife Division, 410 N. 13th Street,*
Edinburgh, Texas 78539 USA

Nest transects in nesting colonies provide one source of information on White-winged Dove (*Zenaida asiatica asiatica*) population status and reproduction. Nests are counted along transects using standardized field methods each year in Texas and northeastern Mexico by personnel associated with Mexico's Office of Flora and Fauna, the Texas Parks and Wildlife Department, and the U.S. Fish and Wildlife Service. Nest counts on transects are combined with information on the size of nesting colonies to estimate total numbers of nests in sampled colonies. Historically, these estimates have been based on the actual nest counts on transects and thus have required the assumption that all nests lying within transect boundaries are detected (seen) with a probability of one. Our objectives were to test the hypothesis that nest detection probability is one and, if rejected, to estimate this probability.

STUDY AREA AND METHODS

Fieldwork was conducted during June 1985 at two whitewing nesting colonies in Tamaulipas, Mexico. The Parras de la Fuente Colony lies adjacent to the Río Soto la Marina about 80 km northeast of Ciudad Victoria. The colony became established in the mid-1970's in response to increased food (grain sorghum) and water (irrigation) and now consists of several million nesting adults in an area approximately 4 × 20 km. The Escandón Colony is a remnant of a much larger colony that existed at least as early as the mid-1960's. Clearing of brush vegetation for agricultural purposes has restricted the colony to an area of about 2 × 4 km, but the nesting population is estimated to be about 1 million whitewings (Tomlinson et al. in prep.). Nesting habitat in both colonies consists of a vegetative complex that is referred to as Tamaulipan thorn scrub. The vegetation is composed of a dense entanglement of small trees (2-5 m in height), shrubs, and cacti, largely impenetrable to humans (Cottam and Trefethen 1968). Whitewing nesting densities in these locations sometimes reach an estimated 1,500 nests/ha.

When we first considered the problem of estimating nest detection probability, it seemed that formal line transect estimators (see Gates 1979, Burnham et al. 1980) would be most appropriate for estimating numbers of nests on transects. Even though nests were located in relatively low vegetation (nest heights seldom exceeded 3-4 m on our transects), however, we were concerned about the critical line transect assumption of seeing nests on the transect line with probability one. We thus used multiple observers in conjunction with capture-recapture model estimators to estimate nest detection probability.

Field methods.—Transects to estimate whitewing nesting densities commonly sample plots of either 0.25 acre or 0.1 ha. Quarter-acre (~0.1 ha) transects are normally 121 yards (110.6 m) long by 10 yards (9.1 m) wide, whereas 0.1-ha transects are 100 m long by 10 m wide. Because earlier studies used the English system, we retained it in this study. White-winged Dove nesting transects are established by cutting a narrow and relatively straight line through the heavy brush and stretching a premeasured length of cord (121 yards, 110.6 m) at chest level to mark the center line of the transect. Two observers then travel the length of the cord, one on each side, counting all nests within 5 yards (4.6 m) of the line. This procedure results in a count of all nests seen within the 0.25-acre (0.1 ha) transect. Data from several transects are combined with an estimate of land area covered by the colony to estimate the total number of nests in a colony.

Our sampling experiments were designed to estimate the probability that an average nest lying within the boundaries of a nest transect is actually detected by observers (call this detection probability, p). Each of 5 observers was provided with a number of small washers painted a distinguishing color (red, black, white, blue, or yellow). We initiated the exercise by cutting a path and laying out the cord in the standard manner. Then a single observer searched for nests on one side of the cord, placing a colored washer in each nest found. When the first observer had proceeded approximately 30 yards (27.4 m) and was well out of sight, a second observer began the same procedure on the same side of the string. This was repeated until the fifth observer had completed his search and washer placement. At the end, all five observers searched the area once again, retrieved the washers, and recorded the different colors found in each nest. Thus, we generated a list of nests with a record of which observers found each one. This exercise was conducted once at the Parras de la Fuente Colony and once at the Escandón Colony, with the same 5 observers participating at each location.

