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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 must be submitted no later than 15 January, with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192 USA.**

Three postdoctoral fellowships were awarded for the 1989 year: Jean-Louis Martin, Avian geographic variation and speciation in the Palearctic: Are there general rules? Richard O. Prum, Phylogeny and behavioral diversification of the cotingas (Cotingidae); and C. Jeffery Woodbury, A taxonomic study of the avian spinal cord.

Three collection study grants for the 1989 year were awarded: Timothy Crowe, for a study of supra-generic phylogenetic relationships within the gamebirds (Order: Galliformes); Nedra Klein, for a study of speciation in the Yellow Warbler (*Dendroica petechia*); and Miguel Lentino Rosciano, for a study of the systematics of *Crypturellus erythropus* and *Tyto alba*.

Chapman grants for 1988, totaling $40,066, with a mean of $598, were awarded: Craig W. Benkman, The ecology and status of the Hispaniolan Crossbill; William L. Benner, How does House Finch color variation affect female choice? James V. Briskie, Dynamics and consequences of copulation patterns in Smith's Longspurs; Kevin J. Burns, The geography of Fox Sparrow ontogeny; Alice L. E. V. Cassidy, Song variation and learning in Song Sparrows (*Melospiza melodia*); Luis M. Chiappe, Continental birds from the Late Cretaceous of Patagonia; Carla Cicero, Stucture and variation in the song of the Lincoln's Sparrow (*Melospiza lincolnii*) in California; David A. Cimprich, Effect of flocking with dominant heterospecifics on nutritional status; Evan G. Cooch, Effect of growth rate on adult body size and fecundity in Snow Geese; Barbara Diehl, Structure and functioning of a bird community in a patchy and changing habitat; Andrea Dinep, The development of social behavior in White Ibis chicks; Keith L. Dixon, Investigation of the Crested Titmouse hybrid zone in Texas; David Eastzer, Allozyme frequencies across a song transition zone; Scott V. Edwards, Molecular evolution in cooperatively breeding Australo-Papuan babblers (*Pomatostomus*); Bruce A. Eichhorst, Genetic variation in the Western and Clark's grebes: color-morphs or species? Lisa M. Ellis, Interaction of testosterone and delayed plumage maturation in Black-headed Grosbeaks; David Enstrom, Mate choice and delayed plumage maturation in Orchard Orioles; Patricia Escalante, Evolutionary relationships of *Geothlypis* warblers; Charles M. Francis, Survival rates of Lesser Snow Geese; Renee D. Godard, Individual discrimination by two wood

(*continued on p. 736*)

MARINE BIRDS FEED AT GRAY WHALE MUD PLUMES IN THE BERING SEA

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ABSTRACT.—Gray whales (*Eschrichtius robustus*) feeding in the northern Bering Sea produce prey-rich mud plumes that provide ephemeral foraging opportunities for seabirds. Approximately 67% of all gray whales were attended by birds. In four whale-associating bird species (Northern Fulmar, *Fulmarus glacialis;* Red Phalarope, *Phalaropus fulicaria;* Black-legged Kittiwake, *Rissa tridactyla;* and Thick-billed Murre, *Uria lomvia*), from 17 to 87% of all individuals that we observed on the water or foraging were in the whales' mud plumes. The combined density of these same four species was strongly correlated with whale density over a broad range of spatial scales. The whale-associating seabirds exhibited species-specific patterns of foraging behavior at plumes, including differences in mean group size, mean residence time, and patterns of movement between plumes. Birds tended to form larger groups and to form more mixed-species flocks in association with whales. The association of marine birds with gray whales in the Bering Sea provides a model system for examining seabird interactions at fine-scale oceanographic patches and demonstrates the importance of these patches in shaping patterns of seabird distribution and behavior. *Received 12 February 1988, accepted 11 April 1990.*

LITTLE information is available on the ways in which patterns of distribution and behavior of marine birds are influenced by patterns of patchiness in the ocean at scales of 1–100 m (i.e. *fine-scale patches*). This is unfortunate, because interactions of foraging seabirds with their prey are bound to occur at relatively small scales (Brown et al. 1979, Brown 1980, Hunt et al. 1985, Obst 1985, Safina and Burger 1985, Heinemann et al. 1989, Piatt in press). Attempts to understand the ways in which birds respond to oceanographic events at larger scales must incorporate information on how individual seabirds make decisions regarding where they will spend their time. Fine-scale patterns are notoriously resistant to study in pelagic systems, because of the difficulties associated with systematically locating and quantifying small, ephemeral patches. These difficulties are compounded by the difficulties presented in tracking and observing the behavior of individual seabirds in the open ocean.

Gray whales (*Eschrichtius robustus*) are plentiful on their summer foraging grounds in the northern Bering Sea. They are unique among large cetaceans in that they are specialized as bottom foragers (Evans 1982, Jones et al. 1984). The whales slurp deep furrows in the sea floor (Oliver et al. 1983, 1984) and strain the sediments through their balleen to remove benthic amphipods, their major food (Rice and Wolman 1971, Nerini 1984). Recent estimates have placed the turnover of sediments by gray whales in the Bering Sea at ca. 10^9 m^3 per summer (Johnson and Nelson 1984). Much of this sediment is carried to surface waters as the whales surface to breathe, which creates large muddy plumes in their wakes (Rugh and Fraker 1981). Large numbers of whole and damaged benthic invertebrates are included in these plumes, some of which may remain at the surface for several minutes after a whale has surfaced (Fig. 1).

In a series of aerial surveys in the northern Bering Sea, Harrison (1979) detected seabirds of several species that apparently feed in muddy patches left by gray whales. He suggested that foraging in association with gray whales may be important for Bering Sea birds. Foraging associations between seabirds and cetaceans are common throughout the world's oceans (see Evans 1982 and Burger 1988 for recent reviews). During three field seasons (1983–1985) of oceanographic cruises in the Bering Sea, we were impressed by the widespread associations between birds and gray whales throughout the Chirikov Basin. In 1985, we studied the association of seabirds with gray whale mud plumes as a model system of the influence of ephem-

eral, fine-scale patches on the species-specific foraging behavior and distribution of marine birds at sea.

Methods

Our study was conducted aboard the 'Alpha Helix' between 28 July and 4 August, 1985, in the Chirikov Basin to the west and southwest of King Island (Fig. 2). On a series of six shipboard transects (cumulative 300 transect miles), the number of birds of each species that occurred within a 90-degree arc 300 m ahead and to one side of the ship was recorded on a portable microcomputer, along with the the birds' behavior when first observed, size of flocks, weather and viewing conditions, and the ship's speed and position (Updegraf and Hunt 1985). The presence, absence, and estimated numbers of gray whales along the transect lines were also noted, as were any observed associations between seabirds and whales or whale plumes.

To observe the behavior of seabirds associated with gray whales, we also stopped the ship within 300–500 m of foraging whales and bird associates. This distance allowed us to view the animals' activities without disturbing them. With three to six observers simultaneously on the bridge, we monitored the diving behavior of the whales, the arrival and departure of birds from the whale-generated mud plumes, and the duration of foraging activities of the birds at the plumes. Observations were recorded onto a cassette tape recorder. The tape was allowed to run continuously throughout an observation period, which lasted up to 60 min for a single whale. We subsequently transcribed the tapes, and determined the temporal course of events.

To determine what the birds ate, we collected birds seen feeding at plumes. We shot birds from the ship's bow or from a small launch and retrieved them from the sea surface by net. We collected 28 birds at whale slicks to the west of King Island on 29 July (n = 12) and 30 July (n = 16), 1985. Stomachs were either removed immediately or first flushed with ethanol to inhibit further digestion of prey and dissected 1–2 hours later. The size, number, and species of recognizable prey items were recorded for each stomach.

Results

Seabird-Whale Associations

Gray whales were abundant in the study area. One or more gray whales were recorded in 39% (77/195) of our 10-min transect segments. Seabird-gray whale associations were also common during our study. Of 95 whales or whale groups seen within 500 m of the ship (i.e. *whale events*) along a cruise track from King Island to St. Lawrence Island, 63 (66%) had associated birds. Northern Fulmars (*Fulmarus glacialis*), Red Phalaropes (*Phalaropus fulicaria*), Black-legged Kittiwakes (*Rissa tridactyla*), and Thick-billed Murres (*Uria lomvia*) were observed at 48%, 28%, 23%, and 12% of all whale events, respectively. The percentages of all individuals recorded on the water and observed in association with whale events ranged from 17% (Thick-billed Murres) to 87% (Red Phalaropes and Black-legged Kittiwakes) (Table 1). For these four species, combined bird density averaged 3.5 times greater in transect segments in which gray whales were present than in those in which whales were absent (Table 1).

Fig. 1. Echogram of mud plumes formed during three successive blows by the same gray whale. To obtain the echogram, we used a 200-kHz echo sounder while the ship was virtually stationary. Settling rates of particles in the plumes ranged between 5–40 m/min. Scale bar is equal to 1 min. Note the high density and the ephemeral nature of the material in the patches.

Other less common surface-feeding species (Sabine's Gull, *Xema sabini*; Glaucous Gull, *Larus hyperboreus*; Herring Gull, *L. argentatus*; Pomarine Jaeger, *Stercorarius pomarinus*; Parasitic Jaeger, *S. parasiticus*; and Long-tailed Jaeger, *S. longicaudus*) were observed with whales at least once during the study. Several species of pursuit-diving alcids were recorded regularly during transects but were never observed feeding in association with whales. They included Least Auklet (*Aethia pusilla*), Crested Auklet (*A. cristatella*), Parakeet Auklet (*Cyclorrhynchus psittacula*), Tufted Puffin (*Fratercula cirrhata*), and Common Murre (*Uria aalge*).

Correlations between bird and whale densities.— For the common, whale-associating species, the density of birds observed either feeding or on the water was strongly correlated with the number of whales in a transect segment. Such correlations were observed at a variety of measurement scales (segment lengths), ranging from

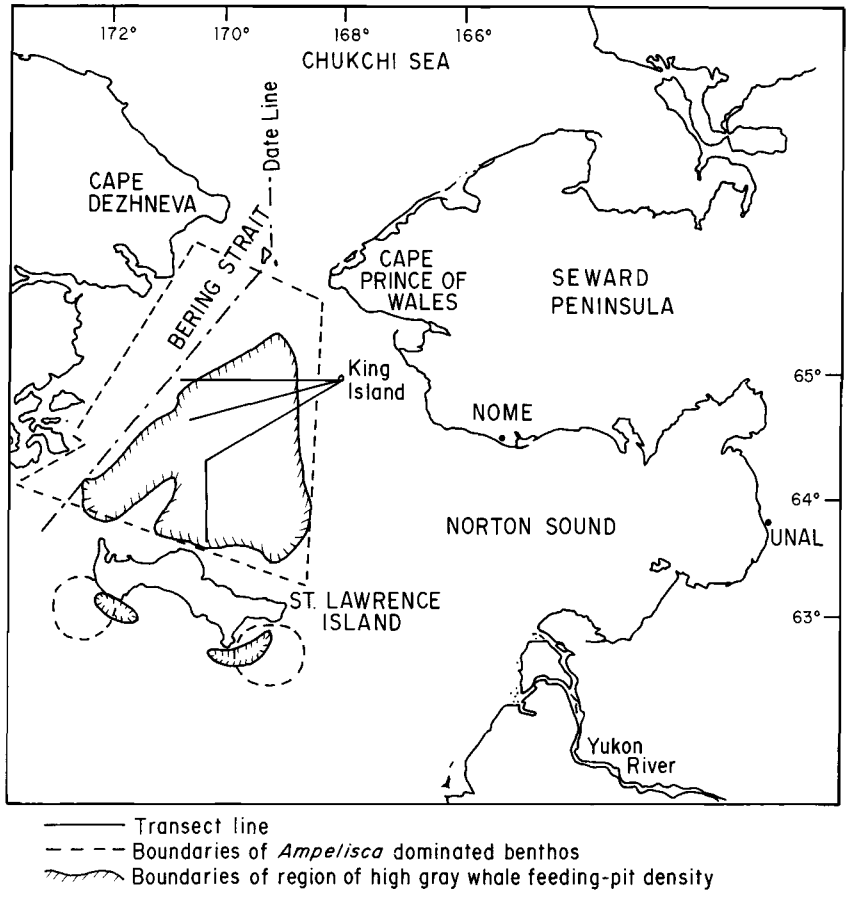

Fig. 2. Location of seabird transect lines in relation to the principal feeding grounds of the gray whale in the Chirikov Basin, northern Bering Sea. Boundaries of the whale feeding grounds are taken from Johnson and Nelson (1984: 1150), and the rough limits of the Ampeliscid benthic community are drawn after Nerini (1984: 423).

approximately 1.5 nautical miles (10 min of transect time) to 10 nautical miles (see Table 2). Correlation coefficients changed little with measurement scale either within individual transect lines (maximum r between 0.73 and 0.89) or for all transects pooled (r between 0.33 and 0.37; Table 2). Correlation coefficients were generally higher when only transect segments along a single transect line were considered than when data from all six transects were pooled. This decrease in correlation reflects a loss of information in the pooled data, which is inevitable because of temporal variation in numbers of birds and whales encountered.

By comparison, the density of Least Auklets—an abundant species that we never saw feeding in whale plumes—was not significantly correlated with whale density at any measurement scale. In fact, correlation coefficients were uniformly negative (r between -0.27 and -0.12) for all six transect lines.

Flock composition.—For each of the four common whale-associating species, the mean number of birds seen to feed or on the water was greater among whale-associating flocks than among those apart from whale events (Table 1). This was true whether the number of each species was considered separately (whale-associating flocks were 1.8–2.4 times larger) or the numbers of all four species were combined (whale-associating flocks 5.7 times larger).

Multispecies flocks were common at whale

TABLE 1. The importance of gray whale mud plumes as foraging sites for Bering Sea birds. Numbers refer only to birds observed feeding or on the water during transects. Differences between means (two-tailed Student's *t*-test) are significant at * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$; sample sizes are in parentheses.

Species	Away from plumes (*n*)	At plumes (*n*)	At plumes (%)	Birds per 10-min transect segment[a] With whales ($\bar{x} \pm$ SE)	Without whales ($\bar{x} \pm$ SE)	Ratio	Birds per flock At plumes ($\bar{x} \pm$ SE)	Away from plumes ($\bar{x} \pm$ SE)	Ratio
Northern Fulmar	157	190	55	2.68 ± 0.69	0.81 ± 0.16	3.3***	3.91 ± 0.55 (46)	1.78 ± 0.25 (87)	2.2***
Red Phalarope	80	505	87	5.17 ± 1.50	1.17 ± 0.51	4.4**	19.28 ± 3.25 (25)	7.89 ± 2.94 (9)	2.4*
Black-legged Kittiwake	23	155	87	1.72 ± 0.56	0.18 ± 0.06	9.6***	4.05 ± 1.02 (37)	1.72 ± 0.30 (18)	2.4*
Thick-billed Murre	271	56	17	1.59 ± 0.26	1.00 ± 0.15	1.6	2.08 ± 0.48 (24)	1.22 ± 0.04 (176)	1.7***
Species combined	531	906	63	11.16 ± 1.92	3.16 ± 0.68	3.5***	9.83 ± 1.44 (90)	1.74 ± 0.18 (289)	5.7***

[a] Sample sizes are 112 transects with whales present, 81 transects without whales.

events. Groups of whale-associating birds comprised from one to six species. Mixed-species flocks accounted for 48% (29/61) of all whale-associating groups. In contrast, only 2 of 67 flocks that fed or were on the water apart from whale plumes comprised more than one species. At plumes, the frequency of flocks encountered declined as species' diversity increased. Monospecific flocks were most common, and two-, three-, and four-species assemblages were progressively rarer. The observed frequency distribution was not significantly different from that predicted by a binomial expansion based upon the independent probability that each species was present or absent at a given whale event ($P > 0.25$). Similarly, among the four common whale-associating species, there was no statistically significant tendency for any pair of species to co-occur in a flock more often than one would predict by chance association alone ($P > 0.25$).

BEHAVIOR AT MUD PLUMES

The foraging behaviors of the individual species feeding at mud plumes varied markedly. We observed differences in the timing of arrival at the plumes, the length of time birds remained at a given plume, and methods of prey capture while they fed.

Black-legged Kittiwakes.—Black-legged Kittiwakes were the most active of the whale-associating species. As a whale surfaced, kittiwakes in the area flew rapidly to the whale and hovered directly above it, dipping and picking in the forming plume. When the whale swam at the surface, usually making several "blows" along the way, kittiwakes would lift and resettle to match its progress, as long as mud was being released. The kittiwakes always fed in the most recently formed plume. After the whale ceased to eject mud, or it dove, the kittiwakes remained on the water, where they continued to peck at the surface for a few minutes. Kittiwakes were often the first birds to arrive at a fresh plume, and were typically the first birds to abandon it (Fig. 3). Black-legged Kittiwake flocks ($n = 14$) spent an average of 6.16 ± 0.60 min at individual whale plumes. Mean time spent in feeding was only 4.46 ± 0.74 min per plume.

TABLE 2. Correlations[a] between seabird density (four primary whale-associating species, on water or feeding) and the density of gray whales sighted along six transect lines in the Chirikov Basin, northern Bering Sea.

Transect segment length (NM)	*n*	Correlation statistics *r*	Variance explained ($r^2 \times 100$)	*P*	No. of transects $P < 0.05$
		For the best of 6 transect lines			
1.5	18	0.73	54%	<0.01	5/6
3.0	15	0.89	79%	<0.01	3/6
5.0	14	0.79	62%	<0.01	3/6
10.0	7	0.79	62%	<0.05	1/6
		For all 6 transects pooled			
1.5	195	0.33	11%	<0.001	
3.0	88	0.37	13%	<0.01	
5.0	59	0.33	11%	<0.02	
10.0	29	0.36	13%	0.06	

[a] Correlation is by least squares, linear regression analysis. Abbreviations: NM = nautical miles, *n* = number of individual transect segments, *r* = correlation coefficient, and *P* = significance level of correlation.

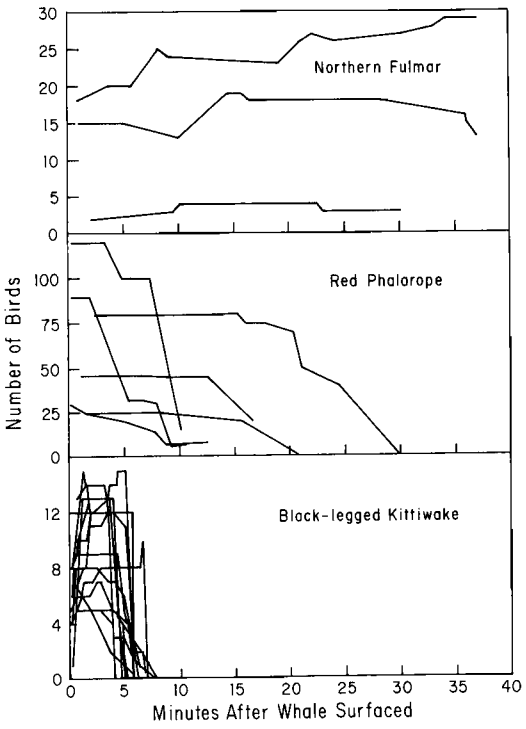

Fig. 3. A comparison of the time spent on gray whale mud plumes by three surface-feeding bird species. Time zero marks the surfacing of the whale and the origin of a mud plume. Each curve tracks the subsequent arrival, aggregation, and disappearance of birds at a single plume. Northern Fulmars commonly feed at plumes for 30 min or more, whereas Black-legged Kittiwakes abandon plumes within 5–10 min after the plumes are formed.

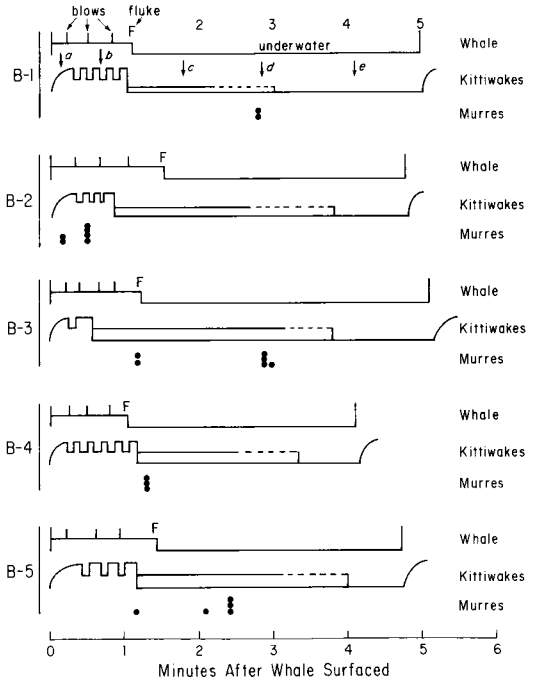

Fig. 4. Synchronization of foraging behavior of a Black-legged Kittiwake flock with the dive cycle of a feeding gray whale. Note that when the whale moved at the surface, the kittiwakes followed; when the whale was submerged, the kittiwakes sat on the water, first feeding, then waiting for it to resurface. Each successive dive cycle represented (B1–B5) began immediately at the end of the cycle depicted above it. Symbols: *a* = flock takes flight; *b* = flock alternately flies and settles in wake of whale; *c* = entire flock on water, all feeding; *d* = flock on the water, occasional pecking; and *e* = flock resting on the water, not feeding. Note that unlike the kittiwakes, the arrival of Thick-billed Murres ● is not synchronized with the whale's behavior.

The behavior of the kittiwakes was synchronized with the behavior of the whales (Fig. 4). Discrete flocks of kittiwakes followed individual gray whales for periods of at least one hour. The flocks spent much of the time resting on the water, waiting for the whale to surface from a feeding dive. Flocks took wing immediately after the whale blew (perhaps first alerted by its sound), flew to it, and fed vigorously while it was at the surface and producing a fresh plume. When the whale submerged for another feeding dive (throwing its fluke up as it dived), the kittiwakes again settled on the water. The rate of surface-pecking declined rapidly, and the birds then waited for the next fresh plume.

The periodicity of the birds' feeding cycle varied with the periodicity of an individual whale's diving cycles. Comparison of the diving rhythms of two gray whales and their attendant kittiwake flocks indicates that the birds remained longer at the plumes of the whale with longer foraging dives. These birds did not spend significantly more time actually feeding at the plumes that were produced (Table 3). The birds with the longer-diving whale spent extra time resting on the water, ostensibly waiting for the whale's next blow.

Red Phalaropes.—Like kittiwakes, phalaropes typically arrived as plumes formed when a whale surfaced. Unlike kittiwakes, however, phalaropes never fed while flying. All phalaropes fed while they swam at the plume. Oc-

TABLE 3. Comparison of the diving behavior of two gray whales (A and B) and the behavior of their two attendant Black-legged Kittiwake flocks. Times (s) are $\bar{x} \pm$ SE (n). Significant differences between means (two-tailed t-test) for the two whales and for the two kittiwake flocks are indicated by * = $P < 0.05$, ** = $P < 0.01$, and NS = not significant.

	Whale A	Whale B	Ratio A : B
	Gray Whales		
At surface	93.0 ± 6.8 (5)	68.8 ± 5.4 (8)	1.35*
Under water	411.6 ± 23.2 (5)	211.1 ± 6.9 (7)	1.95**
Total cycle	504.6 ± 40.5 (5)	279.9 ± 20.0 (7)	1.80**
	Black-legged Kittiwakes		
In air	93.4 ± 13.1 (5)	52.2 ± 6.7 (7)	1.79*
On water	332.2 ± 30.4 (5)	199.5 ± 15.6 (6)	1.66**
Feeding (whole flock)	94.3 ± 10.8 (4)	106.4 ± 13.7 (6)	0.89 (NS)

casional birds spun and dabbed in typical phalarope fashion, but the vast majority simply swam and picked at the surface. As they arrived, flocks of phalaropes usually settled on the freshest part of the plume, but unlike kittiwakes, they did not follow the whale if it repeatedly surfaced. Often, members of the flock spread out by swimming "up-plume" toward the newer portions. The time devoted to a given plume was more variable—and averaged longer—than in kittiwakes (16.80 ± 6.8 min, $n = 6$ flocks; Fig. 2). Moreover, feeding continued in the flock during its entire attendance at a plume, although feeding was always most vigorous upon arrival. We never observed phalaropes landing or attempting to feed on the backs of the whales, as reported elsewhere (Kumlien 1878).

The amount of time Red Phalaropes spent feeding at a given plume exceeded, on average, the period of a whale's dive cycle. Phalaropes rarely moved along with an individual whale. They abandoned plumes by suddenly taking wing and wheeling in tight flocks at heights of ≥50 m. These flocks circled, apparently until they spotted a surfacing whale; then they rapidly settled behind it on the new plume. Among whale-associating species, Red Phalaropes occurred in the largest groups (Table 1). Flocks tended to fragment while the birds fed at plumes, but formed again during the apparent search flights. Phalarope densities were highest in transects with whale groups rather than with isolated whales, and their "whale-hopping" behavior is probably facilitated by their selection of waters with whale groups.

Northern Fulmars.—The behavior of Northern Fulmars at whale plumes was distinctive in several ways. On average, fulmars invested the longest time at a given plume, often >30 min (Fig. 3). In fact, their persistence at plumes usually outlived our patience for monitoring their activities. Although fulmars often occurred in small groups at mud plumes (Table 1), they were distinctly less flock-oriented than kittiwakes or phalaropes. Individual fulmars arrived at and departed from plumes throughout our observation periods. Some fulmars first arrived long after other species had stopped feeding. There was surprisingly little coordination between fulmar activities and whale movements. Fulmars seldom pursued surfacing whales closely, and often settled in older parts of plumes, even as fresh material was being released by a whale.

Northern Fulmars fed by settling on the surface of a plume, paddling slowly, and pecking at the surface film. Rates of pecking remained high throughout the fulmars' residence at a plume ($\bar{x} = 75$ pecks/min, SE = 11, $n = 4$). In contrast, feeding activity of kittiwakes and phalaropes was initially intense, but waned gradually.

Thick-billed Murres.—Among the four most common whale-associating species, Thick-billed Murres were the only pursuit divers. They were irregular visitors at whale plumes; only 17% of all murres seen on the water were conspicuously associated with whales (Table 1). Yet, those murres we observed with whales were clearly keyed in to a whale's presence.

Most often, Thick-billed Murres flew to a surfacing whale, hovered briefly with rapid wing beats, then dropped into the water directly behind or in front of the traveling whale. The murres immediately dove upon hitting the water, and presumably fed in the rapidly settling sediment. In other cases, individual murres

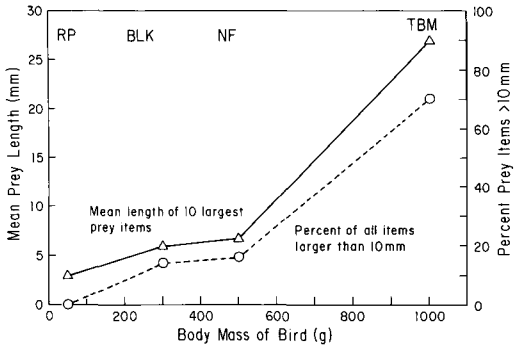

Fig. 5. The length of prey (amphipods) taken from the stomachs of seabird species collected while they fed at gray whale mud plumes as a function of body mass. In general, the average size of the largest prey items increased with the size of the predator, and the majority of large (>10 mm) prey items were found in the largest bird species. Abbreviations: RP = Red Phalarope; BLK = Black-legged Kittiwake; NF = Northern Fulmar; TBM = Thick-billed Murre. Sample size is 7 for each bird species.

swam on the surface to join groups of surface-feeding birds at a plume; they dove when they reached the feeding group. Less commonly, murres surfaced unexpectedly in plumes where we had not previously seen murres arrive. This suggests that some individuals arrived at plumes underwater, either by searching for regions of turbid water or by entering these zones accidentally. Because the murres fed exclusively underwater, we could not track individuals or monitor the time course of feeding activities. Thick-billed Murres occurred mostly as individuals or pairs at whale events (Table 1), and exhibited no obvious coordination as flocks. We saw no evidence that Thick-billed Murres tracked individual whales.

STOMACH CONTENTS

We collected 28 birds as they fed at whale plumes, 7 individuals of each of the four common whale-associating species. A detailed analysis of the stomach contents of these birds and their relationship to the underlying benthic communities will be presented elsewhere (N. Harrison and J. Grebmeier in prep.). We will summarize briefly these data.

Stomachs of the whale-associating birds contained almost exclusively benthic crustaceans. Most important were tube-dwelling *Ampelisca* amphipods (Table 4), a major food of the gray whale and an infaunal form not normally present in surface waters (Rice and Wolman 1971, Nerini 1984). In general, there was a broad overlap in the species and sizes of prey taken by the birds, particularly among the surface feeders. There was a trend for mean prey size to increase with the body size of the predator among the four common whale associates (Fig. 5). In particular, Red Phalaropes took only small amphipods (of the 10 largest items, $\bar{x} = 2.9$ mm), while Thick-billed Murres took most (70%) of the items larger than 1 cm (*Ampelisca macrocephala, Lembos* sp.) present in the 28 birds. Net tows through fresh mud plumes suggest that large amphipods settle most rapidly (Harrison and Grebmeier in prep.) and may therefore be most available to the diving murres. Prey items from Black-legged Kittiwakes and Northern Fulmars were similar in size and species, despite the birds' markedly different behaviors at plumes.

TABLE 4. Percent occurrence of some common, benthic amphipods in the stomachs of seabirds collected near gray whale mud plumes. Sample size is seven for each bird species.

Amphipod	Northern Fulmar	Red Phalarope	Black-legged Kittiwake	Thick-billed Murre
Ampelisca spp.	100	71	100	57
Byblis spp.	100	71	14	57
Protomedia spp.	71	14	29	0
Anonyx spp.	43	14	14	71
Lembos spp.	0	0	0	86

DISCUSSION

Distribution of birds.—Because of the difficulties in systematically locating and quantifying small-scale patches of prey in the open ocean, few investigators have examined the importance of such patchiness in shaping patterns of seabird distribution and behavior. Previous studies have focused on two types of patches: (1) subsurface prey patches located by SONAR, which usually lack a conspicuous surface expression (Woodby 1984, Obst 1985, Safina and Burger 1985, Schneider and Piatt 1986, Hunt et al. MS); and (2) conspicuous surface phenomena, *presumed* to be correlated with increased prey availability (Brown 1980, Au and Pitman 1986, Haney 1986). Correlations between sea-

TABLE 5. Summary of studies that analyze effect of small-scale prey patches on the distribution of seabirds.