Statistical methods.—The above exercises yielded data that were analyzed using the closed capture-recapture methods of Otis et al. (1978). We initially hoped that the data could be analyzed using the heterogeneity model, M_h, of Burnham and Overton (1978). The test results from program CAPTURE, however, indicated the presence of both heterogeneity and observer variation (equivalent to temporal variation in the capture-recapture context) in both data sets (Parras de la Fuente and Escandón). The appropriate model for both data sets was thus M_{th}, for which no estimator is available (Otis et al. 1978). We removed observer variation by restricting the data sets to observers who found similar numbers of nests. By doing this we were able to estimate total nests using model M_h with data from 4 observers at Parras de la Fuente and 3 at Escandón. Note that this restriction of data to subsets of observers was necessary only for the estimation of total nests. Nest detection probabilities were estimated for all observers.

The detection probability, p_i, for each observer, i, was estimated as:

$$\hat{p}_i = n_i/\hat{N}_h, \tag{1}$$

where n_i is the number of nests found by observer i and $\hat{N}_h$ is the estimated total number of nests based on model M_h. The variance was estimated as:

$$\widehat{\text{var}}\ \hat{p}_i = [(n_i/\hat{N}_h)^2\ (\widehat{\text{var}}\ \hat{N}_h/\hat{N}_h^2)] + \hat{p}(1 - \hat{p})/\hat{N}_h, \tag{2}$$

where $\widehat{\text{var}}\ \hat{N}_h$ is based on model M_h. Note that (2) is

TABLE 1. Nest detection probability estimates ($\hat{p}_i$) for 5 observers during sampling experiments at the Parras de la Fuente and Escandón colonies, 1985.

	Parras de la Fuente[a]		Escandón[b]		Both colonies[c]	
Observer (i)	Nests seen	$\hat{p}_i$ ($\widehat{\text{SE}}$)	Nests seen	$\hat{p}_i$ ($\widehat{\text{SE}}$)	Nests seen	$\hat{p}_i$ ($\widehat{\text{SE}}$)
1	56	0.69 (0.055)	44	0.81 (0.058)	100	0.74 (0.040)
2	75	0.93 (0.038)	43	0.80 (0.059)	118	0.87 (0.033)
3	61	0.75 (0.052)	34	0.63 (0.068)	95	0.70 (0.042)
4	66	0.81 (0.048)	42	0.78 (0.061)	108	0.80 (0.038)
5	56	0.69 (0.055)	31	0.57 (0.069)	87	0.64 (0.043)
All observers	314	0.78 (0.029)	194	0.72 (0.034)	508	0.75 (0.022)

[a] Total number of different nests found by all observers, $M_{t+1} = 78$. Total estimated nests, $\hat{N}_h = 81$, $\widehat{\text{SE}}(\hat{N}_h) = 2.19$.

[b] $M_{t+1} = 52$, $\hat{N}_h = 54$, $\widehat{\text{SE}}(\hat{N}_h) = 1.50$.

[c] $M_{t+1} = 130$, $\hat{N}_h = 135$, $\widehat{\text{SE}}(\hat{N}_h) = 2.65$.

written as the sum of two components, the first representing sampling variation associated with the estimation of N and the second representing nonsampling binomial variation.

Equations (1) and (2) were used to estimate p_i for each observer, i, at each colony. An overall $\hat{p}_i$ for each observer was obtained by summing the n_i, $\hat{N}_h$, and $\widehat{\text{var}}\ \hat{N}_h$ on the two transects and using these sums in conjunction with (1) and (2). Estimates for all observers pooled were obtained by computing the following values:

$$n^* = \sum_{i=1}^{5} n_i, \qquad (3)$$

$$\hat{N}_{h^*} = 5\hat{N}_h, \text{ and} \qquad (4)$$

$$\widehat{\text{var}}\ \hat{N}_{h^*} = 25\ \widehat{\text{var}}\ \hat{N}_h \qquad (5)$$

for use in conjunction with (1) and (2).

RESULTS AND DISCUSSION

The hypothesis of $p_i = 1.0$ was rejected for every observer, as none found all of the nests located by all observers. The estimated total number of nests at the Parras de la Fuente Colony was 81 (Table 1). Although 78 of these nests were seen by at least one observer, the number seen by individual observers ranged from 56 ($\hat{p}_i = 0.69$) to 75 ($\hat{p}_i = 0.93$). The total nest estimate at Escandón was 54, 52 of which were seen by at least one observer. The number of nests found by individual observers ranged from 31 ($\hat{p}_i = 0.57$) to 44 ($\hat{p}_i = 0.81$). The ranges in $\hat{p}_i$ illustrate the CAPTURE test results showing individual variation in p_i.

The point estimates of detection probability for individual observers and all observers combined differed to some extent between the two transects. However, none of these differences would be regarded as statistically significant at $\alpha = 0.05$ (based on an approximate z test). We thus conclude that our best estimates of detection probability are those based on both transects (Table 1). The pooled estimate of p over all observers and both colonies was computed using Eqs. (3)–(5) as $\hat{p} = 0.75$. Thus, on average, members of this team of observers would be expected to locate about 75% of the nests on a specific whitewing transect.

This is the first effort, of which we are aware, to estimate nest detection probabilities in White-winged Dove nest transect studies. Although based on only two transects, we believe that use of our pooled detection probability estimate of $\hat{p} = 0.75$ is preferable to assuming that $p = 1.0$. Until more work on detection probability is done, we can "correct" density estimates from previous years by multiplying by $1/\hat{p} = 1.33$.

In future efforts to estimate number of nests in colonies, it may be desirable to estimate $\hat{p}$ for specific teams of observers in specific colonies (and possibly for different levels of other variables that might affect p_i, e.g. nest density, time of day). However, the capture-recapture exercise described here requires 5 observers and approximately 3 h per transect. At least six standard transects can be run with this allocation of time and effort. We suspect that nest detection probability does not vary much among transects or colonies, and that different observers represent the largest potential source of variation in detection probability. Therefore, capture-recapture exercises in representative habitat might be especially useful in estimating team-specific detection probabilities, which could then be used to "correct" or "adjust" counts on all transects run by specific teams.

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Diving Depths of Atlantic Puffins and Common Murres

ALAN E. BURGER[1] AND MARK SIMPSON

Biology Department and Newfoundland Institute of Cold Ocean Science, Memorial University, Corner Brook, Newfoundland A2H 6P9, Canada

The diving ability of an aquatic bird is an obvious, important determinant of its foraging niche. Piatt and Nettleship (1985), for example, showed that the depths attained by four species of alcids in Newfoundland were correlated positively with body mass, which suggests that these similar, sympatric species might exploit different parts of the water column. The development of miniature gauges to measure depth (Kooyman et al. 1971, 1982, 1983; Wilson and Bain 1984a), speed (Wilson and Bain 1984b), and distance traveled (Wilson and Achleitner 1985) has greatly facilitated studies of diving in birds.

We report maximum diving depths, measured with gauges attached to free-living birds, attained by Atlantic Puffins (*Fratercula arctica*) and Common Murres (*Uria aalge*) off Gull Island (47°16′N, 52°47′W) in Witless Bay, Newfoundland. Piatt and Nettleship's (1985) study, on the depths at which alcids were trapped in fishing nets, was made in the same area.

We used depth gauges similar to those used by Kooyman et al. (1971) and Adams and Brown (1983), comprising lengths of flexible plastic tubing sealed at one end and coated internally with water-soluble powder (icing sugar). As water was forced down the tube when submerged, the powder dissolved, recording the maximum depth attained (Adams and Brown 1983). The tubing used was Intramedic® polyethylene (PE 160, i.d. 1.14 mm, Clay-Adams, Inc., New York) and Tygon® (R-3603, i.d. 1.6 mm, Norton Specialty Plastics Div., Akron, Ohio). The latter type was found to be less likely to leak or to be damaged.