Source	Patch type[a]	How identified[b]	Scale[c]	Bird-density increase in transects with prey patch?	*P*	Corr. with patch number or size	*r*
This study	Gray whale plumes	Visual	1.5–10 NM	Yes (3.1)	<0.001	Yes	0.1–0.8
Schneider and Piatt 1986	Fish schools	Acoustic	0.25–15 km	?	—	Yes	0.1–0.9
Safina and Burger 1985	Fish schools	Acoustic	Variable	?	—	No	(NS)
Obst 1985	Krill schools	Acoustic	10 min (1–2 NM)	Yes (2.6)	<0.001	No	(NS)
Heinemann et al. MS	Krill schools	Acoustic	—	Yes	—	Yes	0.2–0.6
Haney 1986	*Sargassum* reef	Visual	15 min (6–10 NM)	Yes		?	—
Woodby 1984	Fish schools	Acoustic	(10–15 min)	No	NS	?	—
	Zooplankton	Acoustic	22–5.6 km	Yes (1–1.8)	<0.05	?	—

[a] All subsurface except whale plumes and *Sargassum* reef.
[b] Visual = visually at surface, and Acoustic = acoustically, using echo-sounding methods.
[c] NM = nautical mile.

bird density and measures of patch density in these studies are typically either weak or not statistically significant (Table 5). The whale plumes were unmistakable in their surface manifestation: a 12-m mammal spewed water 10 or more meters into the air while striping the sea surface with prey-rich mud. Perhaps for this reason, the correlation between the density of patches (whale events) and the density of seabirds was unusually high. Up to 79% of the variability in the density of bird species between segments along a transect line was explained by the number of patches (Table 2).

Although correlations between seabird densities and marine processes have been demonstrated at larger scales, the amount of variability explained by these correlations has often been very low (Abrams 1981, Abrams and Griffiths 1981, Haney and McGillivary 1985, Schneider and Duffy 1985, Briggs and Chu 1986, Schneider et al. 1988). Hunt and Schneider (1987) suggested that patchiness at fine scales (e.g. interactions with prey patches) may be a source of apparent "noise," which can impede the quantification of habitat usage by seabirds at larger scales. The highly significant correlations we found over a wide range of measurement scales indicate the potential importance of identifying and quantifying relevant fine-scale patches in correlative studies of seabird distribution.

Several pursuit-diving alcid species were never observed in association with gray whales, despite the co-occurrence of the birds and whales throughout large areas of the transects. The diets of nonwhale-associating alcids in the Chirikov Basin vary, and they range from diets made up primarily of planktonic crustaceans (Least and Crested auklets) to diets dominated by fish (puffins and the Common Murre; Harrison 1987). None of these species is known to eat substantial quantities of the benthic amphipods that dominated the diets of the whale-associating species. If numbers of all alcids were included in our analyses, correlations between seabird densities and whale densities would certainly have been poorer. This points to the need to use information obtained from behavioral observations of patch use and analyses of stomach contents in distributional studies.

Least Auklets showed negative correlations with whales on all transects, which suggests a tendency to prefer different habitats for foraging. In sharp contrast to our findings, Harrison (1979) reported that small auklets (including Least Auklets) were numerically dominant among the species he observed at mud patches. Kittiwakes and fulmars were comparatively rare. It is difficult to interpret these discrepancies, but the complete absence of auklets from all whale events that we observed suggests a large annual or seasonal difference in the foraging behavior of these birds. Alternatively, Harrison's aerial observations may not have permitted him to distinguish individuals that

happened to be near whale plumes from those that actively entered and fed in them.

Behavior of birds at plumes.—Most studies of seabird behavior at fine-scale patches have suffered from a dearth of information regarding the size, composition, and distribution of the prey patches. In fact, many studies have used the characteristics of the seabird flocks themselves (e.g. size, density, and fixity) to infer characteristics of prey patchiness (e.g. presence/absence, location, size, density, and movement of patches) (Hulsman 1978; Hoffman et al. 1981; Duffy 1983, 1986). This approach may lead to a certain circularity, when differences in predator behavior—first assumed to reflect differences in prey patches—are later offered as evidence for behavioral adaptation (resource partitioning, mutualism) to the varying patch types (Duffy 1983, 1986).

We found that the behavior of the four primary whale-associating bird species varied markedly and consistently from one another at similar patches. That is, a single oceanographic event represented four separate kinds of patches to the birds. For kittiwakes, it represents a highly ephemeral but regularly recurring patch; for phalaropes, clustered patches of intermediate duration; for fulmars, a stable, isolated patch; and for the murres, a subsurface patch of denser-than-background prey. The disparate foraging abilities of these species appeared to define the characteristics of each patch. Kittiwakes are aerial foragers (Hoffman et al. 1981) whose buoyant flight and hovering ability allow them to effectively track resources through time and space. In contrast, fulmars are specialized for sustained, soaring flight, and appear to invest more time in a given patch once they have interrupted their aerial progress by settling. Red Phalaropes are intermediate in their behavior. They invest considerable time and effort in the search for productive patches, and utilize them extensively once they have settled. Thick-billed Murres appear to use their pursuit-diving ability to track settling patches in the vertical plane. Although the foraging behaviors differed, there was a high degree of overlap in type and size of prey that the three surface-feeding species took from whale plumes (Table 4; Fig. 5). We suggest that seabird ecologists must be cautious in interpreting the existence of differing foraging behaviors among species as evidence that they avoid competition by the use of different resources (e.g. Sealy 1973, Hoffman et al. 1981, Duffy 1986).

Flock composition.—Mixed-species flocks are widespread among seabirds and may account for the majority of feeding assemblages in many communities. Previous descriptions of mixed-species seabird flocks have emphasized functional roles of the constituent members, especially the tendency of certain nuclear species to initiate flocks, and the tendency for other kleptoparasitic and "suppressor" species to disrupt them (Sealy 1973, Hoffman et al. 1981, Duffy 1986). Such roles were conspicuously absent among the whale plume flocks. The regular interspecific associations that one might expect if certain species were acting as resource guides or catalysts to flock formation were absent. In particular, Black-legged Kittiwakes (identified as catalysts in other systems; Sealy 1973, Hoffman et al. 1981) were not regularly first to arrive at whale plumes, and they did not contribute to multispecies flocks more often than their general abundance would predict. We observed no kleptoparasitism or flock suppression.

We believe that the absence of functional roles among species sharing gray whale mud plumes is attributable to the characteristics of the patch. Compared with fish shoals or plankton swarms, whale events are highly conspicuous (even at large distances), large relative to the flock size, rich in easily captured prey, and ephemeral but recurring and potentially predictable. Equal access to information regarding the appearance of a patch may mitigate the usual reliance on mobile species as guides. Because prey is briefly but regularly abundant, competition for individual items may be minimized. The dynamics and the plasticity of interspecific behavior as a function of patch characteristics (size, quality, duration) warrant further attention by marine ornithologists.

Gray whales and Bering Sea bird ecology.—Associations between seabirds and gray whales account for the majority of observations of feeding birds of at least three species (Table 2). Whale-generated food may be important ecologically. Nearby King and St. Lawrence islands support large colonies of breeding seabirds, including Black-legged Kittiwakes and Thick-billed Murres, and their breeding seasons coincide with the nearby foraging (June–August) of gray whale herds.

The Northern Fulmars and Red Phalaropes

in the study region represented nonbreeding or postbreeding individuals, but their association with gray whales may also be important. Both species are migratory, and the phalarope winters at sea off Central America and South America. Based on the high densities we observed and their regular attendance at whale events, migratory Red Phalaropes may use the gray whale feeding-grounds of the Bering Sea as an important staging area, perhaps analogous to staging by inland migrating Wilson's (*Phalaropus tricolor*) and Red-necked (*P. lobatus*) phalaropes at terminal lakes of the western United States (Jehl 1981, 1986). Kumlien (1878) reported that associations between postreproductive Red Phalaropes and bowhead whales (*Balaena mysteceti*) were once so regular in waters adjacent to Greenland that early whalers routinely tracked aerial flocks of phalaropes to locate surfacing bowheads. Migratory staging with whales may have formerly occurred widely in this species.

California gray whales in the Bering Sea have returned to historic levels after decimation by whalers during the late 19th and early 20th centuries (Jones et al. 1984). Many other cetacean species have been less fortunate. Although gray whales are unique in their ability to deliver large quantities of benthic sediments within reach of surface-feeding birds, feeding associations between marine birds and various rorquals have been widely reported (Evans 1982). The impact of the virtual extirpation of great whales from many coastal and pelagic ecosystems upon the status and ecology of their former seabird associates is unknown.

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ANNUAL VARIATION OF PRIMARY MOLT WITH AGE AND SEX IN CASSIN'S AUKLET

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ABSTRACT.—In Cassin's Auklet (*Ptychoramphus aleuticus*) on Southeast Farallon Island, California, 1979–1984, we found significant annual and seasonal variation in timing and rate of primary molt in adult males, adult females, and subadults (1–2 years old). Except in 1979, adult males began to molt at least 10 days before adult females, and males molted at a slower rate. Subadult birds initiated molt later and molted faster, but showed less annual variation than adults. Timing of breeding and breeding success varied annually but were not correlated directly with molt. In years of extended breeding, molt rates were slower apparently in response to the energetic demands caused by the overlap of breeding and molt. *Received 17 October 1989, accepted 12 April 1990.*

ANNUAL and seasonal variation in molt, as well as its overlap with other phenological events (e.g. breeding, migration), is rarely studied in wild birds. Only the broadest patterns of molt are known for most pelagic seabirds because they molt at sea, away from breeding colonies where they are most accessible. Minimal data are available for alcids because wing molt for most species is synchronous, which renders them flightless at sea. Consequently, most of the information on molt in alcids is based on museum specimens (Salomonsen 1944, Storer 1952) or on captive birds (Birkhead and Taylor 1977, Swennen 1977, but see Harris and Wanless 1990). The auklets (*Aethia* spp., *Cyclorrhynchus, Ptychoramphus*), however, molt their primaries over an extended period that overlaps with breeding (Payne 1965, Bédard and Sealy 1984).

Cassin's Auklet (*Ptychoramphus aleuticus*) lays a single egg and has an average 38-day incubation and 41-day nestling period. It is the only auklet with a subarctic distribution in the eastern Pacific (Manuwal 1974a, Ainley and Boekelheide 1990). A large breeding colony on Southeast Farallon Island (SEFI), California, is attended by auklets nearly year-round. The accessibility of this colony has accommodated numerous studies on the natural history and breeding biology of Cassin's Auklets (for a summary, see Ainley and Boekelheide 1990).

The Cassin's Auklet also is the only alcid known to double brood, though most Cassin's Auklets do so unsuccessfully (Ainley and Boekelheide 1990). In birds that double brood, molt may overlap extensively with breeding. In addition, this species undergoes significant annual variation in the timing of breeding and the amount of double brooding relative to oceanographic conditions (Manuwal 1974a, Ainley and Boekelheide 1990).

Payne (1965) showed that the progress and rate of molt are slower in Cassin's Auklets that have expended the most energy for breeding, although he was unaware that these birds can double brood. From 1979–1984, we studied the primary molt of Cassin's Auklets on SEFI to investigate further the effects of breeding on molt in consideration of the potentially confounding variables of individual age, sex, and body weight.

STUDY AREA AND METHODS

Southeast Farallon Island is located 42 km west of San Francisco and supports the largest breeding colony of seabirds in the continental United States (Ainley and Boekelheide 1990). Manuwal (1974a, b, 1979) described the breeding colony and habitats used by Cassin's Auklets on SEFI.

We used a 20 × 5 m fish net (1.27-cm² mesh) to capture and band birds as described by Ralph and Sibley (1970). The net was opened 2 to 3 times per month ca. 1 h before dawn when birds began to leave the colony for the day. Sampling dates varied each month until approximately 100 birds were captured. We recorded the following information on each captured or recaptured bird:

1. Weight—Measured to nearest gram.
2. Eye color—To estimate age we modified the methods of Manuwal (1978) to include nine (instead of four) pigmentation categories: from 1.0 (white eye) to 5.0 (dark eye) in scoring increments of 0.5. Birds

with dark eyes (≥3.5) were considered subadults (assumed nonbreeders, 1–2 yr old), and those with light eyes (≤3.0) were considered adult (assumed breeders). Accuracy of these criteria was tested by examination of known-age breeders on SEFI in 1988 and 1989.

3. Bill dimensions—Width and depth (in mm) were greatest at anterior edge of nares (Nelson 1981). Birds with a bill depth (or average bill depth from multiple captures) of >10.3 mm were classified as males, and those with a depth of <9.5 mm, females. Although Nelson (1981) found most females to have a bill depth of <10.3 mm, we used a stricter definition to account for multiple-observer and measurement error. Subadult birds were not sexed.
4. Primary molt—Molting feathers were scored as either old (score 0), missing, or growing. Growing feathers were classified into one of six stages of growth: pin or 1/10, 3/10, 5/10, 7/10, or 9/10 grown, or new. These categories were recoded with standardized methods (e.g. Newton 1966, Ginn and Melville 1983). Accordingly, primaries (P1 to P10) in pin were scored as 1, 1/10 to 3/10 grown were scored 2, 5/10 was scored 3, 7/10 to 9/10 were scored 4, and new primaries were scored 5. Summation of scores for all 10 primaries provided the *molt score* for each captured bird. We did not collect data on body or secondary molt, and hereafter *molt* refers to primary molt.

We used molt score rather than feather mass (see Summers et al. 1983) in our analysis. In Cassin's Auklet, P10 is only 25–29% longer than P1, and P7–P10 are nearly equal in length (within 2 mm; $n = 9$). Thus, we assume that a change in the amount of feather mass replaced during molt in Cassin's Auklet probably does not affect molt rate as it does in other Charadriiformes (Summers et al. 1983, Underhill and Zucchini 1988, Underhill et al. 1990).

We measured birds that were captured before, during, and after the molt period. Birds recaptured within the same month were excluded. These "Type II" data provided estimates of molt parameters with the smallest bias (see Underhill and Zucchini 1988). We did not use Underhill and Zucchini's (1988) numerical algorithm to estimate molt parameters because it relies on a linear relationship of molt rate with time. This relationship is not always linear in Cassin's Auklet (Payne 1965, and data here).

We used linear regression of Julian date on molt score (Pimm 1976) for all birds captured from April through October to estimate molt parameters for each year. The slopes of regression lines produced by this method do not give molt rate, but an inversion of molt rate (rate^{-1}). Although our statistical comparisons are based on the regression values, for clarity in discussing relationships of molt with age and sex, we refer to actual molt rates. All regression analyses were completed with SPSS/PC+ (Nurusis 1986).

Annual variation in molt among sex and age classes was assessed with an analysis of covariance (ANCOVA) on SPSS/PC+. The relationships of molt with body weight, timing of breeding, and breeding success were compared using Spearman's rank correlation (r_s, $P < 0.05$). We determined annual mean (±SD) laying dates (MLD) and breeding success (BS) of Cassin's Auklets from a sample of monitored nest sites (Ainley and Boekelheide 1990). Although MLD implies a normal distribution in laying dates, in Cassin's Auklets this distribution is often skewed towards the earlier part of the laying period (Ainley and Boekelheide 1990). The use of median laying dates resulted in a ranking of years similar to that by mean laying dates. We used data from first clutches only (excluding relays) to calculate MLD. *Breeding success* is the average number of chicks fledged per pair laying.

RESULTS

We confirmed our age classification of Cassin's Auklets by examining eye color of 53 known-age breeders on SEFI in 1988, and 89 in 1989. No breeders in either year had an eye color score of >3.0 (the maximum value used to identify adults captured in the net). The sample included 4 two-year-old birds (the earliest age of first breeding in this species) in 1988 and 10 in 1989. Thus, most birds with an eye color of >3.0 are probably one-year-old subadults.

We used the percentage of birds that initiated molt (P1 missing or growing) each month, from April through December, to assess annual variation in molt timing and duration. Monthly percentages of adult males, adult females, and subadults in molt for breeding seasons 1979–1984 indicate that, in all years except 1983, most birds (>50%) were molting by June (Fig. 1). All captured birds were in molt by July in each year. Any annual variation in these percentages occurred in May and June. Relatively more birds were in molt during May in 1980 and 1984, and fewer during June in 1979 and 1983, than in all other years.

Molt parameters.—The use of linear regression of Julian date on molt score has been criticized because most data are heteroscedastic (lacking homogeneity of variance), sampling dates are not random, and the results often underestimate the timing and rate of molt (Underhill and Zucchini 1988). We evaluated the effects of these problems on our data with an examination of scatterplots of regression variables. Plots for each year of data on adult and subadult auklets (see

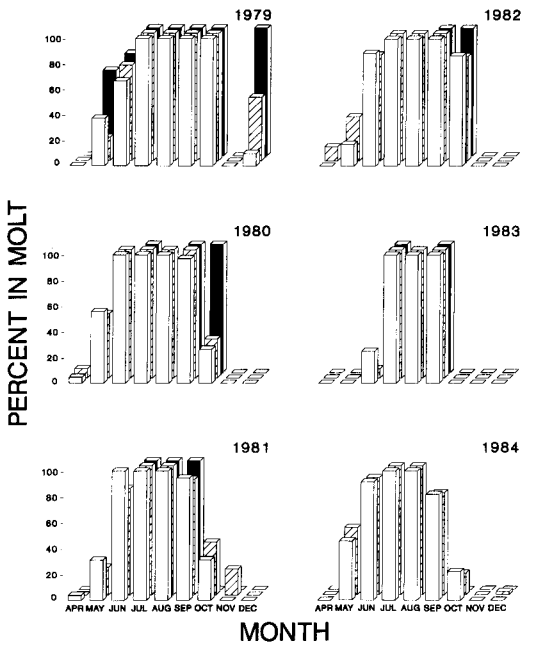

Fig. 1. The monthly percentage of adult males (open bars), females (hatched bars), and subadults (solid bars) in molt (missing or growing at least one primary) captured on Southeast Farallon Island, April through December, 1979–1984. A decrease in percentages after August each year denotes birds that have completed molt. Missing bars indicate absence of data, or when no captured birds were in molt (see Appendix 1 for sample sizes).

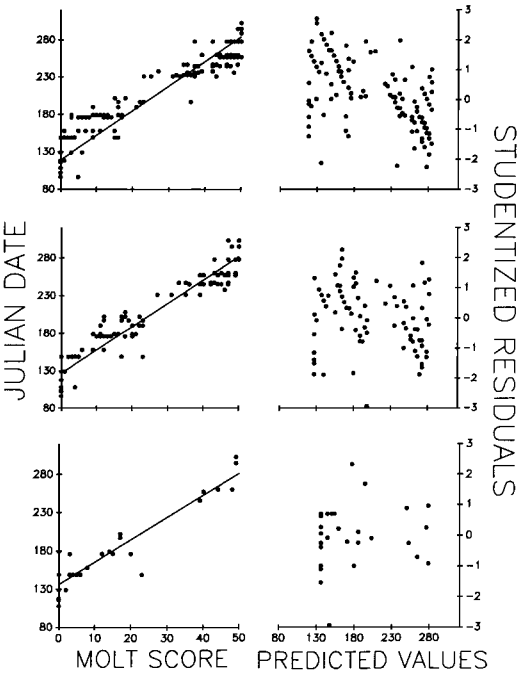

Fig. 2. SPSS/PC+ scatterplots of Julian date with molt score (left) and Studentized residuals with predicted values (right) for adult male (top), female (middle), and subadult (bottom) Cassin's Auklets captured on Southeast Farallon Island, April–October 1980 (see Table 1 for sample sizes and regression equations).

Fig. 2 for 1980) indicated that not all regressions are homoscedastic, which resulted in an underestimate of molt parameters. In most years, fewer than 50% of the birds were in molt by the initiation date estimated from regression (Fig. 1, Table 1). In 1980 and 1984, >50% of the adults were molting by the estimated date, a pattern that supports the regression model. Although most of the molt parameters were slightly underestimated, they provided relative differences in timing and rate of molt for adult males, adult females, and subadults.

Except in 1979, adult males began molt at least 9–10 days earlier than females (Table 1). In 1979, females began 9 days earlier than males. Molt duration was at least 11 days longer in males except in 1979.

Subadults began molt later than adults, and molted more rapidly, in 1979–1982. The 1983 and 1984 samples were too small for statistical comparison (Table 1). Significant variation in molt rate (all years combined) was apparent in adult males and adult females (ANCOVA, $P < 0.01$), but not in subadults ($P = 0.06$). Seasonal variation of molt rates between the sexes was significant in 1981–1984 (ANCOVA, $P < 0.05$, $F \geq 4.52$), but differences between adult females and subadults in 1979–1982, and between adult males and subadults in 1979, were not ($P > 0.05$, $F \leq 3.54$).

Body weight, molt, and breeding.—Mean bimonthly weights of adult male and adult female auklets vary significantly in all years (ANOVA, $P < 0.01$). Auklets of both sexes obtain their peak annual weight in winter, before breeding, and their lowest in summer, during and after breeding (see Fig. 3 for 1979 and 1982). A significant interaction between bimonthly period and sex occurred only in 1982 ($F = 3.31$, $P = 0.011$). In that year, males lost relatively less weight during breeding (May–June) than females, and gained weight at a higher rate after breeding (July–October) (Fig. 3).

Mean weights of adults in February is cor-

TABLE 1. Estimated molt parameters using linear regression of Julian date of capture on molt score for adult males, females, and subadult Cassin's Auklets on Southeast Farallon Island, 1979–1984. For each sample period, the top row is the regression equation (sample sizes in parentheses); the middle row is the standard error of the y-intercept and slope, respectively; and the bottom row is the estimated timing and duration (number of days in parentheses) of molt using molt score (x) values of 0 (no molt) and 50 (molt completed) in the regression equation. The y-intercept is mean Julian date of molt initiation, and the slope is the inverse of the mean molt rate (higher numbers indicate slower rates). All regressions have $r^2 > 0.83$.

Year	Males	Females	Subadults
All	$y = 129.7 + 3.21x$ (887) 0.89, 0.032 10 May–18 Oct (161)	$y = 140.6 + 2.92x$ (1,000) 0.86, 0.032 21 May–14 Oct (146)	$y = 143.9 + 2.92x$ (87) 2.86, 0.132 24 May–17 Oct (146)
1979	$y = 140.5 + 3.19x$ (178) 2.05, 0.075 21 May–27 Oct (159)	$y = 132.3 + 3.47x$ (52) 3.89, 0.159 12 May–2 Nov (174)	$y = 139.2 + 3.35x$ (24) 7.23, 0.278 19 May–3 Nov (168)
1980	$y = 118.7 + 3.32x$ (237) 1.77, 0.057 30 Apr–12 Oct (166)	$y = 126.9 + 3.10x$ (131) 2.45, 0.077 8 May–10 Oct (155)	$y = 136.1 + 2.91x$ (34) 4.03, 0.196 17 May–10 Oct (146)
1981	$y = 132.5 + 2.98x$ (143) 1.81, 0.068 13 May–9 Oct (149)	$y = 141.2 + 2.74x$ (184) 1.91, 0.067 21 May–5 Oct (137)	$y = 155.7 + 2.38x$ (14) 6.57, 0.296 5 Jun–2 Oct (119)
1982	$y = 128.8 + 3.35x$ (151) 2.09, 0.064 9 May–23 Oct (168)	$y = 148.5 + 2.91x$ (213) 1.89, 0.059 29 May–21 Oct (146)	$y = 152.3 + 2.75x$ (15) 3.99, 0.238 1 Jun–17 Oct (138)
1983	$y = 134.3 + 3.13x$ (73) 2.67, 0.117 14 May–18 Oct (157)	$y = 147.3 + 2.77x$ (179) 2.11, 0.089 27 May–13 Oct (139)	— — —
1984	$y = 129.0 + 3.17x$ (110) 2.10, 0.091 10 May–16 Oct (159)	$y = 138.4 + 2.89x$ (254) 1.48, 0.068 19 May–11 Oct (145)	— — —

related with timing of breeding (mean laying date) (Table 2 and Fig. 3; $r_s = 0.83$, $P < 0.05$). Timing of breeding also is correlated with the percentage of double-brooded birds (Table 2). In years of early breeding, relatively more birds attempted a second brood ($r_s = 0.90$, $P < 0.01$). Timing of molt is not correlated with the percentage of birds with double broods ($r_s < 0.3$).

Timing and rate of molt are not correlated with timing of breeding for males or females, or with breeding success ($r_s < 0.6$). The seasonal percentage of birds that molted only one primary versus those that molted two or more primaries simultaneously correlated significantly with the percentage of birds each year that double brood (Table 2; $r_s = 0.83$). Fewer birds molted more than one primary at one time in years of high incidence of double brooding. Annual timing of molt in males ($r_s = 0.94$), but not in females ($r_s = 0.09$), is correlated with timing and rate of weight gain after breeding (Fig. 3). Males initiated molt later in years when weight gain was delayed relative to other years.

Individual molt parameters.—In birds captured at least twice during molt, the mean (±SD) molt rates of recaptured birds ($\bar{x} = 3.06 \pm 1.14$, $n = 128$, all years) are comparable to those estimated by linear regression (Table 1). An exception is 1983 when recaptured birds show a faster mean molt rate ($\bar{x} = 2.32 \pm 0.75$, $n = 30$) than the estimate. In addition, 5 of 13 birds captured three times during molt showed little or no change in molt rate between captures (<1.0 unit difference). Of the remaining 8, 6 slowed their rate by as much as 1.5 to 29.6 units. The bird with the greatest decrease apparently arrested molt in its late stages, between 16 October and 20 December 1979.

Arrested molt in Cassin's Auklets is not unusual. Payne (1965) observed one such bird in July 1965. In June 1989 we captured two birds that had 3–4 new (and all remaining old) primaries. Both birds were incubating a second clutch.

DISCUSSION

We did not collect data on body or secondary molt. Subadult Cassin's Auklets molt body feathers in spring, before adults begin (Manu-

wal 1978). Adult body feathers are molted in relation to breeding status. Payne (1965) found that adults without eggs or young were more advanced in body molt than those with eggs or young. Secondary feather molt begins after primary molt and may overlap slightly. For the entire molt, subadults begin earlier, and complete molt sooner, than adults. Adults overlap body and primary molt with breeding, and may continue molt throughout the autumn.

Our results agree with Payne (1965). Cassin's Auklets can alter timing and rate of molt in relation to breeding effort, apparently as a means to balance the energetic demands of both. Unfortunately, during Payne's study, which occurred for 1 week in July 1964, it was not known that Cassin's Auklets often attempt a second brood (see Manuwal 1974a, b). He was unaware of the true breeding status of birds captured in burrows. Auklets without eggs may have been nonbreeders or individuals that had completed a first clutch, and those on fresh eggs may have been attempting a second brood.

We confirm Payne's conclusion that there is less energy available for molt in auklet breeders than in nonbreeders and postbreeders. The energetic costs of breeding depress molt rates in adults, and the lack thereof for subadults may account for the lower variation in their molt cycle. In two other auklets (*Aethia pusilla* and *A. cristatella*), failed breeders and nonbreeders (and presumably subadults) molted body feathers earlier and faster than breeders (Bédard and Sealy 1984).

Surprisingly, male Cassin's Auklets appeared to be more responsive than females to the energetic demands that render molt incompatible with breeding. In all years except 1979, males molted earlier and slower than females. This difference may be related to body size—mean

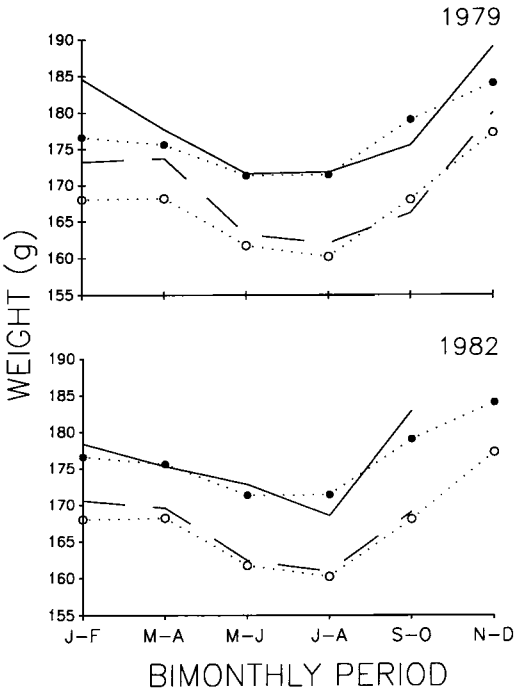

Fig. 3. Mean bimonthly weights (g) of adult male (——) and female (- - - - -) Cassin's Auklets in 1979 and 1982 on Southeast Farallon Island ($n > 10$ for all points). Means (1979–1984) for males (·····●·····) and females (·····○·····) are plotted for comparison. Abbreviations: J-F (January–February), M-A (March–April), M-J (May–June), J-A (July–August), S-O (September–October), N-D (November–December).

(±SD) weight of males (176.0 g ± 11.1, n = 1,492) is significantly greater than that of females (165.7 g ± 11.3, n = 1402; t = 24.73, $P <$ 0.001) and may affect energy demands for molt. These differences do not explain the pattern in 1979, when males molted later and faster than females.

TABLE 2. Annual mean egg-laying date and chicks per pair ($\bar{x}$ ± SD), percentage of adults captured that were molting one versus more than one primary at a time in June and July, and the percentage of birds each year with double broods, for Cassin's Auklets on Southeast Farallon Island, 1979–1984 (sample size is in parentheses; data on double broods from Ainley and Boekelheide 1990).

Year	Mean egg-laying date	Chicks per pair	% molting 1 P	% double brooding
1979	1 Apr ± 8.4 (76)	0.63 ± 0.35 (75)	40 (63)	41.3 (75)
1980	23 Apr ± 6.5 (78)	0.61 ± 0.49 (77)	27 (63)	0.0 (78)
1981	9 Apr ± 7.7 (80)	0.67 ± 0.44 (76)	9 (64)	8.5 (82)
1982	9 Apr ± 14.1 (82)	0.59 ± 0.43 (81)	32 (68)	12.2 (82)
1983	29 May ± 6.2 (39)	0.23 ± 0.42 (39)	1 (73)	0.0 (40)
1984	11 Apr ± 8.4 (77)	0.63 ± 0.44 (77)	28 (107)	5.8 (103)

Primary molt may affect energy requirements for foraging. During chick rearing, both adults spend the day at sea and return to the colony only at night to feed food stored in the gular pouch to the chick (Speich and Manuwal 1974). Foraging occurs primarily in deep waters off the continental shelf, at least 50 km north or south of the island (Ainley and Boekelheide 1990), but may shift closer to the colony (<25 km) in summer (Briggs et al. 1988). The absence of one or more primaries on each wing would increase wing loading, especially with the extra weight of food in the gular pouch ($\bar{x} \pm$ SD of each load = 27.78 ± 9.69 g, n = 22, Manuwal 1974a), and the energetic demands for flight.

It is possible that males expend more energy for breeding. Burrows are reoccupied or excavated by Cassin's Auklets in December and January each year, when most birds return to the colony to begin breeding activities (Manuwal 1974a). Presumably males are responsible for territory defense, and perhaps for burrow construction (Ainley and Boekelheide 1990). Moreover, Thoresen (1964) observed that fighting and chasing behavior at the colony is common in this species, though the sex of the birds was not known. The importance of winter site defense for future breeding is elevated on Southeast Farallon Island by the presence of a "floater" population (Manuwal 1974b). Thus, males may have to defend their nest burrows during the postbreeding season each year. Perhaps as a consequence of extended energy demands for breeding, especially in years of double brooding, body weight of males—but not females—correlates with timing of molt.

That males molted after females only in 1979 may be explained by higher mean body weights in January and February than in any of the next five years (Fig. 3). Breeding also began very early that year, which led to a higher incidence of birds attempting to double brood. Male Cassin's Auklets may delay molt more than females in years of early breeding because they are still expending energy for territory defense when the first clutch has fledged relatively early in the breeding season.

Our results and those of Bédard and Sealy (1984) indicate that extended overlap of molt with breeding in auklets causes considerable energetic stress. In Cassin's Auklet, the energetic demands of breeding and molt are independently unknown, but they are great enough to cause a slowing or suspension of molt. Although Cassin's Auklets apparently vary their timing of breeding and molt in relation to body weight, their ability to delay, slow, or arrest molt with breeding effort may explain why timing and rate of molt do not correlate with timing of breeding. We assume that body weight reflects food availability, which in the Gulf of the Farallons is influenced by sea temperature (Ainley and Boekelheide 1990). Annual variation in timing of body molt in the Black Guillemot (*Cepphus grylle*), a species that does not overlap breeding with molt, also appears to be correlated to sea temperature (Salomonsen 1944, Ewins 1988). Additional study is needed on the physiology of molt in Cassin's Auklets with known breeding status, and on the cost of reproduction for males and females, to understand fully the variation in timing and rate of molt.

Finally, the model proposed by Foster (1974) for birds that overlap breeding and molt is applicable to the molt cycle in Cassin's Auklet. In that model, birds will not overlap these two cycles unless there is a selective advantage to do so. In the Gulf of the Farallones, where annual food availability is often high but unpredictable, it appears that auklets have evolved a compromise of a single egg, an ability to raise a second brood when possible, and a prolonged primary molt overlapping breeding effort to reduce the rate of energy consumption.

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APPENDIX 1. Sample sizes by month of the number of adult male (M), female (F), and subadult (S) Cassin's Auklets captured on Southeast Farallon Island, April through December, 1979–1984.

Year		Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1979	M	13	35	18	30	13	42	27	0	10
	F	10	11	4	7	4	10	6	0	4
	S	3	3	5	3	1	6	5	0	1
1980	M	64	27	28	9	20	34	22	44	21
	F	14	22	20	14	5	31	23	12	10
	S	4	27	7	3	0	5	2	3	2
1981	M	26	29	23	20	9	19	16	15	6
	F	21	28	40	21	22	29	22	10	1
	S	1	0	9	2	1	2	3	0	0
1982	M	24	29	18	2	4	13	60	0	0
	F	9	32	42	9	24	30	67	0	0
	S	0	6	7	0	0	2	1	0	0
1983	M	10	21	8	7	12	13	2	0	12
	F	8	39	14	36	42	28	4	0	5
	S	0	1	0	4	0	11	0	0	0
1984	M	31	35	12	4	7	11	9	0	24
	F	52	50	61	27	12	38	6	0	41
	S	1	1	0	0	0	0	0	0	0

TESTS OF THREE HYPOTHESES OF HATCHING ASYNCHRONY IN THE COMMON TERN

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ABSTRACT.—We examined three hypotheses concerning hatching asynchrony in the Common Tern (*Sterna hirundo*). Survival of third-hatching "C-chicks" was significantly lower than that of "A-" and "B-chicks" in broods of three. In 2 yr when conditions did not appear favorable, survival was significantly higher in manipulated broods in which chicks hatched synchronously (73%) than in nonmanipulated broods (56%). Chicks in synchronous broods grew significantly faster than C-chicks and at a rate similar to A- and B-chicks. These results were inconsistent with the brood-reduction hypothesis, which predicts that hatching asynchrony will maximize brood success under conditions of food limitation. Chicks hatching from C-eggs grew significantly faster and survived at nonsignificantly higher rates when an older sibling was removed experimentally. These results were consistent with the hypothesis that C-chicks serve as insurance against loss of an older sibling. All three siblings, however, survived in 26% of nonmanipulated broods, which indicates that the sole function of the C-chick was not insurance. Predation on tern eggs was common and was correlated with numbers of migrating Ruddy Turnstones (*Arenaria interpres*). The percentage of time adults incubated was lower when only one egg had been laid than when two or three eggs were laid, and egg predation was most frequent during this initial stage. Although hatching asynchrony did not maximize chick survival, incubation before laying is completed may maximize overall nest success by protecting eggs from predators. *Received 19 July 1989, accepted 28 April 1990.*

MANY birds begin incubation before completion of a clutch of eggs. Hatching asynchrony is the result. Survival frequently decreases with hatching order (for reviews, see O'Connor 1978, Clark and Wilson 1981, Hahn 1981). One of the most widely cited explanations of hatching asynchrony is Lack's (1954) "brood reduction" hypothesis (i.e. hatching asynchrony is an adaptation for adjusting brood size to an unpredictable food supply). Asynchrony creates a size hierarchy among siblings. Subsequent sibling competition or more parental attention to larger siblings leads to starvation of the youngest chick when conditions are poor. Resources are not wasted on the chick least likely to survive, and starvation of the entire brood is prevented. Alternatively, the last egg may serve as "insurance" against loss of an earlier-laid egg or an older sibling in species in which the entire brood rarely fledges or survives to breed (Graves et al. 1984). Hatching asynchrony ensures that the last sibling, in which the least resources have been invested, will be the one to die if the older siblings survive. A decrease in egg size with laying order can accentuate the size hierarchy within the brood through which the brood-reduction and insurance strategies operate (Slagsvold et al. 1984).

In Common Terns (*Sterna hirundo*; Nisbet 1973) and in larids in general (e.g. Parsons 1976), hatching is asynchronous, the last egg tends to be relatively small, and survival of the youngest sibling is reduced. Differential mortality by hatching order is usually viewed as adaptive in larids (but see Parsons 1976), either in terms of brood reduction (Langham 1972, Hahn 1981), insurance (Graves et al. 1984, Quinn and Morris 1986), or a strategy that combines both functions (Nisbet and Cohen 1975, Braun and Hunt 1983, Hebert and Barclay 1986). Few studies of larids, however, have offered strong experimental support for either hypothesis (but see Hahn 1981, Graves et al. 1984).

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In contrast, several recent hypotheses view differential mortality within broods simply as a side effect of hatching asynchrony or of incubation before the clutch is completed (reviewed by Hussell 1972, Clark and Wilson 1981). In fact, in apparent contrast to the predictions of the brood-reduction hypothesis, the majority of experimental studies that compare normal, asynchronously hatching broods with manipulated, synchronously hatching broods have failed to detect higher survival rates in asynchronous broods (see reviews in Amundsen and Stokland 1988, Skagen 1988). Specifically, relatively high survival was recorded in synchronous broods of gulls (Hebert and Barclay 1986; but see Hahn 1981), cormorants (Shaw 1985, Amundsen and Stokland 1988), herons (Fujioka 1985, but see Mock and Ploger 1987), and passerines (Slagsvold 1982; Haydock and Ligon 1986; Gibbons 1987; Skagen 1987, 1988; but see Magrath 1989). In most of these studies chick growth was also similar in synchronous and asynchronous broods (see Werschkul 1979). Although only a few of these studies indicated that conditions were food-limited (Hebert and Barclay 1986, Skagen 1988, Magrath 1989), they call into question the general applicability of Lack's hypothesis. Stokland and Amundsen (1988) suggested that selection pressures to begin incubation before clutch completion deserve critical attention.

We tested the brood-reduction and insurance hypotheses in the Common Tern under conditions of food limitation. We also attempted to determine whether onset of incubation before clutch completion could reflect predation pressure during the egg-laying period (the "egg protection hypothesis"; Parsons 1976). In this species, partial incubation begins with the first of 3 eggs (Nisbet and Cohen 1975), and the chicks hatch asynchronously, usually over 1.5–3 days (Courtney 1979). Mortality is higher for last-hatching "C-chicks" than for "A-" or "B-chicks" (Langham 1972, Nisbet 1973). Our objectives were to determine (1) whether manipulated broods with synchronous hatching were as successful as nonmanipulated broods; (2) the frequency with which all 3 chicks in a brood survived; (3) whether chicks hatching from C-eggs had higher survival rates after removal of an older sibling; and (4) whether constancy of incubation was related to frequency of egg predation.

Methods

We studied Common Terns breeding on Oneida Lake, Oswego County, New York, in 1983–1985. Approximately 350 pairs of terns nested on two small, rocky shoals (0.046 and 0.120 ha). We marked each egg with waterproof ink and weighed eggs in 1983–1984 with a 50-g Pesola scale. We weighed most eggs within 24 h of laying; other eggs were weighed twice at a 7–10-day interval, and the initial weight was determined as in Rahn et al. (1976). We checked each nest daily for evidence of egg predation. To aid in the recapture of chicks, in 1983–1984 we enclosed groups of nests with 0.4-m-high wire mesh fences before hatching (Nisbet and Drury 1972a). During the hatching period we checked each nest 1–2 times daily for new chicks. Each chick was weighed at hatching and banded with a USFWS aluminum leg band.

We recorded chick growth and survival in 1983–1984. In 1985 we recorded survival only. We searched for dead chicks daily in 1983–1984. In 1983 each chick was weighed daily until it died or escaped from its enclosure. In 1984 we weighed each chick within its enclosure every 1–2 days until days 11–14, and subsequently we made four colony-wide chick censuses. These censuses, which were facilitated by the small size and sparse vegetation of the islands, were virtually complete (>95%) counts of chicks (Bollinger 1988). Chicks alive at ≥day 18 in 1983–1984 were considered to have survived, because some chicks were able to escape from the enclosures before fledging at ≥22 days of age (Nisbet and Drury 1972a). In 1985 we searched the area around each nest daily until the chicks reached day 10, and subsequently we made three colony-wide censuses. We considered chicks alive at ≥day 10 in 1985 to have survived, because 92% of 73 chick deaths occurred by this age in 1983–1984 (see also Langham 1972, Nisbet and Drury 1972a).

Brood types studied.—We studied nonmanipulated, asynchronously hatching ("asynchronous") broods of 3 chicks, raised by their own parents, in 1983–1985 (n = 16 broods in 1983, 35 in 1984, and 15 in 1985). In 1984 we also created 18 "A/B-removal" broods from nests originally containing 3 eggs. We removed the first or second egg (4 nests) or chick (at ≤2 days of age; 14 nests) before hatching of the C-egg. The chick from the C-egg in an A/B-removal brood was denoted the "B-chick" and its older sibling, the "A-chick."

In 1984 we created 20 "synchronous" broods by placing together 3 randomly selected chicks hatching within 12 (≥70% of the broods) to 20 h of one another. Chicks in synchronous broods (i.e. "synchronous chicks") were transferred when first found, within 12 (≥68% of the broods) to 24 h of hatching. (No deaths had occurred among asynchronous chicks when first found on the day of hatching.) In 1985 we created 15 synchronous broods of 3 chicks, in which siblings

hatched within 24 h of one another and were transferred within 14 (≥60% of the broods) to 24 h of hatching. In each year only adults that laid 3 eggs were given synchronous broods.

Incubation constancy and egg predation.—In 1985 we used a blind to observe 58 nests, each for an average of 5 consecutive days. Three 1-h observations were made daily from 28 May to 9 June, with morning (0845–1300) and afternoon (1300–1800) sessions on alternate days. The presence or absence of incubating terns at each nest was recorded at 5-min intervals. At the beginning and end of each session we recorded the number of eggs depredated at each focal nest and the number of Ruddy Turnstones (*Arenaria interpres*) visible on the island.

Statistical methods.—We calculated individual chick growth rates from weights at days 1–11, a period in which growth was exponential (LeCroy and LeCroy 1974). Linear regressions of ln(weight) vs. age were performed for all chicks for which at least 4 weights were available. We used *t*-tests to compare mean growth rates of groups of chicks, and Chi-square and Fisher's exact tests to compare numbers of chicks that survived in different groups. We combined data from 1984 and 1985 for analysis when significant differences ($P < 0.05$) in survival rates (Chi-square tests) or in means (*t*-tests) and variances (*F*-tests, Snedecor and Cochran 1980: 98) did not occur between years.

RESULTS

Egg weights and hatching asynchrony.—Clutches of 3 eggs represented 70% of all clutches. Egg weight decreased as each egg was laid in 3-egg clutches (two-way ANOVA, $P < 0.0001$, $n = 235$ clutches; paired *t*-tests, $P < 0.05$). Although chicks used in synchronous broods were selected randomly, eggs from which synchronous chicks hatched ($\bar{x} \pm SD = 20.7 \pm 1.3$ g, $n = 50$) were similar in weight to eggs of C-chicks (20.8 ± 1.7 g, $n = 31$; *t*-test, $P > 0.75$) and lighter than eggs of A-chicks (21.4 ± 1.7 g, $n = 25$; $P < 0.05$) in asynchronous broods.

Laying intervals averaged 1.9 ± 0.8 days between the A- and B-eggs, and 1.8 ± 0.6 days between the B- and C-eggs ($n = 118$ clutches). Asynchronous broods hatched over 1–3 days, with mean intervals of 0.7 ± 0.6 days between the A- and B-chicks, and 1.2 ± 0.7 days between the B- and C-chicks ($n = 50$ broods). No asynchronous brood hatched in ≤24 h; in contrast, all synchronous broods hatched within 24 h, with a mean interval of 0.5 ± 0.5 days ($n = 35$).

Seasonal variation.—Clutch initiation occurred from 24 May to 24 July in 1983, 19 May to 25 July in 1984, and 15 May to 23 July in 1985. Approximately 75% of all clutches were initiated in the first one third of the laying period in 1983 and 1984 (i.e. by 10 June), and in the first one half of the season in 1985 (by 15 June). Our analyses included only chicks that hatched from clutches started during or near these major periods of clutch initiation. We studied asynchronous and synchronous chicks that hatched between 21 June and 5 July in 1983, 15 June and 16 July in 1984, and 17 June and 11 July in 1985; chicks continued to hatch at least until 6 August 1983, 11 August 1984, and 1 August 1985.

In no year were there significant correlations between hatching date and chick survival (1983: Spearman's rho = −0.183, $P > 0.10$, $n = 60$; 1984: rho = −0.047, $P > 0.25$, $n = 305$; 1985: rho = −0.120, $P > 0.25$, $n = 90$) or chick growth (1983: rho = 0.40–0.67, $P > 0.10$; 1984: rho = −0.12–0.08, $P > 0.50$). Furthermore, in 1984, the year in which we studied chicks over the longest hatching period, survival of asynchronous chicks was almost identical in the middle of the focal hatching period (27 June–10 July; 56% survival, $n = 45$) and the remainder of this period (57% survival, $n = 58$; $P = 0.90$). Therefore, within each year we combined all chicks for further analyses.

The brood-reduction hypothesis.—In order to evaluate the extent of food limitation in the experimental years, we compared survival rates in 1984 and 1985 with those in 1983. The overall survival rate (i.e. all siblings combined) in asynchronous broods was significantly higher in 1983 than in 1984 or 1985, although 1984 and 1985 did not differ for either asynchronous or synchronous broods (Table 1). Similarly, survival was higher in 1983 than in 1984 and 1985 combined for both A- and B-chicks in asynchronous broods ($P < 0.025$), although survival of C-chicks did not vary significantly between these years ($P > 0.50$; Fig. 1). The average growth rates of A- and C-chicks that survived were greater in 1983 than in 1984 ($P < 0.05$; Table 2). C-chicks that survived grew significantly faster than those that died; similar trends were observed for B-chicks and synchronous chicks (Table 2). These results indicate that food was not plentiful in the experimental years.

Chick survival varied with hatching order in asynchronous broods. A- and B-chicks survived more often than C-chicks (Fig. 1) and at rates similar to one another each year ($P > 0.10$). Growth rates also varied in 1984 (ANOVA, $P < 0.005$): A- and B-chicks that survived had similar

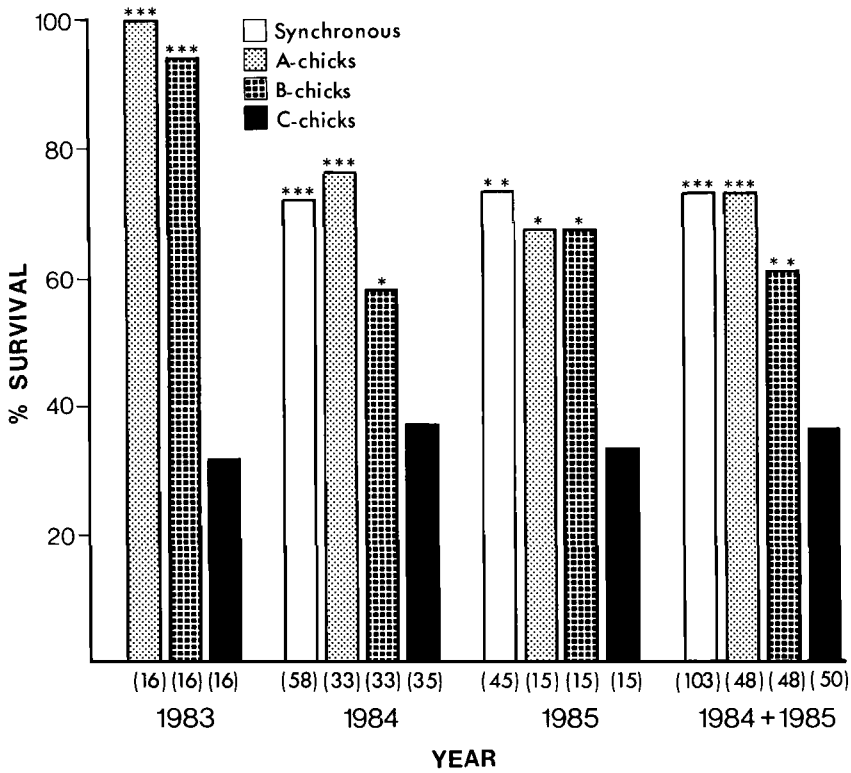

Fig. 1. Variation in rates of survival among synchronous chicks and A-, B-, and C-chicks in asynchronous 3-chick broods of Common Terns. Asterisks indicate differences in survival rates between C-chicks and the other chick classes (Chi-square tests, 1 df). Sample sizes are in parentheses; * = $P < 0.10$; ** = $P < 0.025$; *** = $P < 0.005$.

growth rates, but both grew faster than C-chicks (Table 2). In contrast, in 1983 there were no significant differences in growth rate among A-, B-, or C-chicks that survived (ANOVA, $P > 0.50$; Table 2).

Asynchrony did not maximize brood success. The mean number of chicks that survived per brood and the overall survival rate were higher in synchronous than in asynchronous broods in both 1984 and 1985 (Table 1). Synchronous chicks survived more often than C-chicks (Fig. 1) and at rates similar to those of A-chicks ($P > 0.50$) and B-chicks ($P > 0.10$) in both years. Furthermore, synchronous chicks that survived grew faster than C-chicks ($P < 0.01$) and similarly to A-chicks ($P > 0.25$) and B-chicks ($P > 0.90$; Table 2), with mean weights at days 13–14 similar in both brood types (synchronous: 88.1 ± 17.6 g, $n = 12$; asynchronous: 85.2 ± 9.7 g, $n = 19$; t-test, $P > 0.50$). Age at death also did not differ significantly between synchronous ($\bar{x} = 6.7 \pm 4.2$ days, $n = 28$) and asynchronous chicks (5.8 ± 2.9 days, $n = 64$) in 1984 (t-test, $P > 0.90$) or 1985 ($P > 0.10$). Similarly, the proportion of broods in which all 3 chicks died, and the ratio of partial brood success (1–2 chicks surviving) to complete brood failure, did not differ significantly between brood types (Table 3). However, the proportion of broods in which all 3 chicks survived tended to be higher for synchronous than asynchronous broods (Table 3).

The insurance hypothesis.—Chicks hatching from C-eggs grew significantly faster in A/B-removal broods (B-chicks) than in asynchronous 3-chick broods (C-chicks), and survived at nonsignificantly higher rates (Table 4). B-chicks in A/B-removal broods grew and survived at rates almost identical to those of B-chicks in asynchronous 3-chick broods (Table 4). All 3 siblings survived in 31% (1983, $n = 16$), 20% (1984, $n = 35$), and 33% (1985, $n = 15$) of asyn-

TABLE 1. Comparison of Common Tern brood success between asynchronous and synchronous 3-chick broods and between years.[a] Within each brood type, values followed by the same letter do not differ between years ($P > 0.05$). Values for 1984 + 1985 were compared only with values for 1983. Sample sizes are in parentheses.[b]

Year	Asynchronous	Synchronous	Asynch. vs. Synch.
	No. surviving per brood (±SD)		
1983	2.3 ± 0.6a (16)	—	—
1984	1.7 ± 1.0b (33)	2.2 ± 0.9a (18)	$0.05 < P < 0.10$
1985	1.7 ± 1.2ab (15)	2.2 ± 0.9a (15)	$P > 0.25$
1984 + 1985	1.7 ± 1.0b (48)	2.2 ± 0.9 (33)	$P < 0.05$
	Percent overall survival		
1983	75.0a (48)	—	—
1984	56.3b (103)	72.4a (58)	$P < 0.05$
1985	55.6b (45)	73.3a (45)	$0.05 < P < 0.10$
1984 + 1985	56.1b (148)	72.8 (103)	$P < 0.01$

[a] Chi-square tests with 1 df were used for number surviving (% overall survival); Mann-Whitney *U*-tests were used for no. surviving per brood.
[b] Sample sizes for number surviving per brood were less than one third times those for % overall survival when fates of some of the siblings were unknown.

chronous broods, and in 42% (1984, $n = 19$) and 47% (1985, $n = 15$) of synchronous broods.

Egg predation and incubation constancy.—Predation of at least one egg occurred in 31% of 303 nests from 27 May to 9 June 1983, 51% of 329 from 24 May to 5 June 1984, and 45% of 247 from 28 May to 9 June 1985; by these dates 68%, 59%, and 45%, respectively, of all clutches had been started. Rates of predation were lower after these dates. In 1985 daily numbers of migrating Ruddy Turnstones and egg predation events were positively correlated between 28 May and 9 June ($r = 0.73$, $P < 0.01$, $n = 11$ days). In 9 of 19 instances of predation among focal nests, the eggs either had a small puncture or were split into two pieces; in the remaining instances the eggs were missing. We observed turnstones eating the contents of previously cracked eggs, and we observed a turnstone peck 1 of 2 eggs in a temporarily unattended nest. Ruddy Turnstones were generally ignored by terns. Of 19 focal nests that suffered predation, 16 were attended—at least sporadically—by an adult during the last observation period before egg loss.

Our activity in the colony did not appear to influence egg predation. Of the 19 predation events in focal nests, 13 (68%) occurred while we were off the island or in the blind. Predation patterns among the focal nests were similar to those observed in the entire colony (Table 5), although we created greater disturbance among focal nests. Furthermore, Ruddy Turnstones took flight more readily and returned to the colony more slowly than did the terns after human disturbance.

Incubation constancy varied among egg-laying stages (i.e. 1, 2, or 3 eggs laid) of 3-egg clutches observed at all 3 stages (Friedman's test [Conover 1980: 299], $P < 0.005$, $n = 5$). For clutches observed during more than 1 stage, incubation constancy was significantly lower at the 1-egg stage than at either the 2- or 3-egg stage, but it was similar at the 2- and 3-egg stages (Table 6). Similarly, egg loss occurred more frequently at the 1-egg stage than at either the 2- or 3-egg stage, but the 2- and 3-egg stages

TABLE 2. Mean growth rates[a] (±SD) of Common Tern chicks that survived and chicks that died (1983 and 1984), by hatching order (A = first; B = second; C = third). Within years, values followed by the same letter do not differ significantly (*t*-tests, $P > 0.05$). Sample sizes are in parentheses.

Chick class	Chicks that survived	Chicks that died[b]
	Asynchronous 1983	
A	0.179 ± 0.017a (16)	—[c]
B	0.170 ± 0.016a (16)	—
C	0.173 ± 0.025a (7)	−0.027 ± 0.061 (5)**
	Asynchronous 1984	
A	0.167 ± 0.014a (21)	0.166 ± 0.033 (6)^{NS}
B	0.163 ± 0.019a (15)	0.124 ± 0.078 (13)*
C	0.145 ± 0.016b (12)	0.000 ± 0.085 (17)**
	Synchronous 1984	
—	0.163 ± 0.019 (42)	0.110 ± 0.085 (11)*

[a] Growth rates are ln(g)/day weight gains in the first 11 days.
[b] *t*-tests between chicks that survived and chicks that died: ** = $P < 0.005$; * = $0.05 < P < 0.10$; ^{NS} = $P > 0.50$.
[c] Samples were too small to include in the analysis.

TABLE 3. Rates of partial brood success (PBS; 1–2 chicks survive per brood), complete brood failure (CBF), and whole brood survival (WBS) in asynchronous and synchronous 3-chick broods of the Common Tern (1984 and 1985 combined). Sample sizes are in parentheses.

	Brood type			
	Asynch.	Synch.	Asynch. vs. Synch.	Prediction
No. PBS/No. CBF	3.8 (30/8)	8.5 (17/2)	$P > 0.25$[a]	Asynch. > Synch.[c]
% CBF	16.0 (50)	5.7 (35)	$P > 0.10$[b]	Asynch. < Synch.[c]
% WBS	24.0 (50)	44.1 (34)	$0.05 < P < 0.10$[b]	Asynch. > Synch.[d]

[a] Fisher's exact test.
[b] Chi-square test, 1 df.
[c] Prediction based on brood-reduction hypothesis; from Hahn (1981).
[d] Prediction based on sibling rivalry reduction hypothesis; from Hahn (1981).

did not differ significantly (Table 5). Incubation constancy at the 1-egg stage was similar for nests that were damaged during this stage (65.6% ± 45.6, $n = 10$) and those that were not (68.2% ± 35.7, $n = 25$) (Mann-Whitney U-test, $P > 0.95$). However, incubation constancy at the 2- and 3-egg stages tended to be lower for nests that were depredated during these stages (63.4% ± 25.0, $n = 4$) than for those that were not (92.3% ± 13.8, $n = 21$; $P = 0.07$).

DISCUSSION

The brood-reduction hypothesis.—According to the brood-reduction hypothesis, the competitive weakness of younger siblings facilitates their early death when feeding conditions are poor (Lack 1954). This increases the chances of survival of the older siblings and maximizes the number of young that fledge. Furthermore, brood reduction should minimize the rate of complete brood failure and maximize the ratio of partial brood success to complete failure (Hahn 1981).

Conditions were sufficient for a brood-reduction strategy to operate at our colonies. C-eggs in 3-egg clutches hatched later and were significantly lighter than A- or B-eggs. Chick mortality was common and occurred early in the nestling period. C-chicks survived less often than A- or B-chicks in all three years. C-chicks also grew significantly more slowly than A- or B-chicks in 1 of 2 years. The major cause of chick mortality appeared to be starvation. Growth rates tended to be lower for chicks that died than for survivors. These dif-

TABLE 4. Comparison of survival and growth rates[a] between B-chicks in A/B-removal broods (which hatched from C-eggs) and chicks in asynchronous 3-chick broods of Common Terns in 1984.[b] Values followed by the same letter do not differ significantly between chick classes ($P > 0.05$).[c] Sample sizes are in parentheses.

Brood type/ chick class	Survival (%)	Growth rate of survivors ($\bar{x}$ ± SD)
A/B-removal		
B	55.6ab (18)	0.162 ± 0.018a (9)
Asynch. 3-chick		
A	75.8a (33)	0.167 ± 0.014a (21)
B	57.6ab (33)	0.163 ± 0.019a (15)
C	37.1b (35)	0.145 ± 0.016b (12)

[a] Growth rates are ln(g)/day weight gains in the first 11 days.
[b] Chi-square tests with 1 df were used for number surviving; t-tests were used for growth rate.
[c] For % survival of B- vs. C-chicks in 3-chick broods, $0.05 < P < 0.10$.

TABLE 5. Variation in frequency of egg predation by stage of egg laying (number of eggs laid) in the Common Tern, 28 May–9 June, 1985. Values followed by the same letter do not differ significantly between egg-laying stages (Chi-square tests with 1 df, $P > 0.05$).[a] Nests in the entire colony were checked daily; focal nests (observed during the incubation study) were checked 6 times daily.

	Entire colony	Focal nests
Predation events/nest-day[b]		
1-egg stage	0.15a	0.14a
2-egg stage	0.06b	0.05ab
3-egg stage	0.04b	0.04b
p[c]	<0.005	<0.05
Total predation events (n)	112	19
Total nests (n)	249	58
Total nest-days (n)	1,826	268

[a] For focal nests at the 1-egg vs. 2-egg stages, $0.05 < P < 0.10$.
[b] Nest-days were calculated by summing the number of days each nest was present.
[c] Chi-square test, 1-egg vs. 2-egg vs. 3-egg stage.

TABLE 6. Variation in incubation constancy by stage of egg laying (number of eggs laid), for Common Tern clutches observed during 2 stages, 28 May–9 June, 1985. Sample sizes are in parentheses.

Stage of egg laying	% time spent incubating ($\bar{x} \pm$ SD)	P^a
1-egg	68.3 ± 34.9 (20)	$P < 0.001$
2-egg	94.5 ± 10.7 (20)	
1-egg	53.1 ± 38.2 (6)	$P < 0.05$
3-egg	94.9 ± 8.1 (6)	
2-egg	81.6 ± 23.6 (11)	$0.05 < P < 0.10$
3-egg	90.8 ± 12.9 (11)	

[a] Wilcoxon signed-rank test.

ferences were minimum estimates, as growth was not measured for chicks that died within 4 days of hatching (33% of 105 dead chicks). These chicks showed little or no weight gain. Although bodies of young chicks deteriorated rapidly and were difficult to find among the rocks and vegetation, we found the bodies of 69% of the chicks that died. There was no evidence of predation on chicks, nor was there unusually poor weather in any year.

The brood-reduction hypothesis states that asynchronous broods should be more successful than synchronous broods if feeding conditions are poor. Even if brood reduction is a strategy that augments brood success during poor years and reduces success during good years, it can be adaptive only if gains made in poor years outweigh losses suffered in good years. Conditions did not appear favorable for chicks in 1984 and 1985, when nearly half of all chicks in normal 3-chick broods apparently died of starvation. Rates of chick survival (56% in normal broods) and growth were significantly lower in these years than in 1983. Although chick survival rates vary widely among studies of Common Terns (Morris et al. 1976), starvation rates are difficult to determine given unknown levels of predation. Other studies in which predation on chicks was apparently not a factor reported fledging rates similar to or higher than ours; e.g. 51, 60, and 89% for 3-chick broods (Langham 1972) and, for all brood sizes combined, 68–79% (LeCroy and LeCroy 1974) and 52–67% (Safina et al. 1988). Adult terns frequently stole fish from chicks in 1984, a behavior that may occur during food shortages (Hays 1970, Monaghan et al. 1989). This was not observed in 1983.