Sample gauges were calibrated by being lowered from a boat to depths up to 150 m in the study area. The coefficient of variation of the readings on 10 gauges was within 4% at any depth. The gauges were not affected significantly by the rate of descent (5 gauges lowered at 1.38 and 5 at 0.40 m/s to depths of 50 and 70 m; $P > 0.10$ in each case, Mann-Whitney *U*-test), the duration of immersion (6 gauges immersed at 50 m for intervals of 0.5, 1.0, 2.0, 4.0, and 8.0 min; $P > 0.10$, two-tailed Kruskal-Wallis test with tied ranks), or repeated immersions (6 gauges immersed 5 times to 5 m and 5 times to 50 m; $P > 0.10$ in each case, two-tailed Kruskal-Wallis test).

Gauges were 145 mm long for puffins and 200 mm long for murres. They were attached to metal leg bands with short (10 mm) lengths of string. The tubing caused no discernible impediment to the birds during flight or on land, and was not long or flexible enough to entangle their legs. The string would wear through, releasing the gauge, should it not be recovered. These small, trailing gauges were unlikely to have had the same negative effects on the streamlining and swimming of birds as found with harness-mounted devices (Wilson et al. 1986).

All birds studied were breeding adults tending chicks. Puffins were caught in nooses set in their nesting burrows, and murres were caught with a noose pole. Fifteen gauges, of which 10 were undamaged, were recovered from puffins, out of 46 deployed. Two gauges, both undamaged, were recovered from murres out of 29 deployed. The greatest limitation of this technique is the ability to recapture birds without undue disturbance.

The Atlantic Puffins in our sample, totaling 75 bird-days, usually foraged at depths less than 60 m (Table 1). Only one puffin exceeded this depth, diving to 68 m during 17 days of foraging. Piatt and Nettleship

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[1] Present address: Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada.

TABLE 1. Maximum diving depths (m) attained by Atlantic Puffins and Common Murres breeding at Witless Bay, Newfoundland.

Species	Type of gauge[a]	Dates gauges deployed	No. days deployed	Maximum depth ± 95% confidence intervals
Puffin	P	9-14 July 1984	5	41 ± 1
Puffin	P	9-20 July 1984	11	47 ± 3
Puffin	P	12-21 July 1984	9	43 ± 2
Puffin	P	14-21 July 1984	7	41 ± 1
Puffin	T	23-25 July 1984	2	52 ± 4
Puffin	T	21-26 July 1984	5	52 ± 4
Puffin	P	12-29 July 1984	17	68 ± 7
Puffin	P	16 July-2 Aug 1984	17	40 ± 1
Puffin	T	24-25 July 1985	1	22 ± 1
Puffin	T	22-23 July 1985	1	37 ± 3
Murre	P	15-18 July 1985	3	67 ± 7
Murre	T	11-13 July 1985	2	138 ± 10

[a] P = Intramedic® polyethyelene, T = Tygon® tubing (see text).

(1985) found that Atlantic Puffins were caught regularly in nets at 0-40 m but never in nets set deeper than 60 m.

Our small sample from Common Murres (5 bird-days) shows that these birds dived to at least 138 m (Table 1). Piatt and Nettleship (1985) found that most (80%) Common Murres were caught in nets at 0-50 m but some were caught at 180 m, the deepest that nets were set in the Witless Bay area. Clearly, these birds can dive considerably deeper than the apparent limits for Atlantic Puffins. The proportions of time spent foraging at various depths by these two species remain unknown.

The birds' diving abilities would determine their capacity to exploit deep schools of fish (Brown and Nettleship 1984) and might play a role in ecological segregation of these and other alcids (Piatt and Nettleship 1985). Common Murres and Atlantic Puffins off Newfoundland prey primarily on capelin (*Mallotus villosus*) and occasionally on sand lance (*Ammodytes* spp.) (Brown and Nettleship 1984). These fish are, at times, most common at or near the ocean floor (Winters 1983, Brown and Nettleship 1984), where they might be accessible to murres but not puffins. For example, puffins restricted to the upper 60 m would have access to only 13% of the sea floor, within a 20-km radius of Gull Island, whereas a murre diving to 180 m would have access to 97% of the sea floor (data from Canadian Hydrographic Survey map).