Contrary to the predictions of the brood-reduction hypothesis, survival was significantly higher in synchronous than asynchronous broods. Synchronous chicks also grew significantly faster than C-chicks and similarly to A- and B-chicks. Asynchrony did not reduce the rate of complete brood failure or increase the ratio of partial brood success to complete failure, as predicted. In fact, the differences were in the opposite direction (see also Gibbons 1987, Magrath 1989). The average age at death was similar in both brood types, which indicates that parents of synchronous chicks did not invest unduly in chicks that died (see also Shaw 1985, Skagen 1988; but see Haydock and Ligon 1986, Gibbons 1987). Furthermore, survival of A- and B-chicks varied between years, but that of C-chicks did not (see also Shaw 1985; but see Langham 1972). Thus, it appeared that C-chick survival depended less on food supply than did survival of older siblings (in contrast to one of the major predictions of the brood-reduction hypothesis).

The brood-reduction hypothesis implies that C-chicks are hatched asynchronously so as not to reduce survival of older siblings. However, A- and B-chicks in asynchronous broods did not survive more often than synchronous chicks, which indicates that asynchrony did not reduce costly competition on older siblings. Moreover, survival of B-chicks was significantly lower in 3-chick broods than in naturally occurring 2-chick broods (Bollinger 1988). We suggest that the presence of C-chicks did reduce survival of B-chicks (see also Graves et al. 1984, Hebert and Barclay 1986).

C-chicks in asynchronous broods may have starved unnecessarily (Bryant 1978, Werschkul 1979, Skagen 1988). Adults may have fed siblings more equitably in synchronous broods, as differences in growth rate among siblings tended to be smaller in these broods (Bollinger 1988). The size of a chick relative to its siblings appeared more important than absolute size in influencing its survival, because egg weights were similar for C-chicks and synchronous chicks.

Our results are consistent with several recent experimental studies that have failed to detect higher survival rates in normal, asynchronous broods than in synchronous broods. Among larids, synchronous Herring Gull (*Larus argentatus*) chicks survived as often as asynchronous chicks in a year when conditions appeared poor; syn-

chronous chicks grew similarly to A-chicks and faster than B- and C-chicks (Hebert and Barclay 1986). In contrast, manipulated, synchronous broods of Laughing Gulls (*L. atricilla*) had lower fledging rates, more complete failures, fewer complete successes, and a lower ratio of partial success to complete failure than asynchronous broods (Hahn 1981). It is not clear why Hahn's results differed from ours.

Higher fledging rate is not necessarily equivalent to greater lifetime reproductive success, if increased reproductive effort by parents will lower their future reproductive output. We do not have data to address this point. In addition, survival after fledging may be lower for larid chicks in larger broods (Nisbet and Drury 1972b), although Parsons et al. (1975) recorded lower postfledging survival in larger broods of Herring Gulls in only 1 of 3 years. Within the normal range of brood sizes, Glaucous-winged Gull (*L. glaucescens*) chicks that fledged in larger broods survived at least as well after fledging as those in smaller broods (Ward 1973). In our study, 7 of 75 synchronous chicks (9.3%) and 4 of 83 asynchronous chicks (4.8%) that fledged in 1984–1985 were captured as breeding adults in 1988 (H.-W. Yuan unpubl. data). Chicks that fledged in synchronous broods apparently did not return at lower rates. Furthermore, growth rates between days 1–11 and weights at days 13–14 were similar in both brood types, which suggests that synchronous fledglings were similar in quality to asynchronous young.

The insurance hypothesis.—According to the insurance hypothesis, the full brood rarely fledges (or survives to breed), and the last egg is laid as insurance in case an older chick dies or fails to hatch (Graves et al. 1984). The brood-reduction and insurance hypotheses are not mutually exclusive; asynchronous hatching may provide insurance benefits under poorer conditions and allow the entire brood to be raised under more favorable conditions (Nisbet and Cohen 1975). However, if the sole function of the C-egg is insurance, the C-chick should rarely fledge unless the A- or B-egg or chick dies. Although this has been suggested to be the usual case for Common Terns (e.g. Nisbet and Cohen 1975, Nisbet 1978), we found that survival of all 3 chicks was not rare in asynchronous broods (26%; see also Langham 1972, Nisbet et al. 1984) or synchronous broods (44%). The insurance hypothesis also predicts that survival of chicks from C-eggs will increase if an older sibling dies. Our data were consistent with this prediction. When first or second eggs or chicks were removed (A/B-removal broods), chicks hatched from C-eggs (B-chicks) grew significantly faster than C-chicks in 3-chick broods and survived more often than C-chicks, although the latter difference was not significant (see also Quinn and Morris 1986).

In sum, our data did not strongly support the insurance hypothesis. Given the results of the hatching synchrony experiment, mortality of the C-chick caused by asynchronous hatching does not appear to be beneficial in this species. Although egg size might be expected to increase, rather than decrease, with laying order to offset the negative effects of asynchrony (Slagsvold et al. 1984), we found no effect of egg size on survival in nonmanipulated 3-chick broods (Bollinger in prep.; but see Nisbet 1973, 1978). Decreased egg size may simply reflect the condition of the female as egg laying progresses and incubation begins (Houston et al. 1983, Pierotti and Bellrose 1986). A Common Tern's clutch accounts for approximately 45% of the female's body weight (Wiggins and Morris 1987), and size of the C-egg can be related to food intake by females (Nisbet 1973).

Alternative explanations of hatching asynchrony.—Hussell (1972) and Clark and Wilson (1981) proposed that some birds begin incubation before clutch completion for reasons other than to ensure sibling competition and differential mortality within the brood. Early incubation may speed hatching or fledging, so the young can make full use of declining resources, or so the time during which the nest is vulnerable to predation is reduced (Hussell 1972). However, the incubation and nestling periods of Common Terns are long (6–7 weeks total) relative to the hatching interval (1–3 days), so benefits from earlier hatching or fledging are probably minimal (Shaw 1985). Incubation may help to maintain egg viability (Arnold et al. 1987), but this seems unlikely to be important for the typically small tern clutch. Hatching asynchrony may spread out peak food demands of young (Bryant 1978). This assumption predicts that asynchrony will maximize brood success (this was not observed), or will reduce parental stress. An alternative function of the sibling dominance hierarchy to that of facilitating brood reduction may be to reduce wasteful sibling rivalry, thus increasing the proportion of nests that fledge the whole brood (Hahn 1981). In our study, whole brood success tended

to be less common for asynchronous broods. Degree of hatching asynchrony may also reflect physiological constraints on adults, such as food availability during the egg-laying period (Pierotti and Bellrose 1986).

Clark and Wilson (1981) suggested that early incubation minimizes the vulnerability of the nest to whole nest predation by speeding fledging to an extent determined by the relative risk of predation during the preincubation and fledging stages (see also Briskie and Sealy 1989). Whole nest predation after hatching is not common in Common Terns. Somewhat analogously, other researchers have suggested that, to reduce egg predation, some birds begin incubation before completion of laying (Blaker 1969, Parsons 1976; see also Skipnes 1983). Open-nesting colonial birds such as larids may be particularly susceptible to a variety of egg predators. Although hatching success varies widely among studies of Common Terns (Morris et al. 1976), Ruddy Turnstones can be important predators of tern eggs (Brearey and Hilden 1985, Morris and Wiggins 1986), and egg predation by conspecifics is common among gulls (e.g. Parsons 1976). Incubation may prevent egg predation more effectively than egg guarding (Thompson and Raveling 1987). Common Terns resumed incubation after chasing Ruddy Turnstones from previously unattended nests (Morris and Wiggins 1986, this study). Ruddy Turnstones pecked Sooty Tern (*Sterna fuscata*) eggs when incubating terns momentarily left their nests (Crossin and Huber 1969), and Arctic Tern (*S. paradisaea*) eggs were usually lost only when adults had been scared off their nests by Common Gulls (*Larus canus*) (Skipnes 1983). Furthermore, incubation may reduce predation when terns do not recognize another species as a potential egg predator, as may be the case with Ruddy Turnstones (Parkes et al. 1971).

Alternatively, egg protection may be a side effect—rather than the primary selective agent—of early incubation. This would help explain the consistency in patterns of incubation onset among larids regardless of observed predation pressure. Early incubation itself may be useful for some other reason (see above), or it may be an incidental trait without adaptive significance that results from constraints on hormonal mechanisms that control egg laying and incubation (Mead and Morton 1985).

In our experience egg predation was common during the egg-laying period. Ruddy Turnstone numbers and predation events were positively correlated, and egg losses fit descriptions of turnstone predation in other tern colonies (Parkes et al. 1971, Morris and Wiggins 1986). Although turnstones were present for only a relatively short time, this coincided with the initiation of a large portion (45–68%) of the Common Tern nests each year. Incubation constancy increased and egg predation decreased significantly during egg laying. Incubation also increased through egg laying in other studies of Common Terns (Nisbet and Cohen 1975, Courtney 1979), and Morris and Wiggins (1986) found that Ruddy Turnstone predation on Common Tern eggs occurred most often in nests containing only 1 egg. Predation of A-eggs exceeded that of B- and C-eggs in Herring (Parsons 1976) and Glaucous-winged gulls (Verbeek 1988). These results support the hypothesis that consistent incubation in larids helps to protect eggs from predators, regardless of the reasons for beginning incubation.

We propose that chick mortality due to hatching asynchrony may not be adaptive in Common Terns. If early incubation is a result of selective pressures related to egg predation, it may maximize overall nest success even if it reduces chick survival. Intermittent incubation during early egg laying may reflect a balance between positive effects of early incubation and negative effects of hatching asynchrony. Alternatively, if early incubation is an incidental trait, egg protection may mitigate some of the costs incurred by this behavior.

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SPECIATION, HETEROCHRONY, AND GENETIC VARIATION IN HISPANIOLAN PALM-TANAGERS

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ABSTRACT.—We documented levels of genetic variability for two species of Hispaniolan palm-tanagers. Significant differences between age classes in levels of genetic heterozygosity were concordant with an age dimorphism in foraging behavior and morphology in *Phaenicophilus palmarum*; juveniles ($H = 0.121$) were almost twice as heterozygous as adults ($H = 0.074$). *Phaenicophilus poliocephalus* ($H = 0.104$) was not characterized by a distinct age dimorphism in any character examined. Although *P. poliocephalus* resembled juvenile *P. palmarum* in morphology and behavior, it was not significantly different from either adult or juvenile *P. palmarum* in levels of genetic variability. Both species of *Phaenicophilus* possess levels of genetic variability (9–10%) that are high for birds, and they differ in allele frequencies and presence of private alleles, although they are not characterized by fixed allelic differences. *Phaenicophilus poliocephalus* was probably derived from small founding populations (ca. 50,000–260,000 yr BP), composed mostly of juvenile *P. palmarum* that colonized the south island of Hispaniola formed during the Pleistocene. Rapid divergence between species is consistent with predictions from models of heterochrony by paedomorphosis and speciation by a founder event. *Received 25 August 1989, accepted 28 April 1990.*

HETEROCHRONY (i.e. shifts in developmental patterns) provides a framework for understanding how population processes lead to evolutionary change (Gould 1977). Alterations in body size and shape, fecundity, age-structure, and significant changes in social structure within populations can result by changing individual growth rates or age of sexual maturity (Geist 1971, Gould 1977, Lawton and Lawton 1986). Life history characteristics, such as fecundity and growth rates, are correlated to levels of genetic variability (Cothran et al. 1983, Mitton and Grant 1984), although there is no unifying theory to predict the genetic consequences of heterochrony. Differential selection on various life history stages due to heterochrony can lead to genetic changes within and between species, and it can provide a basis from which to develop a general model predicting the genetic consequences of heterochrony. Furthermore, avian groups are known to be morphologically diverse (Wyles et al. 1983) but genetically conservative (Avise and Aquadro 1982) when compared with other vertebrates. A model of heterochrony may explain this paradox if speciation occurs primarily by regulatory gene changes, as proposed by Gould (1977), although he did not believe heterochrony to be significant in avian evolution.

Heterochrony can be achieved in two ways: *peramorphosis* (i.e. terminal deletion) and *paedomorphosis* (i.e. terminal addition) (Kluge and Strauss 1985). Whereas peramorphosis results in the acquisition of novel characters, paedomorphosis results in the retention of juvenile characters in reproductively capable individuals (Gould 1977, Lawton and Lawton 1986) and it may be achieved by small changes in regulatory genes early in development (Larson 1980). Paedomorphosis may occur by delaying somatic maturation (i.e. *neoteny*) or accelerating sexual maturation (i.e. *progenesis*). Gould (1977) characterized neoteny as a response to limiting resources (i.e. *K*-selected strategy) and progenesis as a response to plentiful resources (i.e. *r*-selected). Only recently has neoteny been equated with delayed maturation in birds (Lawton and Lawton 1986, Foster 1987), although delayed maturation has already been documented for numerous bird species (Selander 1965, Rohwer et al. 1980, Flood 1984, Hamerstrom 1986). Avian groups that are paedomorphic may rep-

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resent ideal systems from which to develop a coordinated theory relating ecological constraints, life history traits, and genetic variability to rapid speciation.

The Neotropical tanagers are good candidates for the study of heterochrony because of their adaptive radiation into a number of ecological niches in the tropics. Moreover, in at least 39 species, first-year birds can be distinguished from adults by plumage. Because molt often does not occur until after the first potential breeding season, many tanagers can breed in juvenile (or subadult) plumage (Isler and Isler 1987). We chose to examine the evolution and speciation of Hispaniolan palm-tanagers using the predictions from the model of heterochrony, because the similarities between the two species suggest one is paedomorphic to the other and may have undergone rapid speciation on a small island (McDonald 1988).

Gray-crowned Palm-Tanagers (*Phaenicophilus poliocephalus*) resemble juvenile Black-crowned Palm-Tanagers (*P. palmarum*) in foraging behavior and morphology. They are also smaller in body size, are more social relative to Black-crowned Palm-Tanagers, and are most likely derived from them (McDonald and Smith in press). We propose that age-related genetic differences observed for *P. palmarum* may be related to the other observed phenotypic differences in this species, and may have relevance to the evolution of *P. poliocephalus*.

Our purpose is to describe the patterns of genetic variation within and between two palm-tanager species and to relate these patterns to their possible mode of speciation. Our specific objectives are to describe age-specific genetic variation within these species and relate it to differences in behavior and morphology, and to quantify the degree of genetic differentiation between these species and estimate divergence time. We discuss speciation of these species as it relates to isolation, founder effect, and genetic variability, and test whether the observed genetic variation is consistent with a paedomorphic derivation of one species from the other.

METHODS

Collections were made of two species of *Phaenicophilus* and their hybrids in Haiti from May through September, 1985. Hybrid specimens and representatives of both parental species are deposited in the American Museum of Natural History. The remaining specimens are deposited in the Florida Museum of Natural History. Tissue samples are deposited in the Louisiana State University Museum of Zoology. Field identifications were based on crown and chin characters (McDonald and Smith in press). Juveniles of both species could be identified in hand by the presence of a yellow wash in the plumage. This plumage character was correlated with a gray—instead of red-brown—iris observed for adults, gray crown, small gonads, and rictal flanges in six of eight specimens.

Because dry ice or liquid nitrogen was not available in Haiti, tissues were stored in 1.5% buffered 2-phenoxyethanol solution 0.5–4.0 h after collection, and vials were stored in a conventional freezer at −20°C within a week after collection until September 1985. Tissues were stored at −60°C thereafter. Little or no degradation, as indicated by mobility changes and subbanding, occurred in most enzymes after 2 weeks storage of tissues in the preservative at room temperature and after 4 months storage in a conventional freezer (McDonald MS).

Liver and muscle extracts were ground in the phenoxyethanol solution. Samples were centrifuged for 5 s to clear the supernatant of particulate matter. Tissue extracts were analyzed using horizontal starch gel electrophoresis, according to the modified methods of Selander et al. (1971) and Harris and Hopkinson (1976).

We assayed for 39 presumptive loci. Locus designations, abbreviations, and buffer conditions are given in Table 1, except where listed below. Loci were numbered according to the mobility of the products (with the most anodal as 1) when two or more isozymes appeared on the same gel. Monomorphic loci included AAT-2 (analyzed using Amine Citrate 6.2 and Tris Maleate 7.4 buffers), CK-1, FH-2, αGPD-1, lactate dehydrogenase (LDH)-1 and -2, malate dehydrogenase (MDH)-1 and -2, malic enzyme (ME), and SOD-2 (all on Amine Citrate 6.2 buffer), and general proteins (GP)-1 and -2 (Lithium Hydroxide 8.2 buffer). Alleles were designated alphabetically, with *A* corresponding to the allele with the fastest migrating product. No locus had more than three alleles. All loci were scored independently from the fresh gels by one or both authors, and then rescored from the pictures by both authors. Photographs are archived with the data at the Savannah River Ecology Laboratory.

General statistical tests were conducted with the Statistical Analysis System (SAS 1985) or Statistical Package for the Social Sciences (SPSS, Norusis 1985). Significance was set at $P \leq 0.05$; highly significant rejection of null hypotheses occurred when $P \leq 0.01$. Acceptance levels for multiple comparisons involving the same data set were adjusted to an experimentwide error of $P_1 \leq 0.05$ (Harris 1975). Tests are reported as two-tailed except where noted.

Allele frequencies and genetic variability were

measured by the proportion of heterozygous loci determined by direct count per individual averaged across 39 loci (H), the average number of alleles per locus, and the percent loci polymorphic with the criterion of a secondary allele frequency of no more than 0.01 (Table 1). The average number of loci observed per individual varied because some of the samples were taken in the absence of ice or cool temperatures. Genetic data were analyzed with BIOSYS-1 (Swofford and Selander 1981). Using a t-test, we performed statistical analyses of individual heterozygosities that were transformed by taking the square-root of the arcsine of the value (Archie 1985). Slatkin's (1985) rare allele model was used to estimate gene flow across palm-tanagers. Hybrids were excluded from this latter analysis. Standard error for the gene flow estimate was evaluated by jackknifing (Lanyon 1987) each of the 31 unique alleles found in one or the other species.

To estimate the relative size of the founding populations required for colonization and maintenance of current heterozygosity levels in *P. poliocephalus*, we calculated expected heterozygosity (H_e) for the colonists as follows (Baker and Moeed 1987):

$$H_e = (1 - 1/2N_o)H_o,$$

where N_o is the size of the founding population and H_o is heterozygosity of the founders. Founding populations derived from ancestral *P. palmarum* were assumed for the calculation to consist of one of three groups: all adults, all juveniles, or a mixture of adults and juveniles collected at random.

Results

Genetic distance (Nei 1978) between *P. palmarum* and *P. poliocephalus* was $D = 0.01$. No significant differences in genetic heterozygosity existed between the two parental species ($t = -0.81$, df = 40), between *P. palmarum* and hybrids ($t = -0.17$, df = 34), or between *P. poliocephalus* and hybrids ($t = 0.54$, df = 32) (Table 1). No fixed allelic differences were found between the species although there were highly significant shifts in five loci between the two species (i.e. AAT-1, DIA-2, FH-1, IDH, and PGD-1).

We found *"private" alleles*, defined as those observed in only one group (Slatkin 1985), at 21 of the 27 polymorphic loci. *Phaenicophilus poliocephalus* had 15 unique alleles in 63 alleles, and *P. palmarum* had 16 in 64. Sample size for each species was sufficient to detect 56.2% and 74.1%, respectively, of the private alleles in at least one individual at the observed frequencies in the other species. The estimated number of migrants per generation was 0.963 (SE 0.011) based on the rare allele method. There were 9 private alleles in juvenile ($n = 8$) and 6 private alleles in adult ($n = 14$) *P. palmarum* at 11 of the 39 loci. Private alleles may be expected to occur in the larger adult sample, but not in the smaller juvenile sample.

Differences in heterozygosity were significant between juvenile ($H = 0.121$) and adult *P. palmarum* ($H = 0.074$) ($t = -3.04$, df = 19, $P_1 \leq 0.007$). We found no significant differences in heterozygosity between age classes within *P. poliocephalus* ($H = 0.104$) ($t = -1.73$, df = 18, $P_1 = 0.10$) or within the hybrids ($t = -1.40$, df = 12, $P_1 = 0.18$), although adult *P. poliocephalus* ($H = 0.115$) were more heterozygous than juveniles ($H = 0.069$). Only five juvenile *P. poliocephalus* and three juvenile hybrids were available for this test. Juvenile or adult *P. palmarum* did not differ significantly from either *P. poliocephalus* or the hybrids in genetic heterozygosity.

Sampling biases due to taking juveniles from the same nest are not likely to account for the observed heterozygosity difference between age classes because 5 of the 8 juvenile *P. palmarum* were collected with another adult in the same habitat, and these habitats were distributed across Haiti. Habitats included cloud forest, disturbed pines, woodland, farms, rural areas, and deserts. One juvenile was collected alone. Two juveniles were collected in the same habitat and could be potential nest mates. Of the 5 juvenile-adult pairs, 4 juveniles had higher levels of heterozygosity than the adults. Of the 2 juveniles collected in the same habitat, 1 ranked highest for individual heterozygosity ($H = 0.143$); the other ranked second to the lowest for juveniles ($H = 0.094$).

Of the 17 variable loci in *P. palmarum* (αGPD-2 was omitted because of low sample sizes), only 4 did not have higher levels of heterozygosity in juveniles than in adults. Data from the 4 loci (GDH, PGM-1, PepA1, and XDH) that did not follow this trend were excluded from the jackknife procedure because removal of these data would result in higher juvenile heterozygosities and bias the following tests. We jackknifed (Lanyon 1987) the remaining data to evaluate single-locus effects on heterozygosity differences between age classes. The data for one locus at a time were removed for the 13 variable loci, and heterozygosities were computed for each age class with the data for the remaining 38 loci. Average heterozygosity for each age

TABLE 1. Allele frequencies, direct count heterozygosity (H), percent polymorphic loci ($P_{0.01}$) (common allele ≥0.99), and mean number of alleles ($\bar{A}$) across 27 variables of 39 enzyme loci. BPA = Adult *Phaenicophilus palmarum*; BPI = juvenile *P. palmarum*; GPT = *P. poliocephalus*; HYB = hybrids; sample sizes are in parentheses in Sample columns.

Name (EC No.)[a]	Buffer pH[b]	Locus/ Alleles	Sample[c] BPA	BPI	GPT	HYB
Aspartate aminotransferase (2.6.1.1)	AC 6.2	AAT-1	(14)	(8)	(20)	(14)
	TM 7.4	A	0.143	0.188	0.000	0.036
		B	0.857	0.813	0.850	0.929
		C	0.000	0.000	0.150	0.036
Aconitate hydratase (4.2.1.3)	AC 6.2	ACON-1	(13)	(8)	(17)	(13)
		A	0.000	0.000	0.029	0.000
		B	1.000	1.000	0.971	1.000
		ACON-2	(12)	(6)	(16)	(12)
		A	0.000	0.083	0.063	0.042
		B	1.000	0.917	0.938	0.958
Catalase (1.11.1.6)	TC 8.0	CAT	(14)	(8)	(20)	(14)
		A	0.000	0.000	0.100	0.214
		B	0.857	0.875	0.750	0.750
		C	0.143	0.125	0.150	0.036
Creatine kinase (2.7.3.2)	AC 6.2	CK-2	(14)	(8)	(16)	(13)
		A	0.000	0.000	0.063	0.038
		B	1.000	1.000	0.938	0.962
Diaphorase (1.6.2.2)	TC 8.0	DIA-2	(12)	(7)	(12)	(12)
		A	0.167	0.143	0.000	0.000
		B	0.792	0.643	1.000	1.000
		C	0.042	0.214	0.000	0.000
(1.6.4.3)		DIA-3	(14)	(8)	(19)	(13)
		A	0.036	0.000	0.000	0.000
		B	0.929	0.875	0.921	0.923
		C	0.036	0.125	0.079	0.077
Fructose diphosphate aldolase (4.1.2.13)	AC 6.2	FDA-1	(8)	(6)	(15)	(8)
		A	0.000	0.000	0.000	0.063
		B	1.000	1.000	1.000	0.938
Fumarate hydratase (4.2.1.2)	AC 6.2	FH-1	(13)	(8)	(16)	(13)
		A	0.885	0.750	1.000	0.962
		B	0.115	0.250	0.000	0.038
Glucose dehydrogenase (1.1.1.47)	TM 7.4	GDH	(12)	(6)	(17)	(12)
		A	0.042	0.000	0.000	0.042
		B	0.958	1.000	0.912	0.917
		C	0.000	0.000	0.088	0.042
Alpha glycerophosphate dehydrogenase (1.1.1.8)	AC 6.2	αGPD2	(1)	(3)	(20)	(9)
		A	0.000	0.167	0.000	0.000
		B	1.000	0.333	1.000	0.833
		C	0.000	0.500	0.000	0.167
Glucose phosphate isomerase (5.3.1.9)	AC 6.2	GPI	(14)	(8)	(20)	(14)
		A	0.214	0.188	0.200	0.107
		B	0.000	0.000	0.000	0.036
		C	0.786	0.813	0.800	0.857
Beta-glucuronidase (3.2.1.31)	TC 8.0	βGUS	(14)	(8)	(20)	(13)
		A	0.000	0.188	0.050	0.192
		B	1.000	0.750	0.925	0.808
		C	0.000	0.063	0.025	0.000
Hexokinase (2.7.1.1)	AC 6.2	HK	(9)	(6)	(17)	(12)
		A	0.000	0.000	0.000	0.125
		B	1.000	1.000	1.000	0.833
		C	0.000	0.000	0.000	0.042
Isocitrate dehydrogenase (1.1.1.42)	JRP 7.1	ICD-1	(14)	(8)	(17)	(14)
	TC 8.0	A	0.000	0.000	0.118	0.000
		B	1.000	1.000	0.853	1.000
		C	0.000	0.000	0.029	0.000

TABLE 1. Continued.

Name (EC No.)[a]	Buffer pH[b]	Locus/ Alleles	Sample[c] BPA	BPI	GPT	HYB
Mannose phosphate isomerase (5.3.1.8)	TC 8.0	MPI	(9)	(5)	(14)	(10)
	EDTA 8.6	A	0.000	0.100	0.000	0.000
		B	1.000	0.800	1.000	1.000
		C	0.000	0.100	0.000	0.000
Purine nucleoside phosphorylase (2.4.2.1)	EDTA 8.6	NP	(14)	(7)	(19)	(12)
		A	0.143	0.214	0.316	0.083
		B	0.107	0.214	0.158	0.833
		C	0.750	0.571	0.526	0.083
Phosphoglucomutase (2.7.5.1)	AC 6.2	PGM-1	(12)	(7)	(17)	(14)
		A	0.042	0.000	0.000	0.036
		B	0.917	1.000	1.000	0.821
		C	0.042	0.000	0.000	0.143
		PGM-2	(5)	(6)	(14)	(9)
		A	1.000	1.000	0.929	1.000
		B	0.000	0.000	0.071	0.000
		PGM-3	(4)	(3)	(13)	(13)
		A	0.000	0.000	0.038	0.000
		B	1.000	1.000	0.962	0.962
		C	0.000	0.000	0.000	0.038
Peptidase[d] (3.4.11)	TM 7.4	PEP-A1	(9)	(6)	(15)	(14)
		A	0.000	0.000	0.000	0.036
		B	1.000	1.000	0.967	0.893
		C	0.000	0.000	0.033	0.071
		PEP-G	(13)	(8)	(16)	(14)
		A	0.038	0.063	0.000	0.143
		B	0.962	0.938	1.000	0.857
		PEP-A2	(14)	(7)	(18)	(14)
		A	0.000	0.071	0.000	0.036
		B	1.000	0.929	0.889	0.964
		C	0.000	0.000	0.111	0.000
		PEP-L	(14)	(7)	(16)	(14)
		A	0.071	0.000	0.000	0.000
		B	0.929	1.000	0.906	1.000
		C	0.000	0.000	0.094	0.000
Phosphogluconate dehydrogenase (1.1.1.44)	TM 7.4	6PGD-1	(14)	(8)	(16)	(12)
		A	0.000	0.000	0.219	0.000
		B	1.000	1.000	0.781	1.000
Superoxide dismutase (1.15.1.1)	AC 6.2	SOD-1	(7)	(6)	(18)	(7)
		A	0.000	0.000	0.167	0.429
		B	1.000	0.917	0.833	0.571
		C	0.000	0.083	0.000	0.000
Xanthine oxidase (1.2.3.2)	TC 8.0	XDH	(10)	(7)	(19)	(14)
		A	0.100	0.000	0.079	0.000
		B	0.900	1.000	0.895	0.964
		C	0.000	0.000	0.026	0.036
Direct count heterozygosity[e]			0.074	0.121	0.104	0.095
SE			0.011	0.009	0.012	0.011
Mean number of alleles			1.4	1.5	1.6	1.7
% polymorphic loci			30.8	35.9	48.7	51.3

[a] Enzyme names and numbers recommended by the Commission on Biological Nomenclature (1973).

[b] Abbreviations for buffers are: AC = Amine Citrate (Clayton and Tretiak 1972); JRP = Tris Citrate 7.0 (Ayala et al. 1972); TM = Tris Maleate; TC = Tris Citrate 8.0; EDTA = Ethylenediamine Tetraacetic Acid (Selander et al. 1971, Harris and Hopkinson 1976). When more than one buffer condition is specified, both were routinely used to assay for multiple loci.

[c] Sample sizes of adults and juveniles for *P. poliocephalus* were 15 and 5, respectively, and for hybrids were 9 and 3.

[d] Peptidase substrates used were PEP-A1 and PEP-A2 = L-leucyl-L-alanine; PEP-G = DL-leucylglycylglycine; PEP-L = L-leucyl-L-leucine.

[e] Genetic variability pooled for adult and juvenile Black-crowned Palm-Tanagers: $H = 0.091$; SE = 0.009; $\bar{A} = 1.6$; $P_{0.01} = 46.2$.

TABLE 2. Mean % heterozygosity for adult (AD) and juvenile (JUV) *Phaenicophilus palmarum* after jackknife simulation (Lanyon 1987) for 13 variable loci. A *t*-test was performed to test the null hypothesis that the average difference across all 13 loci between age classes is not significant. Differences were highly significant ($t = 24.3$, df = 24, $P < 0.001$).

Locus[c] removed	% heterozygosity[a,b] after removal		Locus % heterozygosity before removal		Sample size	
	AD	JUV	AD	JUV	AD	JUV
ACON-2	7.6	12.0	0.0	16.7	12	6
CAT	7.3	11.6	14.3	25.0	14	8
DIA-2	7.0	11.4	25.0	42.9	12	7
DIA-3	7.2	11.7	14.3	25.0	14	8
FH-1	7.0	10.9	23.1	50.0	13	8
AAT-2	6.6	11.3	28.6	37.5	14	8
GPI	6.9	11.3	28.6	37.5	14	8
βGUS	7.7	10.9	0.0	50.0	14	8
MPI	7.6	11.9	0.0	20.0	9	5
NP	6.4	11.0	35.7	57.1	14	7
PEP-C	7.7	12.0	0.0	14.3	14	7
PEP-B	7.4	12.1	7.7	12.5	13	8
SOD-1	7.7	12.1	0.0	16.7	7	6

[a] Standard errors ranged from 0.010 to 0.013 for adults and 0.007 to 0.013 for juveniles.

[b] Probabilities, after removal, ranged from 0.004 to 0.037 for single locus *t*-tests.

[c] Abbreviations for loci in Table 1.

class was then computed across 13 combinations of 38 loci. Heterozygosity differences between the averages for each age class were tested under the hypothesis that the differences were not due to significant single-locus effects. Levels of heterozygosity were still highly significantly different between age classes ($t = -24.33$, df = 24). Therefore, differences in heterozygosity between age classes could not be attributed to the effects of any single variable locus in the study. Moreover, the direction of the difference between age classes remained unchanged. Juvenile *P. palmarum* were always more heterozygous then adults were, regardless of which data were removed (Table 2).

The manner in which the paedomorphic form (i.e. *P. poliocephalus*) was derived could be important in determining its level of genetic variability. Equal or reduced heterozygosity in the derived form relative to that in the antecedent would be consistent with a vicariance model, but equal levels in both forms would not normally be expected given limited dispersal to a relatively isolated area. The required number

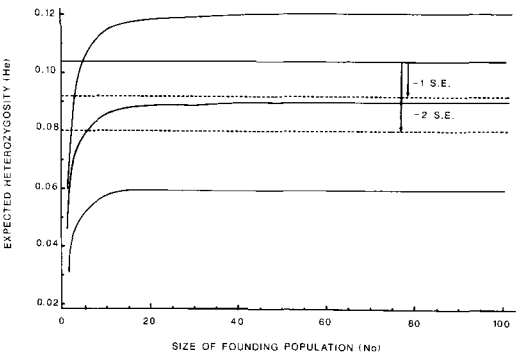

Fig. 1. Expected heterozygosity (H_e) of colonists based on founding population size (N_o) and observed heterozygosity (H_o) in the founders. The lower curve was generated based on the assumption that H_o was contributed by colonists consisting only of adult *Phaenicophilus palmarum*; the middle curve assumed a mixture of adults and juveniles; the upper curve assumed colonists were all juveniles. The solid horizontal straight line is the current heterozygosity observed in Gray-crowned Palm-Tanagers, *P. poliocephalus*. The dotted straight lines are one and two standard errors below this, respectively.

of dispersers to maintain certain levels of heterozygosity may be so high as to make the dispersal model unreasonable. Therefore, we used a modification of Crow and Kimura's (1970) equation to estimate the size of founding populations for given levels of heterozygosity (Baker and Moeed 1987). Three curves were generated and compared with the current levels of heterozygosity in *P. poliocephalus* ($H = 0.104$) (Fig. 1). The curve based on a founding population of all juvenile *P. palmarum* had an expected heterozygosity (H_e) = 0.106 at a founding population size (N_o) = 4, where the curve based on a mixed group of adult and juvenile founders had $H_e = 0.090$ at $N_o = 40$. This latter value is more than one standard error below the current level of heterozygosity of *P. poliocephalus*. The curve based on a founding population of all adults reached an asymptote at $H_e = 0.061$ and $N_o = 10$, more than two standard errors below the current heterozygosity level of *P. poliocephalus*.

DISCUSSION

Paedomorphosis in palm-tanagers.—Before we can discuss the evolutionary patterns observed in *Phaenicophilus* under a model of hetero-

chrony, the polarity of evolutionary relationships (i.e. which species is derived from which) must be established. The problem is to detect whether a terminal addition (peramorphosis) or terminal deletion (paedomorphosis) has been made. This may be resolved by the use of outgroup analysis (Kluge and Strauss 1985). Outgroup analysis involves the choice of a taxon (i.e. sister group) that is closely related to the taxa being compared to determine whether a character is common or unique to one or more of the taxa examined. If a character is shared with the sister group by one but not the other taxa, the first taxon is most likely antecedent to the second.

Three criteria were significant to demonstrate the derivation of *P. poliocephalus* from *P. palmarum*. First, neoteny occurs in *P. palmarum* but not in *P. poliocephalus*. Neoteny is observed in *Piranga*, the most likely sister group to *Phaenicophilus*, based on DNA-DNA hybridization data (Sibley in litt.) and on biochemical evidence (McDonald 1988). Second, *Phaenicophilus poliocephalus* has five alleles not shared with *Piranga*, whereas *P. palmarum* has only three. Third, the presence of a distinct white chin against a gray throat is unique to *P. poliocephalus*. In addition, *P. poliocephalus* is smaller, resembles juvenile *P. palmarum* in foraging behavior, and is relatively more social than is *P. palmarum* (McDonald and Smith in press), a tendency predicted by the retention of juvenile morphology (Lawton and Lawton 1986). The absence of neoteny, the presence of a unique plumage character, the number of unshared alleles with the sister group, and the similarity in behavior and morphology of *P. poliocephalus* to juvenile *P. palmarum* argue strongly in favor of the derivation of the former from the latter species. Once this polarity is accepted, the absence of a black crown in adult *P. poliocephalus* (i.e. a terminal deletion) supports the hypothesis that it is paedomorphic to *P. palmarum*.

Understanding the importance of ecological constraints to the model of paedomorphosis for palm-tanagers is critical to evaluating their probable mode of speciation. There are several assumptions relative to the model. Early sexual maturation is favored when all other factors are equal. However, limiting resources may impose strong intraspecific competition on individuals that attempt to breed. Under these conditions, the relative increase in fitness accrued by inexperienced individuals that breed at an earlier age would be offset by fitness decreased because of intense intraspecific competition for scarce resources. As a result, inexperienced individuals in a resource-limited environment may delay somatic maturation and benefit from cryptic or deceptive morphology by a decrease in intraspecific competition (Rohwer 1978, Lawton and Lawton 1986, Foster 1987). When resources are not severely limiting, these individuals may breed. For example, subadult Northern Harriers (*Circus cyaneus*) breed only when *Microtus* densities are high, but refrain from breeding at other times (Hamerstrom 1986). Paedomorphosis can be achieved by two different reproductive strategies in response to differential resource availability: neoteny and progenesis (Gould 1977). Neotenic species can be characterized by an age dimorphism in morphology and possibly in behavior.

In contrast, progenesis occurs when resources may be relatively more abundant. Species colonizing new habitat represent potential for progenesis to occur. Under these circumstances, early sexual maturation is no longer constrained, nor is there strong competition between age classes for resources. With attainment of sexual maturity, somatic development slows down or stops (Gould 1977), which results in individuals with smaller body size, juvenile morphology, juvenile behaviors associated with juvenile morphology, and a concomitant increase in group behaviors (Geist 1971, Gould 1977, Lawton and Lawton 1986). If the colonizing population becomes isolated from the main stock, divergence can occur, with genetic changes primarily expected at regulatory loci.

Age-related differences in heterozygosity.—Age-related genetic differences may be an expected consequence of neoteny, as are changes in morphology and behavior, particularly because age-related differences are most likely selected in environments with limited resources. We found age-related differences in *P. palmarum* but not in the derived paedomorphic form, *P. poliocephalus* (Table 1). Age-class differences in single- and multi-locus heterozygosity have also been observed for grouse, lizards, deer, toads, and mosquitofish (Redfield 1973, Tinkle and Selander 1973, Cothran et al. 1983, Samollow and Soule 1983, Smith et al. 1989), although higher genetic variability is not always found for juveniles as in *P. palmarum*. Increased heterozy-

gosity seems to be favored in age classes under intense differential mortality or selection (Samollow and Soule 1983). Juvenile *P. palmarum* ($H = 0.121$) are significantly more heterozygous than adults ($H = 0.074$) of their own species. Selection could account for this difference, but other explanations must be considered also.

Age-related differences in heterozygosity in *P. palmarum* might be spurious because of small sample sizes. Because of the small sample size in this study, the magnitude of the differences in heterozygosity between age classes had to be large to yield a probability of <0.007 for rejection of the null hypothesis. It seems unlikely that stochastic processes that were due to small sample size produced such large differences. It is also possible that one or a few loci are responsible for the age-related differences, but higher levels of heterozygosity were observed for juvenile *P. palmarum* for 13 out of 17 variable loci (Table 2). In addition, removal of the data for any single locus did not alter the overall difference (Table 2). Because juveniles were collected across sites, a sampling bias due to their coming from a limited number of nests is not likely. Age-related difference in heterozygosity seems to be a multilocus phenomenon and not due to small-sample biases. However, this result does not provide a basis for understanding the mechanism(s) that generates the differences.

The differences in genetic variability across life history stages may be due to developmental changes in isozyme patterns, negative assortative mating, or nonrandom dispersal of individuals with different genotypes. These processes are not likely to produce the consistent decrease in heterozygosity for adults observed for 13 loci. The decrease in the number of rare alleles in juveniles compared with adults indicates selection is probably operating (Samollow and Soule 1983). Private alleles observed only in juveniles are probably not completely lost in adults, but may occur at much lower frequencies than in juveniles. Our sample size was not sufficient to detect these alleles. Selection may act on both life history stages—first increasing, then decreasing genetic variability—but this hypothesis remains to be tested.

The importance of age-related differences in genetic variability extends beyond its concordance with behavior and morphology in *P. palmarum* and may be related to the process of rapid divergence in *P. poliocephalus*. Lower genetic variability is not characteristic of adults in all species (Cothran et al. 1983, Smith et al. 1989), even for *Phaenicophilus*. Although significant differences in heterozygosity did not exist between age classes within *P. poliocephalus* ($P = 0.10$), the trends are reversed from *P. palmarum*, with adult *P. poliocephalus* ($H = 0.115$) relatively more heterozygous than juveniles ($H = 0.069$). Furthermore, levels of heterozygosity are similar in adult *P. poliocephalus* ($H = 0.115$) and juvenile *P. palmarum* ($H = 0.121$). The similarity in terms of genetic variability between adult *P. poliocephalus* and juvenile *P. palmarum* may be serendipitous, but the pattern across several character sets (i.e. behavior and morphology; McDonald and Smith in press) suggests there may be a single underlying cause related to how and when *Phaenicophilus* diverged.

The genetic divergence between the two *Phaenicophilus* taxa was low ($D = 0.01$), even for avian species where the average $D = 0.044$ (Barrowclough 1980). However, Johnson and Zink (1983) reported $D = 0.004$ for two closely related sympatric species of sapsuckers (*Sphyrapicus*) that were undergoing character displacement and assortative mating. Genetic distance should not be used a priori as the only criterion for species recognition in birds (Hepp et al. 1988). The low D for *Phaenicophilus* is likely an indication of two recently diverged but distinct species. There were no fixed allelic differences between the two taxa (Table 1), but there were a significant number of private alleles (31) not shared by them and significant frequency shifts in alleles for 5 loci. It takes at least one migrant per generation to maintain allelic equivalence between taxa (Crow and Kimura 1970). The significant difference in frequencies for 5 of 17 variable loci and the large number of private alleles supports our contention that gene flow is severely restricted between the two taxa. These characteristics are consistent with the specific designation of the two recently diverged *Phaenicophilus* taxa.

The estimated time of divergence (Nei 1975, Gutiérrez et al. 1983, Marten and Johnson 1986) is from 5.0×10^4 to 2.6×10^5 yr before present (BP). This range in the estimate corresponds remarkably well to the time of the most recent interglacial period, when sea levels rose 8–10 m some 6.5×10^4 yr BP, and multiple times throughout the Pliocene and Pleistocene (Pregill and Olson 1981). The rise in sea level would have inundated the Cul-de-Sac Plain, which runs from west to east across Hispaniola, and

cleaved it into north and south islands. This plain is presently below sea level; during interglacial periods when glaciers melted and sea levels rose it would have formed an open water barrier to gene flow (Pregill and Olson 1981).

Model of speciation.—We propose that *Phaenicophilus* speciated in allopatry on the two islands. Current distributions of the two species suggest that *P. poliocephalus* arose on or dispersed to the south island. If the divergence were a result of a vicariance event, then *P. poliocephalus* would be expected to be similar to *P. palmarum* in having a distinct age dimorphism in behavior, morphology, and genetics, unless neoteny was derived in *P. palmarum* after divergence occurred. A vicariance model might explain similarities in overall genetic variability between the two species, but is inadequate to explain the pattern of similarity of *P. poliocephalus* to juvenile *P. palmarum* in behavior and morphology. In contrast, a model of heterochrony can explain the lack of an age dimorphism in the derived species, the retention of juvenile behavior and morphology in that species, its smaller body size and increased sociality (McDonald and Smith in press), and the retention of high levels of genetic variability (Fig. 1). The absence of a striking age dimorphism in *P. poliocephalus* could have resulted if it were derived from neotenic *P. palmarum* after colonization to the south island. Low competition and relatively abundant resources on the south island would favor the evolution of progenesis, which is characterized by earlier sexual maturation often at smaller body size than normally expected (Gould 1977). *Phaenicophilus poliocephalus* is smaller than *P. palmarum*, as expected for progenetic species. If the colonizers were few in number, then genetic variability might be expected to have declined because of founder effect (Crow and Kimura 1970). Both species have surprisingly high levels of heterozygosity ($H = 9$–10%) for island species (Nevo et al. 1984, but see Yang and Patton 1981). A decline in heterozygosity could be avoided by rapid population growth after colonization (likely for progenetic species), a large number of founders, and multiple invasions.

The simplest explanation for the current situation is that heterozygosity was not reduced on the south island in ancestral *P. poliocephalus*. Multiple invasions or large populations of colonizers could explain the retention of high levels of heterozygosity, but are inconsistent with subsequent divergence and with Templeton's (1980) model of speciation by founder effect. The size of the founder population should be just small enough to cause a rapid accumulation of inbreeding without a severe reduction in genetic variability (Templeton 1980). These conditions enhance the probability of the reorganization of the genome, primarily for regulatory genes (Templeton 1980). Therefore, fixed allelic differences in palm-tanagers may not be an expected consequence of speciation. Changes in regulatory genes are consistent with a model of heterochrony (Gould 1977). Even small changes in regulatory genes can effect significant phenotypic changes (Larson 1980) and provide for the establishment of isolating mechanisms. Few differences in structural loci and radical shifts in ecological niches are expected in either Templeton's (1980) or Gould's (1977) models.

Large or multiple founding populations that consisted mostly of adult *P. palmarum* would not have achieved the high levels of heterozygosity, regardless of the numbers of colonizers (Fig. 1). A small mixed group (<40) of ancestral *P. palmarum* adult and juvenile colonizers would have retained sufficient levels of heterozygosity currently observed in *P. poliocephalus* (Fig. 1). Juvenile dispersal is common in birds (Greenwood and Harvey 1982). Flocks of neotenic Brown Jays (*Cyanocorax morio*) that colonize recently cleared habitats have lower mean ages than flocks in the main populations (Lawton and Lawton 1985). Geographic isolation, small numbers of founders, and few founding events set the stage for rapid speciation (Templeton 1980), and paedomorphosis provides the basis for explaining the resemblance of *P. poliocephalus* to juvenile *P. palmarum* across several character sets and a mechanism (via progenesis) for rapid population growth after founding. An alternative explanation based on a vicariance model does not explain adequately similar levels of genetic variability in both species, the absence of an age dimorphism in *P. poliocephalus*, few structural gene differences, and the resemblance of adult *P. poliocephalus* to juvenile *P. palmarum*.

We conclude that neoteny in *P. palmarum* is expressed both behaviorally and morphologically, and the age dimorphism in these characters is congruent with observed heterozygosity differences between age classes. Hispaniolan palm-tanagers have recently diverged, most likely during the Pleistocene, when higher sea

levels separated Hispaniola into north and south islands. *Phaenicophilus poliocephalus* is distinct from *P. palmarum* based on the distribution of private alleles. Gene flow between species is low. *Phaenicophilus poliocephalus* resembles juvenile *P. palmarum* in behavior and morphology. Higher juvenile genetic variability in *P. palmarum*, combined with a greater amount of juvenile dispersal and the high genetic variability observed in *P. poliocephalus*, is consistent with the derivation of *P. poliocephalus* from small founding populations that consisted mostly of juvenile *P. palmarum* on the south island of Hispaniola during the Pleistocene. The generality of this model of speciation should be investigated for other groups, particularly the tanagers.

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THE ROLE OF PROLACTIN IN PARENTAL CARE IN A MONOGAMOUS AND A POLYANDROUS SHOREBIRD

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ABSTRACT.—We compared circulating prolactin levels in two species of shorebirds which have very different social systems, and which breed sympatrically at La Pérouse Bay, 40 km east of Churchill, Manitoba. Semipalmated Sandpipers (*Calidris pusilla*) are monogamous and share incubation equally, although females normally desert broods earlier than males. Red-necked Phalaropes (*Phalaropus lobatus*) are facultatively polyandrous, and only males care for eggs and young.

High prolactin values were correlated with persistent incubation behavior in male Red-necked Phalaropes, and male and female Semipalmated Sandpipers. Prolactin levels in Semipalmated Sandpipers increased dramatically at the onset of incubation, and were not different between the sexes. Incubating male phalaropes had greater prolactin values than the non-incubating males and females. Changes in prolactin levels, however, did not explain the early brood desertion of female Semipalmated Sandpipers. Prolactin levels did not decline with age of brood in either sex of this species. *Received 16 October 1989, accepted 29 April 1990.*

PROLACTIN is involved in a wide variety of physiological and behavioral events in vertebrates (Bentley 1982). However, controversy continues regarding prolactin's role in initiation and maintenance of incubation in birds. Early studies by Riddle and others (e.g. Riddle et al. 1935, Riddle and Lahr 1944) showed that injections of mammalian prolactin induced incubation behavior in female domestic fowl (*Gallus gallus*) and Ringed Turtle-Doves (*Streptopelia risoria*). Subsequent studies (Saeki and Tanabe 1955, Lehrman and Brody 1961, Opel and Proudman 1980, Höhn 1981) did not yield the same result, although incubation behavior was induced by prolactin in ovariectomized female Wild Turkeys (*Meleagris gallopavo*), after the birds were "primed" with injections of estradiol and progesterone (El Halawani et al. 1986).

Recent development of radioimmunoassays to measure avian prolactin has allowed researchers to follow changes in plasma levels throughout the breeding season, and relate these changes to behavior. The fact that plasma prolactin levels often are elevated before persistent incubation has led some authors to suggest that prolactin induces incubation behavior (e.g. Lea et al. 1981). Others have concluded (from egg-removal studies and studies that involve anesthetization or denervation of brood patches) that either tactile or visual presence of the nest and eggs stimulates incubation and results in elevated plasma prolactin, which in turn maintains incubation behavior (e.g. Hall and Goldsmith 1983). Still others propose a combination of these processes (El Halawani et al. 1986). Other studies of turkeys, bantam hens, and Pied Flycatchers (*Ficedula hypoleuca*) have shown that incubation can persist for at least a short time in the absence of high circulating levels of prolactin (Lea et al. 1981, El Halawani et al. 1980, Silverin and Goldsmith 1984).

The issue is further complicated by the fact that some researchers have found seasonal increases in prolactin levels in the absence of incubation or nestling-feeding behavior. In some instances such increases have been linked to onset of photorefractoriness (e.g. European Starlings [*Sturnus vulgaris*], Dawson and Goldsmith 1983, Goldsmith and Williams 1984; White-crowned Sparrows [*Zonotrichia leucophrys*], Hiatt et al. 1987).

Our primary objective was to examine the pattern of circulating levels of prolactin at dif-

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ferent stages of the reproductive cycle in two species of shorebirds with very different breeding systems. In the Red-necked Phalarope (*Phalaropus lobatus*), only males incubate (Hildén and Vuolanto 1972). Females desert their males as soon as the clutch is completed, and then attempt to obtain subsequent mates (Reynolds 1987). Semipalmated Sandpipers (*Calidris pusilla*) are monogamous, with incubation shared equally by both members of the pair (Ashkenazie and Safriel 1979a, b). If changes in circulating levels of prolactin are primarily related to incubation behavior, prolactin levels should be similar in both sexes of the Semipalmated Sandpiper, and greater in incubating male phalaropes than in females and nonincubating males. In both species plasma prolactin should increase substantially at the onset of incubation behavior. However, if prolactin levels increase seasonally—without a change in behavior—in males and females of both species, its function may primarily relate to photorefractoriness.

The gradual decline of plasma prolactin levels of attending parents of altricial and semialtricial young after hatch has been related to a decrease in feeding or brooding with increased age of nestlings (e.g. Silverin and Goldsmith 1984, Hector and Goldsmith 1985). In contrast to species with altricial young, prolactin levels decline dramatically at hatch (or within two days afterwards) in virtually all species examined with precocial young (Dittami 1981, Goldsmith 1982a, Goldsmith and Williams 1980, Hall and Goldsmith 1983, Wentworth et al. 1983). Spotted Sandpipers (*Actitis macularia*) appear to be an exception, because prolactin levels did not decline in the first two days after hatch (Oring et al. 1986a). In addition, prolactin levels in Wilson's Phalaropes (*Phalaropus tricolor*) declined gradually and reached basal levels by nine days posthatch (Oring et al. 1988). These authors suggested that the gradual decrease is related to the decline in brooding behavior with age of chicks, as found in other shorebirds.

In view of the proposed relationship between prolactin levels and brood-care behavior, particularly in shorebirds, a second objective of this study was to examine hormonal control of brood care in the Red-necked Phalarope and Semipalmated Sandpiper, both of which have precocial young. In phalaropes, however, only males participate in brood care (Hildén and Vuolanto 1972, Reynolds 1987). Almost all female Semipalmated Sandpipers gradually desert their broods to the care of the male soon after hatch (Ashkenazie and Safriel 1979a, b; Gratto and Cooke 1987). Therefore we predicted that prolactin levels of females would decline at rates faster than those of males.

Methods

Field.—Individuals of both species were observed at La Pérouse Bay (58°24'N, 94°24'W), 40 km east of Churchill, Manitoba, on the Hudson Bay coast, in the summers of 1985–1987. The 3-km² study area is situated in the Mast River delta, and consists primarily of low islets of *Salix brachycarpa* or *Betula glandulosa* and mixed sedges and grasses, in fresh water.

Populations of both Semipalmated Sandpipers and Red-necked Phalaropes were studied in the area from 1980 to 1987, and most birds were already individually color-banded. The breeding system of each species was well known. Nonincubating birds were captured in mist nets, and incubating birds in walk-in nest traps. Adults were marked with individual color-band combinations, and observed throughout the breeding season to determine their breeding status and behavior. For Semipalmated Sandpipers, the largest member of a pair (as determined by bill length) was assumed normally to be the female (Prater et al. 1977). Sex determination often was verified by behavior (flight displays, copulation), which indicated that sexing by size was very accurate (Gratto and Cooke 1987). Sexes of autumn migrants were determined by examination of gonads after the birds were collected. Red-necked Phalaropes were sexed by plumage and behavior. Most birds were scored for body molt on the head, back, and breast.

Blood samples were collected during the following stages of the breeding cycle:

1. *Spring transient* (spr)—birds captured in early June that did not remain to nest in the study area (collected for Semipalmated Sandpipers only).
2. *Prelay* (prel)—paired or unpaired birds captured before laying a clutch, that later bred in the study area.
3. *Lay* (lay)—birds captured during the laying period, before the clutch was complete.
4. *Early incubation* (e inc)—birds captured early in the incubation period, normally day 1 (day last egg was laid) to day 4. For female phalaropes, this refers to the time most male phalaropes in the population were in early incubation. Female Red-necked Phalaropes immediately deserted their mates after egg laying and attempted to obtain subsequent mates. Therefore, behavior of "early incubation" females was identical to that of prelay females. These data were collected to determine if changes in steroid levels of female phalaropes were

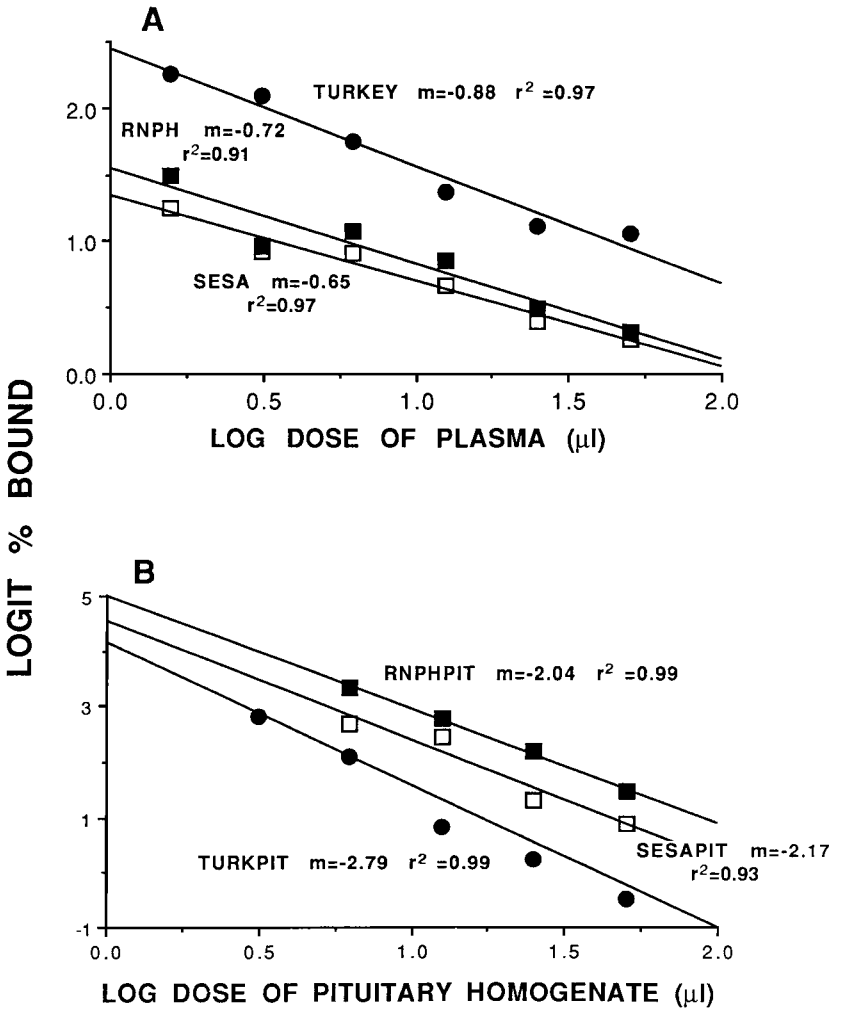

Fig. 1. Radioimmunoassay dose-response series of (A) plasma from broody turkey hens (TURKEY), incubating Semipalmated Sandpipers (SESA), and incubating Red-necked Phalaropes (RNPH); (B) pituitary homogenate of turkey (TURKPIT), Semipalmated Sandpipers (SESAPIT), and Red-necked Phalaropes (RNPHPIT). The slope of each line is indicated by "m."

dependent on season or behavior. Virtually all female phalaropes had left the study area by the time male phalaropes were in late incubation.

5. *Late incubation* (l inc)—birds captured late in the incubation period, before the eggs started to pip, normally day 14-16.
6. *Pip* (pip)—birds captured when at least one egg was pipped and before any hatched, normally day 17-19 (collected only in 1985).
7. *Brood* (brd)—birds captured while they attended the brood, after at least one young had hatched.
8. *Fall transient* (fall)—unbanded adults captured from migratory flocks in late July (collected only from Semipalmated Sandpipers).

Blood was sampled by puncturing the brachial vein with a small (25 G) needle, and collected in heparinized microhematocrit tubes. Most samples (88%, n = 472) were collected between 1100 and 1900. Using the largest consistent subsample of the data (incubating and brooding Semipalmated Sandpipers), we found no significant relationship between sampling time and plasma prolactin level in any year (Pearson correlations: 1985, n = 93, r = 0.03, P = 0.79; 1986, n = 46, r = −0.14; 1987, n = 62, r = −0.20, P = 0.11).

In the field, samples were kept on ice and transported to camp later in the day. At camp, samples were immediately centrifuged. Plasma was drawn off with a microsyringe, placed into labeled plastic tubes,

and stored for transport in liquid nitrogen. At the University of North Dakota, samples were frozen at −20°C until analysis.

Laboratory.—Prolactin values were assayed with the turkey prolactin radioimmunoassay of Burke and Dennison (1980) and Burke and Papkoff (1980). Only two prolactin assays were performed. The first assay (initiated on 24 April 1986) of all 1985 prolactin samples of both species used duplicate 50 μl samples. The second assay (initiated on 2 February 1988) of all 1986 and 1987 prolactin samples of both species used duplicates of 25 μl each. Intra-assay variation was similar in each, with an average of 8.83% based upon differences among multiple-pool sample potency estimates (controls) in the mid-range of the curve, and a minimum detectable dose of 0.307 ng. Statistical comparison of multiple common serum pool estimates in each assay yielded no significant difference between means (ANOVA, $P > 0.05$).

The turkey prolactin radioimmunoassay was previously validated for two other shorebird species, Spotted Sandpipers (Oring et al. 1986a, b) and Wilson's Phalaropes (Oring et al. 1988). This radioimmunoassay was validated for use with Semipalmated Sandpiper and Red-necked Phalarope plasma by comparing the dose-response relationship of plasma from broody turkey hens against plasma from incubating Semipalmated Sandpipers and Red-necked Phalaropes. The dilution series for all three were linear and very similar (Fig. 1A). There was no significant difference between the slopes for turkey and Red-necked Phalaropes (ANCOVA, $P = 0.26$). The difference in slopes between turkey and Semipalmated Sandpipers was marginally significant (ANCOVA, $P = 0.04$). The dose-response relationship of young turkey pituitary homogenate also was compared with pituitary homogenate from both species of sandpipers. Again the dilution series for all three were linear and very similar (Fig. 1B). The difference between slopes for turkey and Semipalmated Sandpipers was not significant (ANCOVA, $P = 0.19$). The difference between slopes for Red-necked Phalarope and turkey pituitary homogenate was marginally significant, because of the strong linearity of the dilution series in these two species (ANCOVA, $P = 0.04$).

Further evidence to support the validity of the assay for the shorebird species was generated by comparing molecular size of the immunologically reactive component of Semipalmated Sandpiper, Red-necked Phalarope, and young turkey pituitary homogenates. Each pituitary homogenate was subjected to molecular sieve column chromatography. The supernatant from each was applied to a 1.5 × 50 cm Sephadex G100 column and eluted with 0.1 M phosphate-buffered saline containing 0.1% BSA. One-milliliter fractions were collected from the column and 50-μl aliquots of each were assayed for immunoreactive prolactin. Using the turkey prolactin assay, we compared the elution patterns of each species for immunological reactivity. These patterns were very similar with primary peaks in the same molecular size range (Fig. 2).