The maximum depths (180 m and 60 m, respectively) usually attained by Common Murres (average body mass 930 g) and Atlantic Puffins (510 g) were comparable to those usually reached by penguins of much larger mass. Chinstrap Penguins (*Pygoscelis antarctica;* 3.5 kg) had a maximum diving depth of 70 m, and 90% of their dives were less than 40 m (Lishman and Croxall 1983). Maximum depths of 19 Gentoo Penguins (*P. papua;* 5-6 kg) did not exceed 40 m except for one bird that exceeded 70 m (Adams and Brown 1983). Wilson (1985) reported a maximum depth of 130 m for Jackass Penguins (*Spheniscus demersus;* 3.2 kg), although most birds foraged at depths of less than 30 m. Only the very large penguins have been recorded to dive far deeper than Common Murres. King Penguins (*Aptenodytes patagonica;* 12-14 kg) frequently dived beyond 100 m and one was recorded below 240 m (Kooyman et al. 1982), while Emperor Penguins (*A. forsteri;* 20-24 kg) have been recorded deeper than 265 m (Kooyman et al. 1971). Our impression is that the underwater swimming abilities of alcids are comparable to those of the penguins.

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The **Roger Tory Peterson Institute for the Study of Natural History** has been established in Jamestown, New York. Information about the Institute and its membership program may be obtained by writing **Roger Tory Peterson Institute, 525 Falconer Street, Jamestown, New York 14701.**

Wisconsin Project Loon Watch is accepting applications for its second annual **Sigurd T. Olson Common Loon Research Award** for research on Common Loons in the Lake Superior–Lake Michigan region of the United States and Canada. To apply, a brief description (maximum 10 pages) of the proposed research program and curriculum vitae should be submitted to **Dr. Paul I. V. Strong, Coordinator, Wisconsin Project Loon Watch, Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806** no later than **15 February 1987.** Guidelines for prospective applicants can be requested from WPLW. Proposals by students should be accompanied by two letters of recommendation. The $1,000 award will be granted on the basis of the project's potential to better understand and manage Upper Great Lakes populations of Common Loons.

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GABAR (Growth and Biology of African Raptors) is a new journal that publishes material on African raptors. Contents will include short papers on completed studies, progress reports on ongoing research, short notes, unusual sightings, conservation problems, and a Forum in which opinions, continuing controversies, constructive criticisms, and new ideas are aired and challenged. For sample copies and subscription rates contact **Robert Simmons, Editor, GABAR, Department of Zoology, University of Witwatersrand, Johannesburg 2001, South Africa.**

The following application has been received by the **International Commission on Zoological Nomenclature** and has been published in vol. 43, part 2, of the *Bulletin of Zoological Nomenclature* (9 July 1986). Comments or advice on it is welcomed and should be sent **c/o The British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.** Comments will be published in the *Bulletin.*

Case No. 1051 *Bubo* Dumeril, 1806 and *Surnia* Dumeril, 1806 (Aves): proposed confirmation on the Official List.

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The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and should be submitted (in duplicate) no later than January 15th—with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, c/o Jane Connelly, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192.**