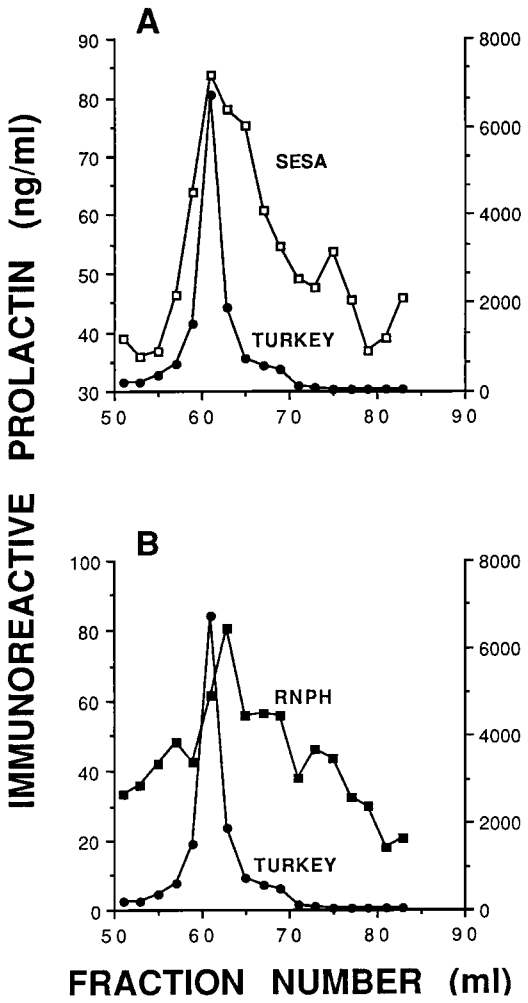

Fig. 2. Elution profiles of pituitary homogenates from incubating Semipalmated Sandpipers (SESA) and Red-necked Phalaropes (RNPH), and young turkeys (TURKEY) after chromatography on a 1.5 × 50 cm Sephadex G100 column. Scales on the left refer to sandpipers; all turkey values should be read from the scale on the right.

Effects of blood sampling on behavior of the birds, and on hormone levels, was minimal (Colwell et al. 1988, Gratto-Trevor et al. 1991). Virtually all samples were collected in <15 min.

An ANOVA was used to compare all status groups for each species and sex each year (e.g. female phalaropes in 1985). Status groups with a sample size of one were deleted from this analysis (e.g. laying female phalaropes in 1985). If the ANOVA revealed

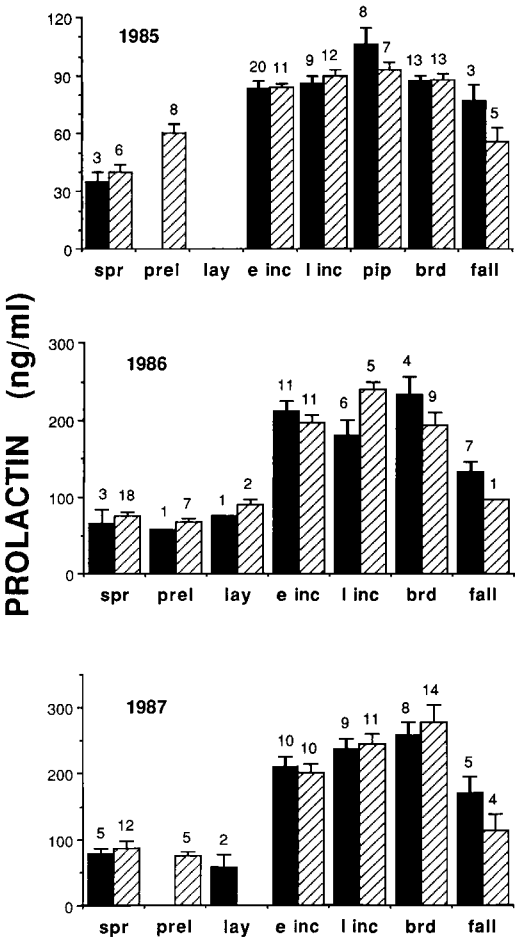

Fig. 3. Mean circulating prolactin levels in male (hatched bars) and female (solid bars) Semipalmated Sandpipers during the 1985 to 1987 breeding seasons at La Pérouse Bay. Abbreviations of status groups are explained in text. Error bars denote SE; numbers above bars are sample sizes.

significant differences ($P < 0.05$), we used the *GT2* test for multiple comparisons and unequal sample sizes to determine specific significant differences between status groups: for example, prelay vs. early incubation (SAS Institute Inc. 1982). Unless otherwise stated, any differences noted were significant at $P < 0.05$. Because samples from 1985 and those from 1986–1987 were assayed separately, it is not possible to compare actual hormone levels between years, just patterns of change. We combined data from different years only when we examined changes in individuals during a single season (or differences between members of a pair) when there were no significant differences among years (ANOVA, $P > 0.05$).

RESULTS

PROLACTIN AND INCUBATION

Semipalmated Sandpipers.—Prolactin levels were low in both sexes during spring, prelay, and lay. Levels increased significantly during early incubation, and did not change significantly until they declined at autumn migration (Fig. 3, Table 1).

When all preincubation values (spring, prelay, and lay) were combined within a year, there was never a significant difference between prolactin values of males and females (Table 2). There also were no significant differences between the sexes during incubation or brooding.

The difference in prolactin levels between members of a pair was compared when both birds were captured during incubation, no more than four days apart. Again, there was no significant difference between the sexes (paired *t*-test, all years combined, $n = 26$, mean (±SE) female–male = 11 ± 8 ng/ml, $P = 0.17$).

We captured a number of birds several times during a single breeding season. Prolactin levels increased in all seven instances where birds were caught first during prelay and later during incubation or brooding. This increase was significant (paired *t*-test, all years and sexes combined, $n = 7$, $\bar{x} = 95 \pm 28$ ng/ml, $P = 0.02$). In the 12 instances where birds were caught first in early incubation and subsequently in late incubation, 6 increased, 5 decreased, and 1 remained the same. The difference was not significant (paired *t*-test, all years and sexes combined, $\bar{x} = 19 \pm 11$ ng/ml, $P = 0.10$). Of the 19 Semipalmated Sandpipers captured first during incubation and later at brooding, 15 prolactin values increased and 4 decreased. The difference was not significant (paired *t*-test, all years and sexes combined, $\bar{x} = 28 \pm 16$ ng/ml, $P = 0.10$).

Red-necked Phalaropes.—We found no significant differences between prelay and "early incubation" prolactin levels (Fig. 4, Table 3) for female Red-necked Phalaropes. In phalarope males, few differences between status groups were significant (Fig. 4, Table 3). Levels appeared to increase between prelay and early incubation in 1985 and 1987 (only significant in 1987), but not in 1986. Prolactin levels at prelay were always less than those at late incubation or brooding, although the differences were not always significant.

TABLE 1. Semipalmated Sandpiper: statistical comparison of prolactin levels across breeding stages; results of ANOVA and *GT2* multiple comparison tests (Type I family error rate = 5% across each year-sex comparison). Probability and *F*-values are for ANOVA, while only significant differences are shown for *GT2* tests. Abbreviations of status groups are in text.

Year	ANOVA		Significant *GT2* tests
	F	*P*	
		Female	
1985	8.8	0.0001	spr < e inc, l inc, pip, brd, fall e inc < pip
1986	10.7	0.0001	spr < e inc, l inc, brd fall < e inc, brd
1987	15.0	0.0001	spr < e inc, l inc, brd, fall lay < e inc, l inc, brd fall < brd
		Male	
1985	23.9	0.0001	spr < prel, e inc, l inc, pip, brd prel < e inc, l inc, pip, brd fall < e inc, l inc, pip, brd
1986	49.5	0.0001	spr < e inc, l inc, brd prel < e inc, l inc, brd lay < e inc, l inc, brd
1987	19.1	0.0001	spr < e inc, l inc, brd prel < e inc, l inc, brd e inc < brd fall < l inc, brd

In 1985 and 1987, there were no significant differences in prolactin levels between females and preincubation males (Table 4). In 1986, preincubation males had significantly higher values than females. Incubating males in all three years had significantly higher prolactin values than those of females (when the one extremely high value for 1985 "lay" females was excluded). Incubating males also had significantly higher values than preincubating males in all years except 1986, when prolactin levels did not increase in males until late incubation.

Two female phalaropes were captured during prelaying and "early incubation" in one season, and prolactin levels in each changed only −2 ng/ml. Prolactin levels in 7 of 8 male phalaropes increased between preincubation and incubation or brooding, but the difference was not significant (paired *t*-test, all years combined, $\bar{x} = 39 \pm 19$ ng/ml, $P = 0.08$). The mean difference for males between early incubation and late incubation was 79 ± 44 ng/ml, which also was not significant (paired *t*-test, all years combined, $n = 7$, $P = 0.12$). In these 7 birds, levels increased in 6 and decreased in 1. There was no significant change in males captured first during incubation and later during brooding (paired *t*-test, all years combined, $n = 7$, $\bar{x} = -3 \pm 23$ ng/ml, $P = 0.89$). Levels increased in 3 birds and decreased in 4.

TABLE 2. Comparison of circulating prolactin levels between sexes in the Semipalmated Sandpiper at different times in the breeding season. "Preincubation" refers to all spring, prelay, and lay birds.

Stage/yr	Prolactin (ng/ml)				
	Females			Males	
	n	$\bar{x} \pm$ SE	*P*[a]	*n*	$\bar{x} \pm$ SE
Preincubation					
1985	3	35 ± 5	0.10	14	51 ± 4
1986	5	66 ± 10	0.35	27	75 ± 4
1987	7	72 ± 8	0.45	17	83 ± 8
Incubation					
1985	37	89 ± 3	0.73	30	88 ± 2
1986	17	201 ± 11	0.55	15	210 ± 10
1987	19	224 ± 11	0.96	21	223 ± 11
Brooding					
1985	13	87 ± 3	0.88	13	88 ± 3
1986	4	232 ± 23	0.21	9	194 ± 16
1987	8	259 ± 18	0.61	14	278 ± 26

[a] *t*-test.

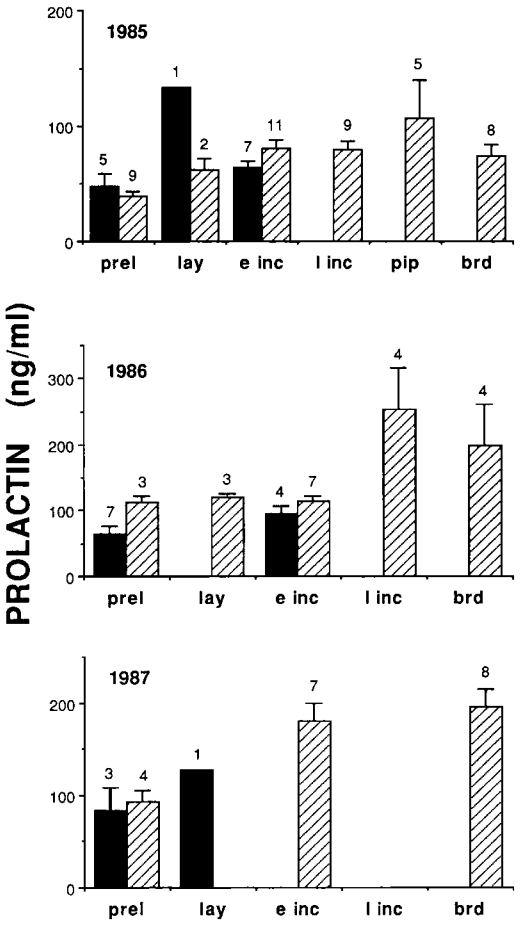

Fig. 4. Mean circulating prolactin levels in male (hatched bars) and female (solid bars) Red-necked Phalaropes during the 1985 to 1987 breeding seasons at La Pérouse Bay. Abbreviations of status groups are explained in text. Error bars denote SE; numbers above bars are sample sizes.

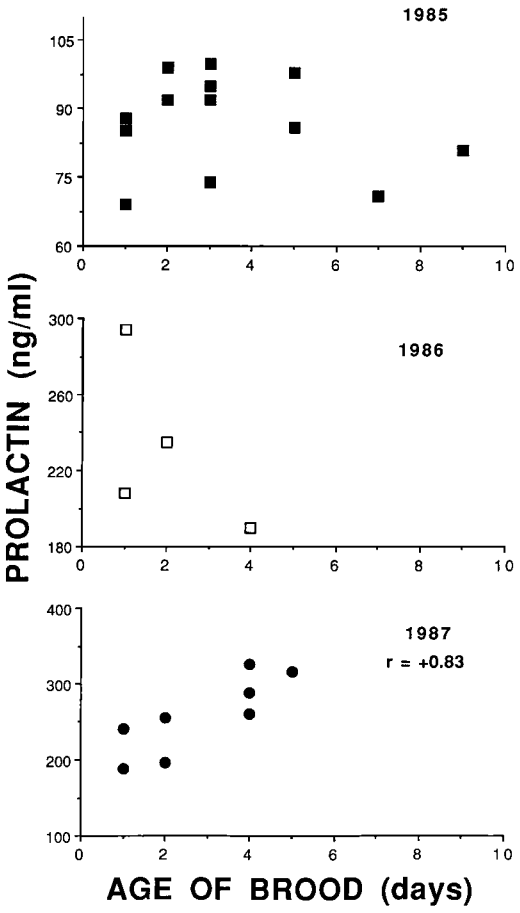

Fig. 5. Relationship between circulating prolactin levels and age of brood for female Semipalmated Sandpipers in each year at La Pérouse Bay. Only 1987 was significant ($r = +0.83$, $P < 0.05$).

PROLACTIN AND BROODING

There were no negative correlations between circulating prolactin levels of female Semipalmated Sandpipers and age of brood (Fig. 5) in any year. There was a significant positive correlation in 1987 ($r = +0.83$, $P < 0.05$).

There were no significant correlations between prolactin and brood age for male Semipalmated Sandpipers (Fig. 6). As noted previously, there was no significant difference between male and female prolactin levels during brooding in any year (Table 2). There also was no significant difference between members of the same pair caught with the brood on the same day (paired t-test, all years combined, $n = 17$, mean female-male $= -23 \pm 23$ ng/ml, $P = 0.32$).

In male Red-necked Phalaropes, there was a significant negative correlation between prolactin and age of brood in 1985, one of the two years (1985, 1987) with sufficient brood data (Fig. 7, $r = -0.70$, $P < 0.05$). Results from 1987 were not significant, although there was a suggestion of a decline.

DISCUSSION

PROLACTIN AND INCUBATION

High levels of circulating prolactin were correlated with incubation behavior in the Semi-

TABLE 3. Red-necked Phalarope: statistical comparison of prolactin levels across breeding stages; results of ANOVA and *GT2* multiple comparison tests (Type I family error rate = 5% across each year-sex comparison). Probability and *F*-values are given for ANOVA, while only significant differences are shown for *GT2* tests. Abbreviations of status groups are explained in text.

	ANOVA		
Year	*F*	*P*	Significant *GT2* tests
	Female		
1985	1.9	0.49	
1986	3.4	0.10	
	Male		
1985	3.5	0.01	prel < pip
1986	2.8	0.06	
1987	5.8	0.01	prel < e inc, brd

palmated Sandpiper. Prolactin levels increased significantly at the onset of persistent incubation. Sexes incubate equally, and prolactin values were not significantly different between the sexes at any time during the breeding season.

Only two previous studies have examined avian species in which both members of the pair participate equally in incubation. No differences in prolactin levels between the sexes were found during incubation and brood care in male and female Ringed Turtle-Doves (Cheng and Burke 1983). The sexes incubate equally, and both produce crop sac "milk." In the Black-browed (*Diomedea melanophris*) and the Gray-headed (*D. chrysostoma*) albatross, in which species the sexes incubate equally in bouts lasting a number of days, prolactin values also were not different between the sexes. By contrast, in the Wandering Albatross (*D. exulans*), in which males and females also incubate equally, pro-

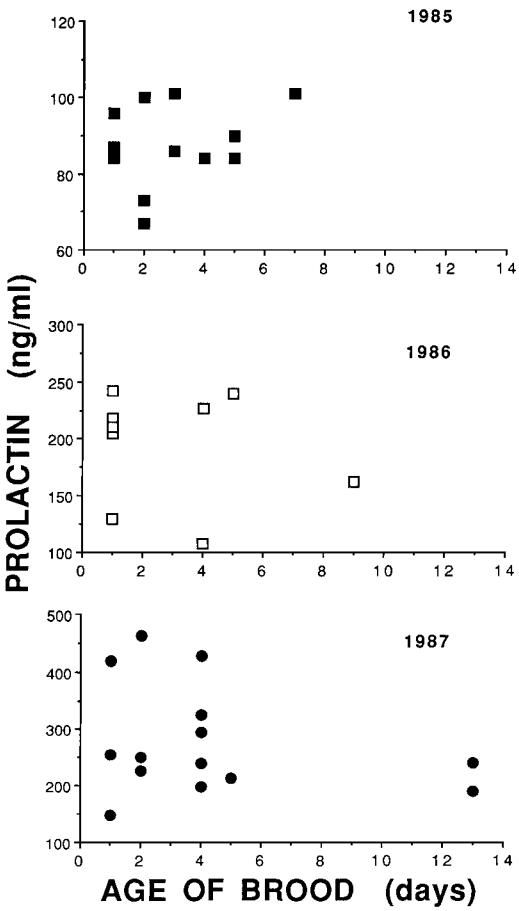

Fig. 6. Relationship between circulating prolactin levels and age of brood for male Semipalmated Sandpipers in each year at La Pérouse Bay. None was significant (Pearson correlations, $P > 0.05$).

TABLE 4. Comparison of circulating prolactin levels among incubating male, and nonincubating male and female Red-necked Phalaropes. The highly elevated value for the only laying female in 1985 was excluded. Comparisons are *t*-tests.

	Prolactin (ng/ml)								
	Preincubation males			Females			Incubating males		
Year	*n*	$\bar{x} \pm$ SE	P^a	*n*	$\bar{x} \pm$ SE	*P*	*n*	$\bar{x} \pm$ SE	P^b
1985	11	43 ± 17	0.08	12	57 ± 6	0.005	25	86 ± 7	0.0001
1986	6	116 ± 5	0.002	11	75 ± 9	0.01	11	165 ± 30	0.14
1987	4	92 ± 12	0.94	4	95 ± 20	0.02	7	181 ± 19	0.01

[a] All comparisons are *t*-tests.

[b] Incubating vs. preincubation males.

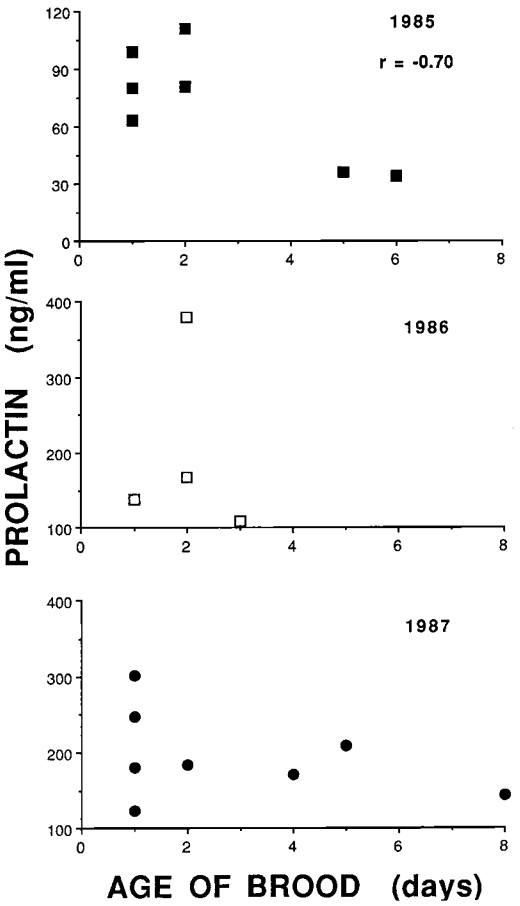

Fig. 7. Relationship between circulating prolactin levels and age of brood for male Red-necked Phalaropes in each year at La Pérouse Bay. Only 1985 was significant ($r = -0.70$, $P < 0.05$).

lactin levels were significantly higher in females than in males. Possible reasons for this difference were not discussed (Hector and Goldsmith 1985).

In species where only one sex incubates, that sex has higher levels of prolactin than the other during incubation (e.g. Mallard [*Anas platyrhynchos*], Goldsmith and Williams 1980; Barheaded Goose [*Anser indicus*], Dittami 1981; Common Canary [*Serinus canaria*], Goldsmith 1982b; Pied Flycatcher, Silverin and Goldsmith 1983; White-crowned Sparrow, Hiatt et al. 1987; Wilson's Phalarope, Oring et al. 1988). In the Black Swan (*Cygnus atratus*), females participated in incubation more often than males, and also had slightly higher plasma prolactin levels (Goldsmith 1982a). Female Spotted Sandpipers normally incubated much less than their mates did late in incubation, and females had lower prolactin levels at that time (Oring et al. 1986b).

It is not surprising that we found incubating male Red-necked Phalaropes had levels of plasma prolactin higher than those of females. Nevertheless, the fact that early-incubating males in 1986 did not have elevated prolactin levels seems to contradict the hypothesis that high values of circulating prolactin coincide with incubation behavior. However, in this case the exception seems to support the rule. Red-necked Phalaropes often desert their nests for extended periods (sometimes days) in cold or wet weather, when food is presumably difficult to obtain. At the time that most phalaropes began their nests in 1986, minimum temperatures were lower than normal, and precipitation much higher (average June minimum temperature: 1985 = 2.0°C, 1986 = 1.0°C; total June precipitation: 1985 = 30 mm, 1986 = 117 mm [Churchill Weather Office Reports unpubl.]). Extensive observations on two nests at this time indicated that incubation was greatly reduced (dropped from the normal 50–70% of daytime 1-h observation period to 0% on particularly poor-weather days; Mallory 1987). This finding further emphasizes the relationship between high prolactin values and persistent incubation. Perhaps periods of poor weather and low insect availability result in decreased prolactin release from the pituitary, and produce low circulating prolactin levels. Certainly a decrease in incubation behavior when foraging conditions are poor has been noted in the Pectoral Sandpiper (*Calidris melanotos*), with single-sex incubation (Norton 1972). Because both sexes incubate in the Semipalmated Sandpiper, incubation constancy is near 100% (Norton 1972), and no decline in incubation is evident under poor weather conditions. As expected, the poor weather conditions early in incubation in 1986 did not affect prolactin levels in sandpipers.

Even though the 1986 "early incubation" phalaropes had low prolactin levels and reduced incubation, they were sufficiently tenacious to enter a nest trap. This supports the idea that once a bird is "primed" by high gonadal steroids and eggs are present, high plasma levels of prolactin are not necessary for at least short periods of incubation. The presence of eggs, and the act of incubation itself, may result

eventually in elevated prolactin levels (e.g. Goldsmith 1983, Lea 1987).

The extent of male Red-necked Phalarope incubation is variable and depends upon weather conditions. Therefore, it may be expected that their overall patterns of circulating prolactin levels changed from year to year. Even within a year, the period of incubation varied from 18 to 24 days in this species (e.g. 1985, $n = 14$, $\bar{x} \pm SD = 20.3 \pm 1.9$ days). Semipalmated Sandpipers with biparental care, on the other hand, incubate constantly, and the length of the incubation period varied little (e.g. 1985, $n = 16$, $\bar{x} \pm SD = 19.6 \pm 0.73$). The patterns of circulating prolactin were much more consistent in this species.

Prolactin and Brooding

Our results for Red-necked Phalaropes agree with those from Wilson's Phalaropes (Oring et al. 1988): prolactin levels declined gradually with increasing age of the brood. Because diurnal brooding behavior generally decreases during the first week posthatch in male Red-necked Phalaropes that attend young, it is possible that circulating prolactin levels in this species are directly related to both incubation and chick brooding. However, this pattern of decline was significant only in one year. Cold weather is not uncommon after hatch in the subarctic. By affecting the amount of brooding, ambient temperature might produce a more inconsistent pattern of prolactin decline after hatch, compared with patterns in more southern study areas.

Although diurnal brooding behavior also generally decreased during the first week posthatch in Semipalmated Sandpipers, we found no evidence in either sex of a decline in plasma prolactin with increasing brood age. This should have been particularly evident in females, because they gradually separate themselves from the chicks much earlier than males (Ashkenazie and Safriel 1979a, b; Gratto and Cooke 1987). In fact, prolactin levels increased significantly in one year. We cannot explain this result, and reasons for the overall lack of decline in prolactin after hatch are not obvious. All previous studies on birds that attend young report either an immediate precipitous decline or a gradual decrease in prolactin (for review, see Goldsmith 1983). Perhaps these high prolactin levels posthatch are related to molt and migratory fattening (e.g. Dawson and Goldsmith 1983, 1984). Both sexes of Semipalmated Sandpipers initiated body molt during incubation, and began premigratory fattening soon after leaving the brood. Red-necked Phalaropes, on the other hand, did not initiate molt during incubation or brooding.

Meier proposed that the timing of seasonal conditions in birds is based upon changing temporal relations among hormones, including prolactin (for review, see Meier and Russo 1985). Although we found no evidence for circadian rhythm of prolactin secretion, our sampling regime was not designed to maximize detection of daily changes. Therefore, it is possible that a phase shift in the timing of prolactin release is the basis for prolactin's role in both incubation and photorefractoriness.

The patterns of circulating prolactin levels in Semipalmated Sandpipers and Red-necked Phalaropes breeding in the subarctic indicate that high prolactin levels are correlated with persistent incubation behavior. This is made evident by the fact that there was no difference in prolactin levels between the equal incubating sexes of the Semipalmated Sandpiper, and by the fact that incubating male Red-necked Phalaropes had greater prolactin values than the nonincubating females. The apparent effect of poor weather conditions on plasma prolactin levels in male phalaropes emphasizes the difference in incubation constancy between these two species. However, changes in prolactin levels did not explain the early brood desertion of female Semipalmated Sandpipers. Although we cannot explain why plasma prolactin levels do not decline during brooding in Semipalmated Sandpipers (and is not pronounced in Red-necked Phalaropes), this phenomenon appears unique among avian species examined.

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VARIATION IN PIED FLYCATCHER (*FICEDULA HYPOLEUCA*) MITOCHONDRIAL DNA

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ABSTRACT.—Pied Flycatchers (*Ficedula hypoleuca*) in Sweden have low levels of variation in nuclear genes relative to most other bird species. This lack of variation has been attributed to population bottlenecks caused by Pleistocene glaciations. We studied mitochondrial DNA (mtDNA) variation in 20 Pied Flycatchers from four Swedish localities. Eight restriction endonucleases yielded a total of 207–212 DNA fragments (approximately 5% of the mtDNA genome). The mean pairwise divergence between the individuals was 0.35 ± 0.16% (range 0.00–0.82%), which suggests that the 18 identified mtDNA clones diverged within the past million years, and that the majority of clones evolved within the last 100,000 years.

If genetic variation was reduced by prolonged bottlenecking during the last glacial period, low protein heterozygosity and high variability in mtDNA can be explained by a difference in rates of recovery of nuclear and mtDNA variation. The Pied Flycatcher in northern Europe may have only recently begun to regain variation in nuclear genes, whereas considerable variation in mtDNA has already accumulated through mutation. *Received 7 December 1989, accepted 11 May 1990.*

GENETIC variability and relationships among clones of mitochondrial DNA (mtDNA) can provide background data to hypotheses on biogeographical history and population structure. As a clonally transmitted marker, the distribution of the maternally inherited mtDNA will reflect founder or rare immigration events more directly than nuclear DNA (Wilson et al. 1985). The study of mtDNA variability is highly relevant for avian species because of the relative lack of observed differentiation in proteins as assessed by electrophoresis (Barrowclough 1983).

The last glacial period probably played a major role in determining the amount of diversity and the distribution of mtDNA clones in North American and Eurasian species. During the Pleistocene glacial period, populations were isolated in refugia and subjected to severe reductions in effective population size, which decreased the number of mtDNA clones within populations (Wilson et al. 1985, Gyllensten and Wilson 1987). Postglacial recolonization involved founder events and population bottlenecks, and further reduced mtDNA variation. Multiple range expansions from one or a few refugia have led to a geographic structuring of mtDNA clones, especially in small mammals (Avise et al. 1983, Avise et al. 1987, Tegelström 1987a) where female dispersal is restricted compared with that in most avian species.

Most studies of avian mtDNA have concentrated on genetic differences between species or subspecies (Kessler and Avise 1985a; Mack et al. 1986; Ovenden et al. 1987; Shields and Wilson 1987a, b; Avise and Nelson 1989; Zink and Avise 1990). Studies of mtDNA variation within bird populations (Shields and Wilson 1987a, Tegelström 1987b, Ball et al. 1988, Avise and Nelson 1989, Zink and Avise 1990) indicate small genetic distances between mtDNA clones and, with one exception (Avise and Nelson 1989), an absence of structure in mtDNA variation. The most thorough study of mtDNA variation within an avian species was a continent-wide survey of the Red-winged Blackbird (*Agelaius phoeniceus*). The morphological subspecies exhibited little allozyme divergence (Ball et al. 1988). Red-winged Blackbirds also had only small genetic distances between mtDNA clones, and the different mtDNA clones showed widespread geographic distributions.

We studied mtDNA in the Pied Flycatcher (*Ficedula hypoleuca*), a species whose main breeding area is in rich deciduous woodlands in northwestern Europe. The Fennoscandian populations are probably descended from populations isolated in refugia during the Pleistocene period (von Haartman 1949). Protein electrophoresis of 35 loci revealed a low amount of genetic variation compared with other avian species (Gelter et al. 1989). The proportion of observed polymorphic loci was 11.4 ± 0.3% (mean of 24.0% in other avian species; Evans

TABLE 1. Eighteen mtDNA clones in the Pied Flycatcher (*Ficedula hypoleuca*) from 4 localities in Sweden. Letters in the composite mtDNA genotypes refer (left to right) to restriction morphs for enzymes *Hae*III, *Dde*I, *Rsa*I, *Mbo*I, *Hin*fI, *Hpa*II, *Sau*96 AI, and *Taq*I, respectively.

Clone no.	Locality	Composite mtDNA genotype	No. of individuals
1	A	BBAFBCEA	1
2	A, B	BBADBCBA	2
3	A	BCABBCDA	1
4	A	BGADFCBA	1
5	A	BFAFEAFC	1
6	A	BCABCCEA	1
7	B	BBAEBCBA	1
8	B	BFAGECBA	1
9	B	BFAHBCGA	1
10	B	ABBAABCA	1
11	B	BCAFEAFC	1
12	C	BCAABCEA	1
13	C	BBAADCBA	1
14	C	BAACBAAC	1
15	D	BAAFBCEA	1
16	D	BDAEBCBB	1
17	D	BAAFEABC	2
18	D	CEAIECBA	1

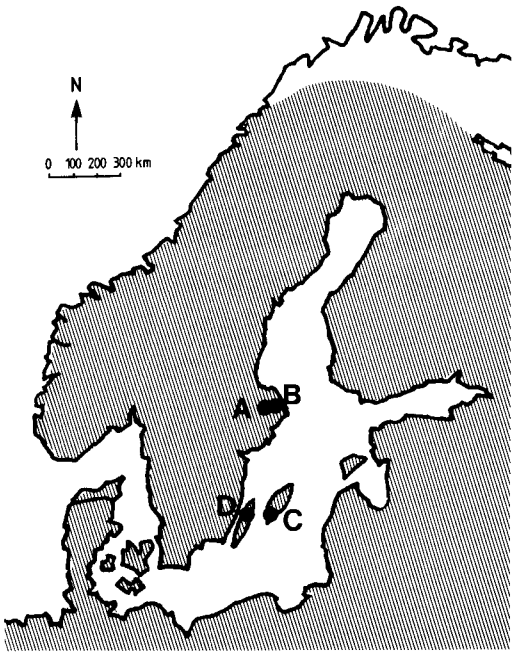


Fig. 1. Sampling localities (A–D) for individuals of the Pied Flycatcher (*Ficedula hypoleuca*). The shaded area indicates the geographic distribution of the species.

1987), and the observed mean heterozygosity was 0.9% (compared with a mean of 4.4% in other avian species; Evans 1987). Our objectives were to investigate whether mtDNA in *F. hypoleuca* exhibits low genetic variation and whether mtDNA clones are geographically structured.

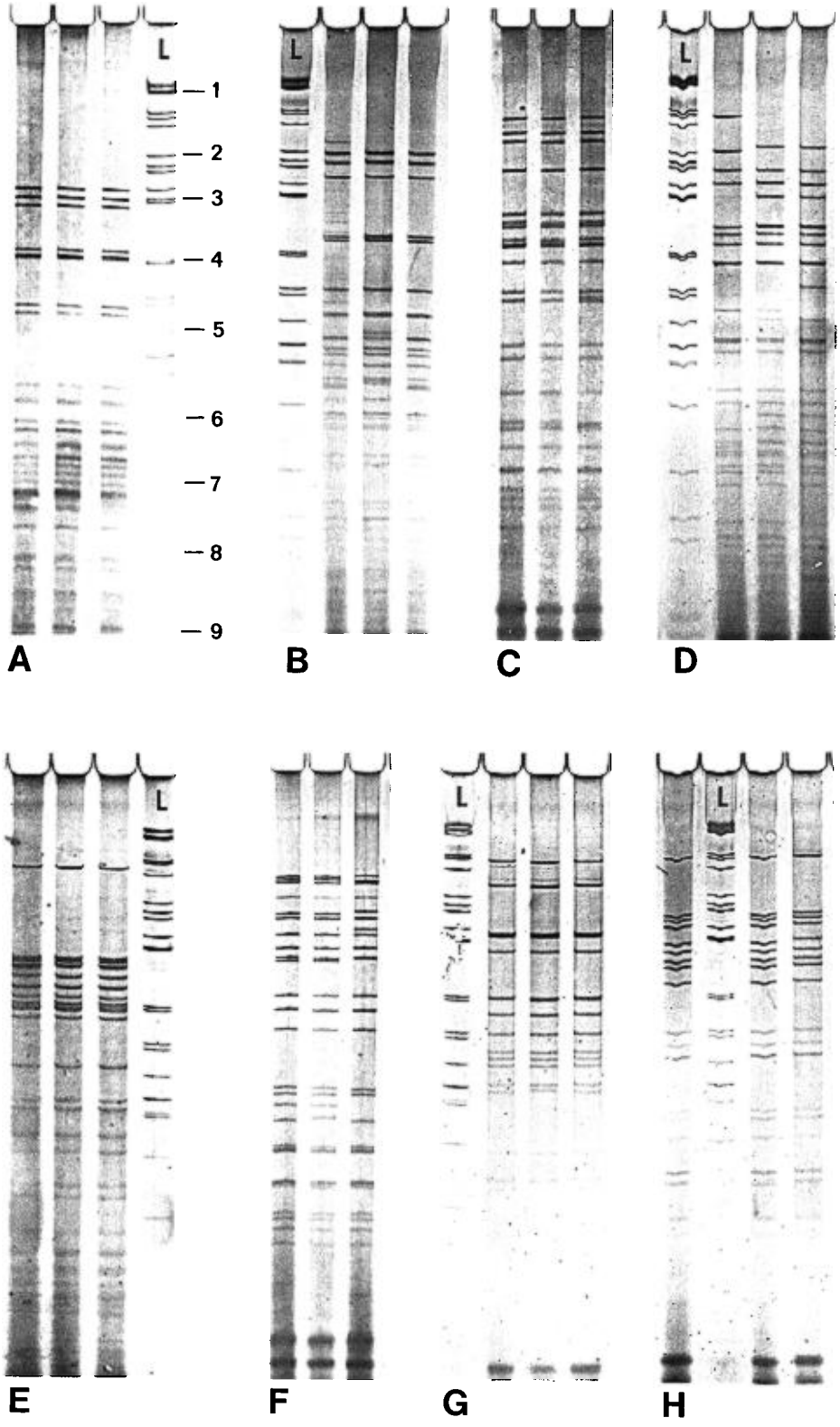
METHODS

Twenty *Ficedula hypoleuca* were live-trapped at their nest boxes (Fig. 1, Table 1). We isolated mitochondria from fresh or frozen liver and heart according to Lansman et al. (1981). We isolated mtDNA by ultracentrifugation in CsCl density gradients (Beckman SW 50.1 swing out rotor) for 48 h at 35,000 rpm. After collection, 10–40 ng of mtDNA was digested according to Tegelström (1986). Eight type II tetranucleotide restriction endonucleases (Boehringer Mannheim or Pharmacia P-L Biochemicals) were used to characterize mtDNA (recognition sequences in parenthesis): (1) *Hae*III (GGCC); (2) *Dde*I (CTNAG); (3) *Rsa*I (GTAC); (4) *Mbo*I (GATC); (5) *Hin*fI (GANTC); (6) *Hpa*II (CCGG); (7) *Sau*96 AI (GGNCC), and (8) *Taq*I (TCGA). These eight enzymes have a GC:AT ratio of 2.2, which is similar to that of other studies of avian mtDNA (mean 1.9, range 1.3–3.3; Tegelström and Gelter 1990). Fragments of mtDNA were separated in 5% polyacrylamide-gels according to Tegelström (1986) and Tegelström and Wyöni (1986), and visualized by silver staining (Guillemette and Lewis 1983). Each of the distinctive mtDNA restriction fragment patterns produced by a given restriction endonuclease was designated by a letter. Every specimen was assigned a composite mtDNA phenotype of eight letters to characterize the restriction fragment patterns given by the eight endonucleases used in the study. Individuals that shared a common composite phenotype were regarded as belonging to the same mtDNA matrilineal clone.

We calculated the total proportion of shared fragments between two individuals as

$$F = 2Nxy/(Nx + Ny),$$

where Nx and Ny are the numbers of fragments in individuals X and Y, respectively, and Nxy is the number of fragments shared by X and Y. Values of F were converted to estimates of nucleotide sequence divergence, p, by eq. 20 (Nei and Li 1979). Phenograms were constructed from matrices of p-values by the unweighted pair-group method (UPGMA; Sneath and Sokal 1973). Fragment data are not presented in their entirety, but are available on request from Tegelström.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Results

The eight restriction endonucleases yielded a total of 207–212 fragments per mtDNA clone, corresponding to approximately 850 nucleotides per individual (ca. 5% of the mtDNA genome). Altogether 40 different fragment patterns were identified and representative examples are shown (Fig. 2). Each of the enzymes detected more than one clone. *Rsa*I was the least discriminating and yielded 2 phenotypes. *Mbo*I detected 9 phenotypes. Among the 20 individuals, 18 different mtDNA clones were identified (Table 1). The estimated total number of base pairs (bp) in the *Ficedula hypoleuca* mtDNA molecule varied between 12,900 bp (*Hae*III) and 16,980 bp (*Taq*I). Excluding *Hae*III (which often gives a high number of smaller fragments not detectable on the gels), the remaining seven endonucleases give a mean molecular size of 16,225 bp, which is comparable to values obtained for 40 other bird species (16.3–17.3 kb; Shields and Helm-Bychowski 1988). No mtDNA size variants were identified, and each bird was homoplasmic for the identified genotype.

The mean pairwise-divergence among the 20 individuals (including identical clones) was 0.35% (SD = ±0.16%) and the range of pairwise genetic distances between clones was 0.00–0.82%. The majority of clones had low pairwise genetic distances (Fig. 3), which indicates a recent divergence. Assuming a rate of 2% sequence divergence per million years (Shields and Wilson 1987b), all the clones identified in *F. hypoleuca* have diverged within the last million years (largest *p*-value: 0.82%). The majority of clones evolved within the last 100,000 years ($p < 0.2\%$).

The phenogram (Fig. 3) implies little geographic structuring of the clonal branches. Clones in neighboring localities in Uppsala (locality A and B) and clones from the islands of Öland and Gotland are mixed randomly. For example, the four clones from Öland (locality C; clones 15, 16, 17, and 18) appear in different parts of the phenogram and always have a clone from the mainland as the closest relative.

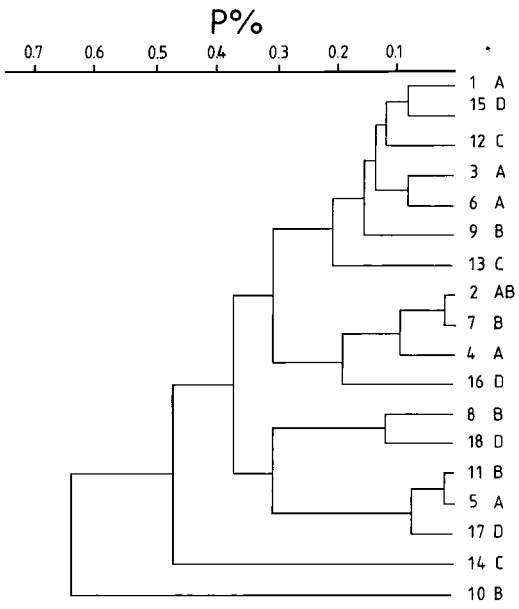

Fig. 3. Phenogram derived from an UPGMA cluster analysis (Sneath and Sokal 1973) of 18 mtDNA clones in the Pied Flycatcher (*Ficedula hypoleuca*). Clones are numbered 1–18 (Table 1). Letters refer to sampling localities (Fig. 1).

Discussion

We identified a large number of mtDNA clones in the Swedish Pied Flycatcher populations. The 20 individuals studied yielded 18 different maternal lineages. The different clones showed no obvious geographic structuring and were closely related. However, the small sample sizes meant that population subdivision cannot be ruled out. Larger population sample sizes would allow estimates of within vs. between population variation (cf. Takahata and Palumbi 1985). The presence of closely related mtDNA clones at different geographic locations could have two explanations. Either an ances-

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Fig. 2. Representative examples of fragment patterns after restriction endonuclease digestion of mtDNA from individuals of the Pied Flycatcher (*Ficedula hypoleuca*): (A) *Hae*III, (B) *Dde*I, (C) *Rsa*I, (D) *Mbo*I, (E) *Hin*fI, (F) *Hpa*II, (G) *Sau*96, and (H) *Taq*I. Lanes marked L contain λ DNA digested with restriction endonuclease *Bgl*I to produce fragment size markers: (1) 9,649 base pairs, (2) 1,650 bp, (3) 1,138 bp, (4) 790 bp, (5) 562 bp, (6) 366 bp, (7) 267 bp, (8) 186 bp, and (9) 115 bp.

tral retention of clones (Neigel and Avise 1986) after the colonization of the European continent and Scandinavia from one or several refugial areas (von Haartman 1949) or recent interconnections through gene flow, which would prevent mtDNA differentiation of populations by stochastic lineage sorting (Avise et al. 1987). A more extensive sampling of populations is necessary to distinguish these explanations.

Even though electrophoresis of proteins in the Pied Flycatcher reveals a low level of heterozygosity, mtDNA shows relatively high levels of variation—comparable to the "DNA-fingerprinting" level of the mtDNA variation found by Avise et al. (1989). Other studies of mtDNA variation have revealed lower levels of variation (Spolsky and Uzzell 1984, Kessler and Avise 1985b, Saunders et al. 1986, Shields and Wilson 1987a, Avise and Zink 1988, Ball et al. 1988, Avise and Nelson 1989, Lamb et al. 1989, Mulligan and Chapman 1989). Explanations for the difference in amounts of nuclear and mtDNA variation may be found in demographic factors such as differences in dispersal between the sexes. Alternatively, populations may have incurred bottlenecks during the colonization of the European continent and Scandinavia from previously glaciated regions.

A demographic situation that affected the distribution of diversity in mtDNA and nuclear genes has been described in Canada Geese (*Branta canadensis;* Shields and Wilson 1987a), where males disperse more widely than females. Founding of new breeding populations by a low number of closely related females and many males from diverse lineages has led to the fixation of different mtDNA-variants in different populations. Nuclear diversity, however, is high, and there is little differentiation even between subspecies, because of nuclear gene flow between populations through male dispersal. Demographic factors that characterize the Pied Flycatcher, such as female-biased dispersal (which would increase the effective population size for both mtDNA and nuclear genes) or polygynic males (which would decrease the effective population size for nuclear genes) cannot explain low levels of nuclear variation accompanied by substantial levels of variation in mtDNA.

Low levels of protein variation (Sage and Wolff 1986) as well as mtDNA (Wallis and Arntzen 1989, Gyllensten and Wilson 1987) occur in species from previously glaciated regions and imply past genetic bottlenecks. In diploid organisms, the effective population size for mtDNA will always be less than that for nuclear genes, which makes variation in mtDNA more sensitive to population bottlenecks (Wilson et al. 1985). If genetic variation in both nuclear and mtDNA genes was reduced during the last glacial period, the current genetic variation in the Pied Flycatcher will be the sum of the variation that survived the bottleneck and mutations that have been incorporated subsequently.

We suggest that differences in recovery time for nuclear and mtDNA variation after a population bottleneck explain the pattern of mtDNA and nuclear genetic variation in the Pied Flycatcher. The majority of mtDNA clones in the Pied Flycatcher have diverged less than 0.2% (cf. Shields and Wilson 1987b). This implies that most mtDNA variation has been accumulated during the last 100,000 years, which supports the suggestion that the species may have been exposed to population bottlenecks during the alterations of the last glacial period. In contrast to the situation with mtDNA, the regeneration of genetic variation in nuclear DNA is a comparatively slow process. Assuming a large population size, the recovery time for reaching equilibrium allele frequencies for neutral alleles at one nuclear locus is in the range of 100,000 to 10 million generations (Lande and Barrowclough 1987). Thus, the Pied Flycatcher in northern Europe may be at the beginning of the process of regaining genetic variation in nuclear genes whereas considerable mtDNA variation already may have accumulated through mutation.

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GENETIC VARIATION AND DIFFERENTIATION IN THE SPOTTED OWL (*STRIX OCCIDENTALIS*)

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ABSTRACT.—We used starch-gel electrophoresis to investigate genetic variability at 23 loci in 107 individuals from seven populations of the Spotted Owl (*Strix occidentalis*). These populations sample all three currently recognized subspecies. No genetic variation was found in six populations from Oregon and California. Average heterozygosity in owls from New Mexico was 0.022. The low level of genetic variability will make it more difficult to monitor the genetics of this threatened species; the paucity of variation is possibly due to a small overall effective population size or bottlenecks in the past. At one locus there was a major allelic frequency difference between the Pacific Coast populations (*S. o. caurina* and *S. o. occidentalis*) and the allopatric taxon (*S. o. lucida*) found in New Mexico; our estimate of F_{ST} is 0.55. We believe the two allopatric populations have long been isolated, and it is probable that they represent two species. The data do not help elucidate the subspecific status of *S. o. caurina*. *Received 11 December 1989, accepted 11 May 1990.*

OVER the last two decades, evolutionary and systematic biologists have devoted a major effort to assessing the extent of genetic variation within, and differentiation among, populations (Lewontin 1985, 1986). This has been true of many disciplines, including ornithology (for recent reviews, see Avise and Aquadro 1982, Avise 1983, Barrowclough 1983, Corbin 1983, Barrowclough et al. 1985, Barrowclough and Johnson 1988). These results have allowed biologists to make inferences about the evolutionary history of a species and, perhaps, to generalize about evolutionary processes (e.g. Lewontin 1974). In addition, these studies provide systematists with data, independent of classical morphology and phenotypes, to assess biogeographic and taxonomic patterns (e.g. Barrowclough 1985).

Conservation biologists now realize that such data permit monitoring threatened populations for evidence of genetic deterioration (Lande and Barrowclough 1987) as well as identifying evolutionary and taxonomic units for conservation (e.g. Ryder 1986a, b). The recent report on genetic variation in the endangered New Zealand Kakapo (*Strigops habroptilus*; Triggs et al. 1989) is an example. One North American species that is the subject of much concern among conservationists, foresters, and wildlife biologists is the Spotted Owl, *Strix occidentalis* (e.g. Gutiérrez and Carey 1985, Dawson et al. 1987, U.S. Dep. Agric. For. Serv. 1988).

We report on an electrophoretic examination of genetic variation within and among populations of the Spotted Owl over much of its range. This study adds to the small, but growing, body of reports on the extent of genetic variation and differentiation in natural populations of birds; it also provides a survey of the population genetics of a species of particular environmental concern.

METHODS

Study areas and populations.—We sampled Spotted Owls from eight populations representing all three currently recognized subspecies (AOU 1957) (Fig. 1; Table 1). Populations differed greatly in their habitat characteristics and their population size. The Oregon and northwest California populations were large, continuous populations within a mix of old growth and younger age conifer forests. The Sierra Nevada and New Mexico populations were large and continuous. The habitat was characterized by a mixture of old growth, mixed age, and young forests. The southern California owls existed in small isolated populations located primarily in mixed age conifer stands.

We probably sampled <5% of the birds from the large continuous populations. Because we sampled only two birds from the Black Range, we combined the New Mexico samples for the purpose of analysis. We sampled approximately 20% of the San Bernardino range population. The two smallest populations were sampled most intensively: approximately 90% of the San Jacinto mountain population and approximately 50% of the Palomar Mountain birds. All estimates of

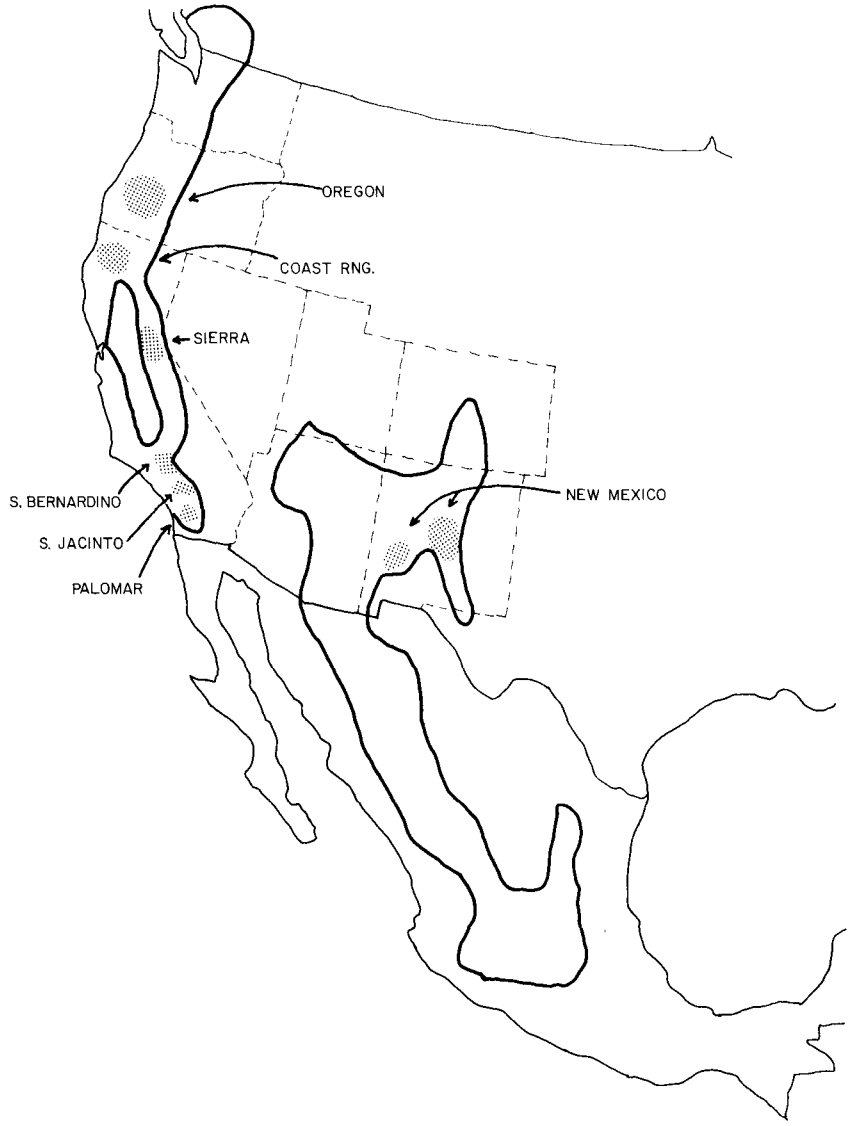

Fig. 1. Approximate distribution of the Spotted Owl. Localities from which genetic samples were obtained are indicated.

the proportion of the population sampled were derived from extensive census and banding studies (Franklin et al. 1990).

Capture methods.—Spotted Owls were located by imitating their calls to elicit a response (Forsman 1983, Franklin et al. 1990). Responding birds were captured with noose poles, mist nets, or pan traps (Forsman 1983, Bull 1987). Blood was taken from a brachial vein with a 23-ga needle and 1-cc syringe washed with EDTA as an anticoagulant. Each blood sample was immediately transferred to a cryogenic vial and frozen in liquid nitrogen within one hour of extraction. A few (<6) blood samples were not frozen for several hours because the sampling location was remote. Samples were maintained in liquid nitrogen, dry ice, and ultracold freezers until used for electrophoresis.

With a few exceptions (accounted for in the analyses), only unrelated individuals were sampled. Although we did not know the exact lineage of each bird, we inferred from previous banding and population studies that most of the birds were probably not closely related. However, the small isolated populations must have a substantial background level of relatedness.

TABLE 1. Taxa, localities, sample sizes, and estimates of genetic heterozygosity in Spotted Owl (*Strix occidentalis*) samples.

Population	n^a	$\hat{H}^b$	Subspecies
Oregon; Cascade & Coast ranges; Douglas County	20	0.0	*S. o. caurina*
California; Coast Ranges; Humboldt & Mendocino counties	19	0.0	*S. o. caurina*
California; Sierra Nevada; Placer & El Dorado counties	11	0.0	*S. o. occidentalis*
California; San Bernardino Mtns.; San Bernardino County	20	0.0	*S. o. occidentalis*
California; San Jacinto Mtns.; Riverside County	19	0.0	*S. o. occidentalis*
California; Mt. Palomar; San Diego County	9	0.0	*S. o. occidentalis*
New Mexico; Sacramento & Black ranges; Grant & Lincoln counties	9	0.022	*S. o. lucida*

[a] Number of individuals sampled from population.
[b] Averaged over 23 genetic loci.

Analysis.—Thawed blood was diluted with deionized water to lyse cells, then centrifuged at 6,000 rpm for 20 min. The supernatant was used for standard starch-gel electrophoresis. The electrophoretic conditions, buffer systems, and staining methods have been described previously (Harris and Hopkinson 1976, Barrowclough and Corbin 1978, Richardson et al. 1986). Nomenclature of enzymes, multiple isozymes, and alleles follows standard conventions.

Genotypic and allelic frequencies were computed from the starch-gel results. These data were analyzed using Hardy-Weinberg tests (Crow and Kimura 1970), contingency Chi-square tests (Workman and Niswander 1970), Slatkin's (1985) rare allele procedure, Rogers' (1972) genetic distance, Wright's (1978) F_{ST} statistics, and Nei's (1978) standard genetic distance and heterozygosity. The latter three statistics all included corrections for sampling error due to finite numbers of individuals.

RESULTS

We scored 23 loci that yielded consistently strong staining patterns. Additional enzymes that are typically scored using liver and skeletal muscle in birds were found to be weak, inconsistent, or absent in these red cell lysates.

Genetic variation.—Of the 23 loci examined, 22 were monomorphic in all populations (EC numbers in parentheses): ACP (3.1.3.2), ADA (3.5.4.4), CK (2.7.3.2), EST-2 (3.1.1.1), G6PDH (1.1.1.49), GPT (2.6.1.2), HGB (hemoglobin), IDH (1.1.1.42), LDH-1 and LDH-2 (1.1.1.27), MDH-1 and MDH-2 (1.1.1.37), NP (2.4.2.1), PEP-A, PEP-B, and PEP-C (3.4.11), 6PGDH (1.1.1.44), PGI (5.3.1.9), PGM (2.7.5.1), PT-1 and PT-2 (plasma proteins), and SOD (1.15.1.1). One locus, EST-D (3.1.1.1; by the methylumbelliferyl fluorescent method), was variable in the New Mexico sample. It was, however, monomorphic in all the Pacific Coast populations. The allele fixed in the coastal populations had a frequency of 0.389 in the New Mexico sample; a single alternate allele in that population had a frequency of 0.611.

Sample sizes and estimates of overall heterozygosity are in Table 1. Esterase-D is dimeric (Harris and Hopkinson 1976); the heterozygotes for this locus all had the characteristic three-banded pattern of such proteins. The observed three genotypic frequencies do not differ from Hardy-Weinberg proportions ($\chi^2 = 0.255$, df = 1, $P > 0.05$) in the New Mexico sample.

Genetic differentiation.—At the Esterase-D locus, the differences in allelic frequencies among the populations are statistically significant ($\chi^2 = 1273.4$, df = 6, $P < 0.005$; Workman and Niswander 1970). For this single locus, the estimate of F_{ST} among the seven populations is 0.55. Of course, this is actually an estimate of F_{ST} between the New Mexico population and those of California and Oregon. Similarly, our estimate of Nei's distance between New Mexico and the west coast is 0.016; for Rogers' distance, the estimate is 0.027.

Slatkin (1985) provided a method of estimating the extent of gene flow among populations from the frequency of private polymorphisms. The Esterase-D allele found segregating in the New Mexico population is an example of such a situation. From Slatkin's formula, we obtain an estimate of $Nm = 0.021$. This is equivalent to an average of one individual exchanged among populations every 50 generations.

DISCUSSION

Genetic variation.—This is the first published report on genetic variability in a natural population of owls. The estimated level of genetic variation (heterozygosity) in the samples of *S. o. occidentalis* and *S. o. caurina* (0.0) is remarkably

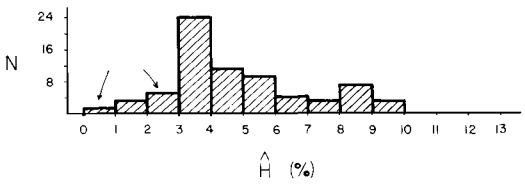

Fig. 2. Distribution of reports of genetic heterozygosity in birds based on 20 or more loci and 10 or more individuals. (Based on summaries of Barrowclough et al. 1985, Corbin 1987; and additional reports of Braun and Robbins 1986, Baker and Moeed 1987, Haig and Oring 1988, Seutin and Simon 1988).

low. This is one of very few cases of an apparent lack of detected variation in a population of birds for which a relatively large number of individuals and loci have been examined. For example, in recent reviews of genetic heterozygosity in birds (Barrowclough 1983; Corbin 1983, 1987; and Barrowclough et al. 1985), only one species with such an estimate is tabulated. This is the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*), based on 13 individuals and 23 loci (Gutiérrez et al. 1983). There are other nominal estimates of H of 0.0 (e.g. Patton and Avise 1986), but these are based on samples of one or a few individuals. We summarized (Fig. 2) estimates of H reported for birds calculated from at least 20 loci and 10 individuals. The west coast Spotted Owl populations lie at the extreme of the distribution. Outside of birds, estimates of H of zero are not common, but are known from a variety of taxa (e.g. see Nevo 1978).

The population of *S. o. lucida* has an estimate of H more typical of birds. It may seem odd that within the same species there should be populations with such disparate values, but the variability in *S. o. lucida* is the result of one polymorphic locus, and we will argue that these taxa probably have been isolated from each other for a long time.

We emphasize that these results do not mean that there is no genetic variability in the coastal populations of Spotted Owls. They indicate only that at some of the loci routinely screened by electrophoresis, the birds are invariant. Other structural genetic or regulatory loci, or the loci coding for quantitative traits, may be variable.

There are several possible reasons for the lack of genetic variability reported for the Pacific coast populations. First, the 23 loci we examined may be a particularly poor choice in that they are relatively monomorphic compared with "average" loci. This is equivalent to arguing that some genetic loci show more variability than others, across all taxa, and that members of the subset we examined are relatively invariant. Consequently, examination of another—complementary—set of loci may reveal substantial variation. We believe this is not a likely explanation. Some of the loci we examined (e.g. ADA, EST, NP, PEP, 6PGDH, and PGM) are among the most variable in birds (Evans 1987).

Second, it is possible that *Strix* owls, or large predators in general, because of their elevated position on the food chain, inherently have lower population sizes than do, for example, insectivores and granivores. Hence, they might have lower heterozygosity if H scales positively with effective population size (N_e), as neutralist theory suggests (Barrowclough et al. 1985). This possibility cannot be ruled out easily. Unfortunately there have been few studies of genetic variability in raptors. Barrowclough and Coats (1985) suggest that the genetic population structure of *S. occidentalis* in the Pacific Northwest consists of a series of overlapping demes of approximately 220 individuals each. If there are ten or so such demes in the range of the owls, then the total effective size of the coastal population might be only a couple of thousand (i.e. much smaller than the overall population size of taxa such as thrushes, warblers, and sparrows, etc., that include hundreds, if not thousands, of interconnected demes in their ranges). A way to check this hypothesis would be to compute correlations of heterozygosity on trophic level. However, this is not a strong test and is subject to many difficulties (Schnell and Selander 1981).

Third, the low variability observed could be due to extended population bottlenecks or founder effects in the past few thousands of years. Nei et al. (1975), for example, demonstrate that the heterozygosity of a population, following a long period of reduced numbers, will require 10^5 to 10^6 generations to recover to equilibrium levels. Likewise, a founder effect could also produce low levels of genic variation, but only if the founder population remained small for a very long period of time. This class of explanations can neither be ruled out easily, nor tested readily.