Chapman grants during 1986, totalling $35,717.00, with a mean of $576.08, were awarded to: Michael L. Avery, Post-breeding territoriality and foraging in Costa's Hummingbirds; Lenir Alda do Rosario Bege, Estudo da biologia de *Sula leucogaster* e *Fregata magnificens* atraves do anilhamento; Craig Louis Berman, Tactics of intraspecific brood parasitism in the House Sparrow (*Passer domesticus*); Dr. Keith L. Bildstein, Use of museum specimens to test RSD hypotheses in raptors; Janet S. Boe, Colony and nest site selection by Eared Grebes; Bonnie Sue Bowen, Genetic structure and paternity in communally breeding jays; Randall Breitwisch, Mate choice, parental care, and sexual selection in a monogamous passerine, the Northern Mockingbird (*Mimus polyglottos*); Dr. Michael de Leighton Brooke, Assessment of the night vision capabilities of Gough Island Petrels; Albert E. Burchsted, Song dialect interpretation of range expansions of the House Finch on Cape Cod; Dale H. Clayton, Experimental study of avian-ectoparasite coevolution; Thomas I. Crossman, Habitat characteristics of Savannah and Grasshopper sparrows in Connecticut; Michael D. Dennison, Morphological and ecological evolution of Chaffinches; Emile D. DeVito, Fine-grained landscape heterogeneity within a forest ecosystem: effects on the habitat use and distribution of birds; Robert M. Dickerman, Morphological variation in interface zone of the subspecies of Great Blue Heron; Susan Leigh Earnst, The behavior and energetics of polyandrous Red Phalaropes; Carl Edelstam, Molt in large birds of prey and owls; and Mimicry in birds; Marit Evans-Layng, The influence of visual and acoustic stimuli on the kinship preference of female Zebra Finches (*Taenopygia guttata*); Greg Hunt Farley, Comparative breeding strategies of two coexisting passerines: Bell's Vireo and Bewick's Wren; Dr. Julian Ford, Phylogenetic studies on Australo-Papuan birds and some studies on hybrid zones; Charles M. Francis, The growth and development of nestling swiftlets; John A. Gerwin, Relationships of species and genera of hummingbirds: a biochemical perspective; Rosemarie Gnam, Breeding biology of the Bahama Parrot (*Amazona leucocephala*); Jeffrey G. Groth, Systematics of the North American *Loxia curvirostra* complex; Lisa Guminski, The breeding behavior of the White-cheeked Pintail in the Bahamas; Shannon Hackett, Evolutionary genetics of shorebirds: relationships of genera and families; Brian Thomas Henen, *In vivo* determination of body lipid content using cyclopropane gas; James D. Hengeveld, Does the starvation of Red-winged Blackbird (*Agelaius phoeniceus*) nestlings benefit the surviving nest mates?; Geoffrey E. Hill, The reproductive consequences of subadult plumage in male Black-headed Grosbeaks; Kelly M. Hogan, Foraging behavior of fledgling Bat Falcons (*Falco rufigularis*); Torgeir S. Johnsen, The influence of plasma testesterone levels and territorial experience on male behavior and reproductive biology in the Red-winged Blackbird; Mark J. Kasprzyk, Estimates of turnover rates for Semipalmated Sandpipers; Catherine P. Kittleman, Parameters influencing the absence of parasitism on the Yellow-headed Blackbird; David Lemmon, Social dominance and scanning behavior in Black-capped Chickadees (*Parus atricapillus*); William S. Longland, Great Horned Owl predation and predator avoidance by desert rodents; Paul M. Mayer, Population ecology of the Piping Plover in the northern Great Plains; Mara A. McDonald, The evolution and biology of Hispaniolan Palm Tanagers, genus *Phaenieophilus*; Dona J. Milinkovich, Variation in the reproductive characteristics and reproductive success of the House Wren (*Troglodytes aedon*); Randall J. Mitchell, Mechanisms of competition for pollination; David C. Morimoto, Avian community structure in

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The **Kathleen S. Anderson Award** has been established to encourage significant avian research in areas of interest to Kathleen Anderson and Manomet Bird Observatory, and to support promising biologists in their work. Requests for support of projects in one or more of the following areas will be considered: migration, feeding ecology, habitat fragmentation, populations, competition, shorebirds, and endangered species. All proposed projects must take place in the Americas, and work based at MBO is encouraged. A total of $1,000 will be awarded annually, either to one person or divided among two or more recipients. Any person, of any age, beginning a career in biology is eligible. Enrollment in an academic program is desirable, but not required. Applicants should submit a proposal by **1 December 1986.** For proposal guidelines, write to **Kathleen S. Anderson Award, Manomet Bird Observatory, Box 936, Manomet, Massachusetts 02345.** Award announcements will be made 1 January 1987.

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A **symposium on Birds of Evergreen Forest,** organized by the Southern African Ornithological Society, will be held **8-10 September 1987** at The Wilderness, Cape Province, South Africa. Papers and posters will be presented on the following topics: forest bird communities, biogeography of forest birds, population biology of forest birds, and conservation of forest avifaunas. Prospective participants should contact the **Symposium Organising Committee, E.C.W.B.S., P.O. Box 1305, Port Elizabeth 6000, South Africa.**

The **Third New England Regional Hawk Conference** will be held **4 April 1987** at the Holiday Inn, Holyoke, Massachusetts. Registration forms are available from **HAWKS, P.O. Box 212, Portland, Connecticut 06480.** There are special rates for lodging at the Conference center. Registration will be limited.

The **Third World Conference on Birds of Prey** will be held **22-27 March 1987** at Eilat, Israel. It will be organized by the World Working Group on Birds of Prey in conjunction with the Israel Raptor Information Center and the U.S. Hawk Mountain Sanctuary Association. The conference will consist of 7 paper sessions on conservation, migration, population biology, education, and legislation. For further information write to the Hon. Secretary of the World Working Group: **Mr. R. D. Chancellor, 15 Bolton Gardens, London SW5 0AL, U.K.**

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the pine barrens of southeastern Massachusetts; Lauraine C. Newell, The breeding status of Ross' Geese in an eastern arctic Lesser Snow Goose colony; Reed F. Noss, A critical evaluation of edge effects on north Florida forest birds: the influence of habitat juxtaposition, heterogeneity, and predation; Marc Odin, The mating system of the Ruddy Duck (*Oxyura jamaicensis*); David N. Pashley, Distribution of wood warblers in Mexico; Walter H. Piper, The effect of dominance rank on survival in the White-throated Sparrow; Richard O. Prum, Continuing field work on the behavior and systematics of manakins (Pipridae); Juan Carlos Reboreda, Foraging behavior in the Rufus Hornero (*Furnarius rufus*); Alistair S. Robertson, Life history indices of *Falco* and *Accipiter* spp.: a comparative study of separate populations; Argelis C. Roman, The importance of woodlots to birds in deforested habitats; Peter E. Scott, Competition between hummingbirds and carpenter bees for nectar: effects on foraging behavior and pollination; Peter T. Sherman, The White-Winged Trumpeter (*Psophia leucoptera*): Why defend a feeding territory when you are a frugivore?; Paul Sniegowski, Field experiments in the role of experience in controlling avian migration; Glenna K. Stewart, Variation in egg size of the American Kestrel (*Falco sparverius*); Hannah Bonsey Suthers, Pesticide residues and death in backyard songbirds; Michael E. Tarburton, White-rumped Swiftlets—clutch size determination; Dr. Jill M. Trainer, Development of singing synchrony in cooperatively displaying Long-tailed Manakins; Pablo Luis Tubaro, Adult song modification in the Chingolo (*Zonotrichia capensis*); Lisa Valburg, The role of choice in the foraging behavior of the Common Bush-Tanager (*Chlorospiagus opthalmicus*); David Mercer Ward, The comparative ecology of *Vanellus coronatus*, *V. melanopterus* and *V. lugubris*; Ian G. Warkentin, Wintering ecology of the Richardson's Merlin in Saskatoon, Saskatchewan; David A. Wiedenfeld, Ecomorphology of resident and migrant populations of Yellow Warbler; Licia Wolf, Biparental care in the monogamous Dark-eyed Junco: a test of the adaptive hypothesis; Eileen Zerba, The interaction between activity metabolism and thermoregulation in Gambel's Quail.

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Received 5 February 1986, accepted 16 May 1986.

The **Roger Tory Peterson Institute for the Study of Natural History** has been established in Jamestown, New York. Information about the Institute and its membership program may be obtained by writing **Roger Tory Peterson Institute, 525 Falconer Street, Jamestown, New York 14701.**

Wisconsin Project Loon Watch is accepting applications for its second annual **Sigurd T. Olson Common Loon Research Award** for research on Common Loons in the Lake Superior-Lake Michigan region of the United States and Canada. To apply, a brief description (maximum 10 pages) of the proposed research program and curriculum vitae should be submitted to **Dr. Paul I. V. Strong, Coordinator, Wisconsin Project Loon Watch, Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806** no later than **15 February 1987.** Guidelines for prospective applicants can be requested from WPLW. Proposals by students should be accompanied by two letters of recommendation. The $1,000 award will be granted on the basis of the project's potential to better understand and manage Upper Great Lakes populations of Common Loons.