A fourth possibility is that the low heterozygosity in these owls is the result of habitat

destruction caused by timber cutting. This might have led to a reduction in the numbers of owls and hence to a loss of variability. This is an unlikely explanation, and is equivalent to arguing that the owls are now in a bottleneck because of logging. However, Spotted Owls are not yet rare (e.g. Gould 1977, Forsman et al. 1987, Franklin et al. 1990), even though this activity probably has reduced the population substantially in the past 100 years. It takes tens to hundreds of generations of reduced population size to reduce genetic variability (Nei et al. 1975).

Finally, it is possible that genic heterozygosity is less affected by population processes and demography than by internal genetic processes, physiology, and the efficacy of DNA repair mechanisms. From the point of view of whole organism biologists, heterozygosity might be a stochastic variable and Spotted Owls just happen to have variability of zero for these loci at this time. If so, then genetic data are uninformative about any aspect of the population biology of a species. This explanation is basically a null hypothesis best adopted as an alternative to specific causative models. It is not tested easily.

Clearly, at present we are unable to discriminate among the competing explanations of the reduced heterozygosity in the Spotted Owl. Nevertheless, only three of the possible explanations are particularly plausible, and these allow us to draw inferences of interest.

None of the most probable causes for the low variability lead to the conclusion that the owls are currently at risk because of genetic difficulties such as inbreeding. This may seem counterintuitive, but observed variation in an electrophoretic study has to be viewed simply as a genetic marker for monitoring the genetic makeup of a population (Lande and Barrowclough 1987). Variation in the loci studied should not be interpreted as being critical per se.

A second conclusion we can draw is that, unfortunately, it will be difficult to monitor the genetics of Pacific Coast populations of these owls for conservation purposes. If further testing of structural genes does not yield easily observed variation, then more difficult and expensive techniques, such as mtDNA restriction mapping or heritability of quantitative traits, will have to be used to monitor the genetic structure of this species. In the populations of

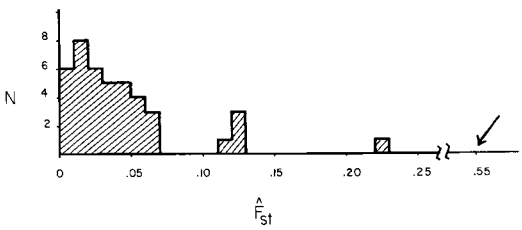

Fig. 3. Distribution of reports of Wright's F_{ST} in birds. (Based on summaries of Barrowclough 1983, Barrowclough and Johnson 1988; and additional reports of Van Wagner and Baker 1986, Baker and Moeed 1987, Grudzien et al. 1987, Haig and Oring 1988, Seutin and Simon 1988).

S. o. lucida, EST-D is readily available, easy to monitor with blood samples, and polymorphic.

Genetic differentiation.—No variation was observed in the samples of *S. o. occidentalis* and *S. o. caurina*. Thus it was not possible to observe any differentiation or to estimate its magnitude. Therefore, our data were neutral with respect to the taxonomy of these two currently recognized subspecies. Our results cannot be used to argue either for or against lumping of the taxa. Other molecular or morphological studies will be required to address that issue.

The extent of differentiation observed between the New Mexico sample of *S. o. lucida* and the California and Oregon samples is large by avian standards (see Fig. 3 for estimates of F_{ST} among conspecific populations of birds from the literature). The observed value for this species (0.55) is the largest reported to date. Of course, this estimate is based on a single locus and has an unknown, but probably quite large, standard error.

The estimates of Nei's and Rogers' genetic distances are also large in comparison with reports of the same statistics from other conspecific avian populations (e.g. see summary in Barrowclough 1980). The estimate lies in the range of overlap between the average differentiation among subspecies and that among species. Some subspecies with larger genetic distances are known (e.g. Baker and Strauch 1988, Capparella 1988). Likewise, some species show smaller distances (e.g. Hackett 1989).

The geographical extent of the EST-D polymorphism found in the New Mexico birds requires analysis. We presume the polymorphism characterizes the entire *S. o. lucida* taxon, but that should be established through further sam-

pling. If the polymorphism is widespread, then we find this pattern of variation interesting because of its implications for the past evolutionary history and taxonomic status of the owls.

The most frequent allele (at the EST-D locus) in our sample of *S. o. lucida* was absent in the relatively large sample of the Pacific Coast birds, which represents six populations including those geographically nearest to the range of the interior taxon. We suggest that there is currently no gene flow between the taxa, *nor has there been any for an evolutionarily long period of time.* We draw this inference because the period of time required for an allele to go from rare to common, or from common to lost (either may be the case in this situation because we do not know the ancestral state), is on the order of the inverse of the effective population size. Certainly, in this case, this is more than a thousand generations. Barrowclough and Coats (1985) estimated that generation time for Spotted Owls is approximately seven years. The private polymorphism analysis using Slatkin's technique reinforces this conclusion. The magnitude of estimated gene flow (one individual per 50 generations) is an upper bound that may seriously *overestimate* current gene flow (Larson et al. 1984, Rockwell and Barrowclough 1987).

Species status.—Allopatric populations of birds, with their own evolutionary histories and a lack of gene flow for thousands of years, present taxonomic problems. In the worldview of the Biological Species Concept (e.g. Mayr 1970), these populations are not in contact. Whether they are behaviorally or genetically reproductively isolated is unknown. One might suppose, given our knowledge of the propensity for hybridization among birds in general (e.g. Rising 1983), that they would interbreed if given a chance, However, treating the owls as conspecific based on that line of reasoning does not reflect the status quo. It is essentially a prediction about what the owls might do at some indefinite time in the future if environmental changes facilitate contact.

In the framework of the Evolutionary Species Concept (*sensu* Wiley 1978), the populations apparently have had their own separate evolutionary histories indicated by the major allelic frequency difference. Consequently, they would be considered separate species.

Within the Phylogenetic Species Concept (e.g. Cracraft 1983), these owls are not quite diagnosable. The frequency of the EST-D allele in the New Mexico sample is such that 90% of those birds can be unambiguously distinguished from the *S. o. occidentalis* and *S. o. caurina* populations. This is a more extreme case of the pattern in the *Empidonax difficilis* complex (Johnson and Marten 1988), a situation in which the biogeography is concordant with that of these owls. However, based on our interpretation of the available data, we suggest that the past period of isolation has been sufficiently long that further examination will reveal fixed differences when more genetic loci are assayed. Thus, there exists the distinct possibility that these are two species of birds.

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AMERICAN WOODCOCK WINTER DISTRIBUTION AND FIDELITY TO WINTERING AREAS

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ABSTRACT.—We examined winter distribution and fidelity to wintering areas for the American Woodcock (*Scolopax minor*), which exhibits reversed, sexual size dimorphism. Band-recovery data revealed no difference in winter distributions of different age/sex classes for woodcock from the same breeding ares. Similarly, band recoveries from woodcock banded on wintering grounds revealed no difference in fidelity to wintering sites. Males may winter north of a latitude that is optimal for survival based on physiological considerations, but they gain a reproductive advantage if they are among the first to arrive on the breeding grounds. This may explain our results, which indicate males and females have similar distribution patterns during winter. *Received 5 December 1989, accepted 12 May 1990.*

MANY migratory bird species exhibit sex- and age-specific differences in where they winter (see reviews in Ketterson and Nolan 1976, 1983; Nichols and Haramis 1980; Myers 1981). Three hypotheses have been invoked to explain differences. One concerns physiological differences associated with body size, another considers behavioral dominance of age/sex classes, and a third concerns differences in time of arrival on breeding grounds (see Hypotheses and Predictions). Unfortunately, most previous investigations of differential distribution patterns on the wintering grounds have been conducted on species for which the observed distributional differences are consistent with predictions of two or all three of these hypotheses.

We investigated winter distribution patterns of American Woodcock (*Scolopax minor*). They are an appropriate choice for two reasons. First, the hypothesis of behavioral dominance among age/sex classes can likely be rejected *a priori* for this species, while the two remaining hypotheses yield opposite predictions (see Hypotheses and Predictions). Second, band-recovery data are available. Band-recovery data permit unambiguous inferences about distribution patterns during winter of birds from specific breeding areas (Nichols and Haramis 1980, Nichols et al. 1983, Perdeck and Clason 1983, Nichols and Hines 1987, Diefenbach et al. 1988a, b). Most studies of winter distribution patterns use samples (e.g. museum specimens) of birds obtained at specific wintering locations without prior knowledge of their origin on the breeding grounds. The geographic variation in age or sex ratios of such samples is ambiguous. Previous investigators have inferred that such variation reflected variation in wintering-ground destination among birds from the same breeding areas. An alternative explanation is that geographic variation in age or sex ratios exists on the breeding grounds and that birds from the same breeding areas migrate together to the same wintering areas (see Nichols and Hines 1987: 35). In this instance, age or sex ratios on the wintering grounds simply reflect ratios on breeding grounds, and proposed explanations of different migration patterns may be unnecessary.

In addition to examining winter distribution of the different age/sex classes of American Woodcock, we tested hypotheses about age- and sex-specific variation in fidelity to wintering areas. To date, such questions about fidelity to wintering grounds have been restricted primarily to waterfowl (Nichols et al. 1983, Nichols and Hines 1987, Diefenbach et al. 1988a, b).

Our objectives were to test two null hypotheses. First, male and female woodcock from the

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same breeding areas have the same pattern of distribution in winter. Second, male and female woodcock have similar degrees of fidelity to specific wintering areas. Both of these hypotheses were tested for young, adult, and both age-classes combined.

METHODS

BAND RECOVERIES

Records of band recoveries for woodcock were obtained from the U.S. Fish and Wildlife Service (USFWS) Bird Banding Laboratory in Laurel, Maryland. For the analyses of distribution patterns, we used all recoveries from preseason (10 April to 31 August) 1961–1984 bandings of normal wild birds that were shot or found dead during December and January. Band recoveries were restricted to December and January because autumn migration should be nearly complete and spring migration not yet begun (Pursglove and Doster 1970). Each banded bird was sexed and aged as either young (calendar year of hatching) or adult (older than one year) (Martin 1964).

Band recoveries from normal wild birds banded in Louisiana in December, January, and February, 1939–1960, and shot or found dead in December and January at least one year later, were used to compare the fidelity to wintering areas of male and female woodcock. Banders after 1960 also aged birds, which allowed comparisons between males and females for both young and adults banded during 1962–1977.

STATISTICAL TESTS

Our analysis of distribution patterns of woodcock compared the bivariate distributions (latitude and longitude) of band recoveries from each age/sex class. We used a nonparametric test (Mardia 1967, 1972: 197) to test the null hypothesis that distribution patterns of band recoveries of males and females for both adults and young, and both age-classes combined, were equivalent for birds banded in the same breeding area. Data for comparisons were limited, so we combined recoveries from bandings in all years. When band recoveries from the same 10-min block occurred for both samples (i.e. ties), the test statistic was computed as suggested by Robson (1968).

Our analysis of the fidelity of woodcock to wintering areas compared the location of band recoveries with the location of winter banding. We tested the null hypothesis that males and females exhibited similar tendencies to return to the same wintering area from one year to the next. To test this null hypothesis, we selected degree-blocks of banding and based our tests on all band recoveries of these birds in December and January. A recovery in either the degree-block of banding or one of the eight degree-blocks contiguous to the block of banding was defined as occurring in the vicinity of banding. The proportion of recoveries occurring within the area of banding is an indication of fidelity to a wintering area. We used the *Z*-test for proportions to compare males and females for each class.

HYPOTHESES AND PREDICTIONS

Distribution patterns.—Female woodcock are larger than males. Because larger birds can endure longer periods of fasting (Calder 1974: 110), female woodcock may have the ability to winter in colder environments. Thus, based on physiological considerations alone, we would predict that female woodcock should winter farther north than male woodcock (Ketterson and Nolan 1976).

However, two additional factors may influence age/sex segregration on the wintering grounds (Ketterson and Nolan 1976, 1983) and may work in combination (see Byrkjedal and Langhelle 1986). One potential influence on age/sex segregation on the wintering grounds is behavioral dominance among age/sex classes. We rejected this possibility in woodcock because no evidence of age/sex dominance on the wintering grounds has been reported, and detailed observations of woodcock feeding in groups (Mendall and Aldous 1943) and woodcock maintained in captivity (Stickel et al. 1965, Vander Haegen unpubl. data) have failed to demonstrate social aggression. Another potential influence involves arrival times on breeding grounds. Under this hypothesis, segregation by sex on the wintering grounds occurs because the first individuals of one sex to return to breeding areas gain a reproductive advantage. Members of this sex winter closer to the breeding grounds. Based on the arrival-time hypothesis, we would predict that male woodcock should winter north of females. The physiological and the arrival-time hypotheses applied to woodcock give opposite predictions about sex-specific distribution patterns in winter. Presumably our analyses would permit us to reject one of these alternatives.

Fidelity to wintering areas.—If one age/sex class is more sensitive to environmental changes, then we might expect differences in fidelity to wintering grounds. Female woodcock are larger than males and can endure longer periods of fasting (Calder 1974: 110). Therefore, during periods of harsh weather conditions, we might expect male woodcock to exhibit greater facultative migration than females (Pulliam and Parker 1979, Nichols et al. 1983, Terrill and Ohmart 1984), and less fidelity to wintering areas.

RESULTS

Distribution patterns.—Only 2 of 9 comparisons from the Mardia tests indicated differences in distribution patterns during winter ($P < 0.05$)

TABLE 1. Results of testing the null hypothesis of equivalent winter band-recovery distributions for recoveries of male and female American Woodcock banded during the preseason (10 April to 31 August) in 1961–1984. For each test, df = 2.

Banding location	Age	No. of recov.	Center of recoveries: Males Lat.	Males Long.	Females Lat.	Females Long.	χ^2	P
Maine	Young	39	34.4	82.3	34.0	83.6	2.16	0.34
	Adult	21	32.8	84.6	34.7	79.8	7.22	0.03
	Both[a]	61	34.0	83.1	34.3	82.2	2.63	0.27
New York	Both	18	34.1	83.0	32.5	86.2	0.78	0.67
Michigan	Both	13	33.1	86.3	31.2	91.5	9.16	0.01
Wisconsin	Young	63	31.5	92.1	31.6	91.0	1.13	0.57
	Both	71	31.4	92.0	31.6	91.1	2.40	0.30
Michigan, Wisconsin, Minnesota	Young	73	31.5	91.8	31.6	91.2	0.22	0.90
	Adult	18	31.9	89.5	31.2	91.3	0.19	0.91

[a] Includes one bird of unknown age.

(Table 1). Furthermore, the center of the distribution pattern of females was north of that of males in only 1 of 2 tests with significant results, and 5 of 9 tests overall.

Fidelity to wintering areas.—We found no difference between sexes in fidelity to wintering areas during the period 1939–1960 ($P = 0.13$) (Table 2). Likewise, we found no sex-specific differences during the period 1962–1977 for adults ($P = 0.47$), young ($P = 0.75$), or ages combined ($P = 0.30$).

DISCUSSION

Distribution patterns yielded little evidence for sexual segregation on the wintering grounds. Several studies that examined sex ratios on localized wintering areas found disproportionate numbers of males or females (Stamps and Doerr 1976, Pace and Wood 1979, Stribling and Doerr 1985). However, these results may reflect differences in collecting methods or in habitat use (Stribling and Doerr 1985). Our results indicate that male and female woodcock from the same breeding grounds do not winter in different geographic areas.

The power of our statistical tests to detect differences in distribution patterns may have been reduced by small sample sizes and the relatively small latitudinal wintering range of woodcock (e.g. compared with the Dark-eyed Junco [*Junco hyemalis* Ketterson and Nolan 1976]). The power of Mardia's test is sufficient, even with small sample sizes, to detect differences in distribution patterns likely to be of biological relevance (Diefenbach et al. 1988b). Whereas the latitudinal range of woodcock may be limited, the size dimorphism of woodcock (M:F ratio = 0.81; Owen and Krohn 1973) is greater than for species in which differences in distribution patterns have been detected (e.g. Dark-eyed Juncos, F:M ratio = 0.93; data in Ketterson and Nolan 1976: 689). We also recognize that the northern extent of the winter range probably fluctuates with winter severity (Sheldon 1967, Wood et al. 1985), and combining data over years masked any intra- or inter-year variation in distribution patterns. These factors should not have reduced significantly our ability to test differences in central tendencies of distribution patterns.

Migratory birds would be expected to winter in areas that optimize their overall fitness. We suggest that mechanisms of both the body-size and arrival-time hypotheses may act together

TABLE 2. Test of the null hypothesis that the proportion of December and January recoveries of male vs. female American Woodcock occurring within the area of winter banding in Louisiana are equivalent. Number of recoveries is in parentheses.

Years	Age	Proportion of recoveries in banding area: Males	Females	Z	P
1939–1960	Both	0.75 (20)	0.55 (31)	1.51	0.13
1962–1977	Young	0.64 (33)	0.68 (25)	−0.32	0.75
	Adult	0.44 (18)	0.65 (23)	−0.73	0.47
	Both	0.57 (51)	0.67 (48)	−1.03	0.30

to produce the observed pattern of winter distribution of woodcock. Females probably winter in areas that are a compromise between the energetic cost of migration and food availability. They migrate just far enough to ensure an adequate food supply. Males may winter farther north than is optimal with respect to their energetic requirements and have reduced survival. However, the risk of dying for a male may be offset by greater reproductive success with earlier arrival on the breeding grounds. The effect on winter distribution of woodcock is that both sexes may winter on the same areas to optimize their fitness, but as a result of different influences on their reproductive success.

Along with the advantage of an early arrival on the breeding grounds, male woodcock may gain an additional reproductive benefit by wintering sympatrically with females. Unlike many shorebirds, woodcock do not have disjunct wintering and breeding ranges, and considerable reproduction occurs on wintering areas (Wood et al. 1985). Thus, males that winter with females may have the opportunity to breed before and during the flight north. Nesting has been observed as early as January in North Carolina (Stamps and Doerr 1977) and Alabama (Roboski and Causey 1981), and February in Texas (Whiting and Boggus 1982), although most nesting occurs later. Because males initiate migration sometime in February, receptive females are available for breeding before and during migration. How female woodcock select mates is unknown, as is the likelihood that a male courting on his wintering grounds or migration stopovers could mate with a female. Nevertheless, the opportunity for wintering or migrating males to breed on wintering areas does exist and could influence the winter distribution of males.

The winter banding data indicate no difference between sex and age classes in fidelity to wintering grounds. This was unexpected considering the size difference between sexes, nor does it support our hypothesis that males are wintering north of optimal latitudes. A possible explanation for this discrepancy lies in the origin of the winter banding data. A sufficient number of recoveries was available only for woodcock banded at sites in south-central Louisiana, which is near the southern edge of the winter range for woodcock. Similar analyses for woodcock banded in northern regions of their winter range, where weather conditions are harsher or more variable, might yield different results.

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ERRATUM

In "Renesting by American Woodcocks (*Scolopax minor*) in Maine" by Daniel G. McAuley, Jerry R. Longcore, and Greg F. Sepik (1990, Auk 107: 407–410), the range of distance moved by females that abandoned nests or had nests destroyed by predators (p. 408) should read: "range = **1.0–15.5**" and the values in the "Distance moved (km)" column in Table 2 (p. 409) should read down the column: "**1.01, 11.34, 1.22, 4.17, 15.54, 0.65, 0.36, 1.14, 0.88, 0.24, 0.80, 0.16.**" Corrected values are in boldface type.

INDIVIDUAL VARIATION IN BEHAVIOR AND BREEDING SUCCESS OF NORTHERN FULMARS

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ABSTRACT.—In a sample of breeding Northern Fulmars (*Fulmarus glacialis*) observed in 4–5 years, up to 43% of the variability in 13 attributes of breeding behavior was consistent among individuals or pairs. Sample means for most attributes were correlated in a predictable way with annual levels of breeding success. Except for laying dates, there was little evidence that individual differences in these attributes contributed to variation in breeding success. A test of breeding experience as a contributing factor revealed an interaction between individual and annual components of variation. During years when the whole population did relatively poorly, pairs with no previous breeding experience were affected disproportionately. Late-nesting fulmars were more successful than early layers, possibly because delayed breeding ensured that food availability was adequate for successful incubation. *Received 7 November 1989, accepted 15 May 1990.*

IF the same sample of breeding birds is monitored in several years, the observed variance in breeding success has annual and individual components. Annual variation arises from variability in environmental factors such as food supply, predation, disease, weather, or disturbance. Any added component of individual variation arises from differences in the quality of the habitats occupied by individuals (Nettleship 1972, Birkhead 1977, Hudson 1982), or from differences in the quality of the individuals themselves (Coulson 1968, Potts 1969, Reilly and Cullen 1981). Interaction between the two components of variation is expected because annual changes in the environment need not affect all individuals equally.

In a 6-yr study of breeding Northern Fulmars (*Fulmarus glacialis*), I found that young were more likely to be raised successfully in some sites than others (Hatch 1988). Fulmars are long-lived and have a strong fidelity to the same mate and nest site between years (Hatch 1987, Ollason and Dunnet 1988). Many of the birds in my sample were individually known from plumage differences, and all direct evidence indicated that few undetected changes of site ownership or pair bonds occurred during the study. I therefore hypothesized that the among-pairs component of variance in breeding success could be explained by individual differences in breeding biology and behavior. Consequently, I assessed individual variation in laying dates and time allocation as factors that affect breeding success. I also considered the influence of breeding experience under the varying conditions that occurred during the years of study.

METHODS

The study was conducted from 1976 to 1981 on the Semidi Islands, western Gulf of Alaska (56° N, 156° W). The islands and their seabird populations are described elsewhere (Hatch and Hatch 1983). I usually arrived between 29 March and 3 May, 4–8 weeks before the first eggs were laid, and I departed 26 August to 9 September, 1–3 weeks before the first young fledged. In 1978 I was present only from 26 May to 29 June (egg laying) and on 30 August and 8 September to assess chick survival. Behavioral data were also incomplete for 1976; therefore much of the analysis pertains to observations from 1977 and 1979–1981.

By 1977 my sample of active breeding sites totaled ca. 400, and I monitored the same sites every year thereafter. I used a binocular or spotting scope to check sites once daily to record adult attendance and egg or chick survival. Laying dates were thus known to within ±24 h. A pair of breeding fulmars produces only one egg a season. Chicks ranged from approximately 21 to 45 days old when last observed, but fledging does not occur until a mean age of 53 days (Mougin 1967). Thus, the measure of breeding success I use is the survival of chicks through the mid- to late chick stage.

Fulmars occurred in a wide range of plumage types, although most (85%) were dark phase (see Fisher 1952

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or Hatch 1985 for a description of the color phases). Approximately half of the sites in my sample contained mixed pairs (i.e. the male and female were of different color phases). I sexed the birds from their position in copulation.

A bird whose mate failed to return in spring often skipped a year before it resumed breeding with a new—usually inexperienced—partner at the same site (Hatch 1987). Therefore I minimized the influence of undetected mortalities and mate changes by including in the analysis only sites that had a continuous record of breeding over 5 or 6 yr. Other recruits to the breeding population paired with similarly inexperienced birds and began to breed after one or more years of site occupation as nonbreeders, whereas experienced pairs rarely failed to lay (Hatch 1987). Thus, when a site changed to breeding status from nonbreeding, there was a high probability that one or both members of the pair had no previous experience. I tested the effect of breeding experience on success by comparing pairs from sites grouped according to whether or not an egg was or was not laid the year before.

I created three variables, all measured in days, to quantify individual attendance patterns during the prelaying period. First, I counted the number of days a bird was recorded as absent from its site during the 40 days immediately preceding its laying date. Second, I determined the longest period of continuous absence for each individual in the last 30 days before laying. Third, I defined a *pre-egg feeding interval* to include the days between departure of a bird on its longest absence (as above) and the start of its last uninterrupted presence at the breeding site before laying. The latter two values were frequently the same, especially in females. They are alternative measures of what is commonly called the "prelaying exodus" (see Macdonald 1977 and Hatch 1990a for details).

Most pairs had a well-synchronized rendezvous at the time of egg laying after an extended prelaying absence. Normally the female returned to find her mate waiting at the site or the male arrived soon afterward. The female often laid and departed within 24 h, leaving the male to take the first long shift of incubation (up to 2 weeks). I quantified behavioral coordination at egg laying by calculating the difference between male and female arrival dates. Male-female synchrony, so defined, ranged from −11 days (among early-arriving males) to +12 days (indicating late-arriving males).

The attributes of incubation behavior I considered included first shift durations for the male and female, mean shift length for the pair through 48 days of incubation, the overall ratio of male to female shares, and the number of days the pair was recorded at the site during incubation.

On the premise that variation in the amount of time spent at sea reflected differences in food availability (between years) or foraging efficiency (between individuals), I expected all three measures of time allocation in the prelaying period to vary inversely with breeding success, both within and between years (Hatch 1990a). By the same reasoning, I expected attendance by pairs during incubation to be correlated positively with success (Hatch 1990b). I expected synchrony at laying to be inversely related to success, because a late-returning male risked nest desertion and egg loss by the female. Principles of central place foraging (Orians and Pearson 1979) predict shorter incubation shifts in successful pairs and better years. I had no predictions concerning the ratio of male to female shares in incubation or the effect of annual variation in laying dates. However, I expected laying date to be negatively correlated with breeding success within years, as reported for many other species (Burger 1981, Perrins and Birkhead 1983).

I tested the significance of annual variation in behavior using a repeated measures ANOVA, an extension of the paired observations t-test (Sokal and Rohlf 1981). Individual differences were modeled as random effects and estimated from the ratio of between- to within-pairs variation in a one-way ANOVA. Both types of analysis were performed on a balanced subset of the data that consisted of all pairs observed in all years.

Results

Annual and individual variation in behavior.—There was significant variation among years in 10 of 13 behavioral attributes examined (Table 1). Because 4 years' data were included in most of the analyses, it is necessary to determine whether the deviations of annual means from their grand means followed the expected patterns (i.e. whether higher annual breeding success was associated with more time spent on land in the prelaying period, shorter incubation shifts, etc.). Pearson correlation coefficients had the predicted sign, with two nonsignificant exceptions involving attendance patterns of the female.

There was significant variation among pairs in 11 of the 13 variables examined. This component ranged from approximately 7% to 43% of the total variance (Table 1).

Time allocation and breeding success.—Repeated measures ANOVA failed to show significant relationships between breeding success and any of the 12 measures of time allocation (Table 1), with the following exceptions. Synchrony of attendance at egg laying was significantly related to hatching success (but not to overall breeding success) in 1980 and 1981 ($F_{1,188} = 11.2$, $P < 0.001$ in 1980; $F_{1,193} = 18.8$, $P < 0.001$ in

TABLE 1. Annual and individual components of variation in breeding behavior of Northern Fulmars.

Variable	Source of variation: Among years F ratio	df	P	Among pairs F ratio	df	P	Correlation of annual mean and success[a]: r	P	Predicted sign?	Among-pairs variance component (%)
Laying date	7.80	3, 165	0.000	3.01	55, 168	0.000	−0.47	0.257	—	33.4
Cumulative prelaying absence, ♂	6.97	3, 162	0.000	4.03	54, 165	0.000	−0.96	0.014	yes	43.1
Pre-egg feeding interval, ♂	2.64	3, 132	0.052	1.38	44, 135	0.081	−0.49	0.249	yes	8.8
Longest prelaying absence, ♂	3.28	3, 162	0.023	3.35	54, 165	0.000	−0.84	0.066	yes	37.0
Cumulative prelaying absence, ♀	11.86	3, 162	0.000	2.45	54, 165	0.000	0.56	0.211	no	26.6
Pre-egg feeding interval, ♀	0.83	3, 162	0.480	1.87	54, 165	0.001	−0.97	0.009	yes	17.8
Longest prelaying absence, ♀	0.57	3, 162	0.636	2.50	54, 165	0.000	−0.88	0.047	yes	27.3
Synchrony at laying; ♂, ♀	17.12	3, 150	0.000	1.38	50, 153	0.069	−0.34	0.326	yes	8.7
First incubation shift, ♀	6.26	4, 372	0.000	1.37	93, 376	0.023	0.15	0.404	no	6.8
First incubation shift, ♂	22.48	4, 276	0.000	2.10	69, 280	0.000	−0.12	0.422	yes	18.0
Mean incubation shift length	8.21	3, 132	0.000	3.32	44, 135	0.000	−0.93	0.008	yes	36.8
Pair present during incubation	2.86	3, 183	0.038	2.61	61, 186	0.000	0.80	0.087	yes	28.6
Incubation ratio, ♂:♀	1.46	3, 129	0.230	3.29	43, 132	0.000	−0.82	0.040	—	36.4

[a] Data points for correlations are annual means for all pairs observed plotted against breeding success (n = 4–5 yr). A significant correlation is possible in spite of a nonsignificant component of variation among years because tests for annual variation were limited to the sample of pairs observed during all years of study (repeated measures ANOVA).

1981). The sign of both relationships was as predicted (i.e. males that arrived after their mates had laid had a higher risk of egg loss). Duration of the pre-egg feeding interval in males was significantly related to hatching success in 1977, but in the opposite direction from my expectation (i.e. males that spent more time at sea before laying were more successful than males that spent less; $F_{1,172} = 8.2$, $P < 0.01$).

Effect of laying date.—There is no significant correlation between annual breeding success and mean laying dates (Table 1), but the probability of success within years is related to a pair's position in the laying distribution. Pairs that laid early had lower success than pairs that laid in the middle or late portions of the distribution, a significant effect in 2 of 6 yr (Table 2). When I combined the data for all years, there was a substantial increase in success in middle layers over early layers (57% vs. 46%), and an additional small increase among late layers (59% success overall).

Considering only pairs that failed, there was a significant tendency for early-breeding pairs to fail early in the breeding cycle (within the first 14 days), whereas those in the middle group tended to fail at a later stage ($\chi^2 = 6.3$, df = 2, $P < 0.05$). Failure in the late-laying group was distributed about as expected between early and late stages.

TABLE 2. Effect of laying date on breeding success.

Year	Overall breeding success[b]	Relative laying date[a]: Early n	Early Success	Early Residual[c]	Middle n	Middle Success	Middle Residual[c]	Late n	Late Success	Late Residual[c]	χ^2	P
1976	0.143	47	0.085	−2.7	117	0.128	−1.7	25	0.320	4.4	7.89	0.019
1977	0.510	59	0.458	−3.1	254	0.492	−4.6	73	0.616	7.7	4.28	0.118
1978	0.461	78	0.321	−11.0	233	0.502	9.6	86	0.477	1.4	7.87	0.020
1979	0.594	79	0.570	−1.9	249	0.602	2.2	73	0.589	−0.3	0.28	0.872
1980	0.661	109	0.587	−8.0	208	0.697	7.6	72	0.667	0.4	3.87	0.144
1981	0.719	41	0.634	−3.5	290	0.728	2.5	64	0.734	1.0	1.64	0.440
All yr	0.550	413	0.462	−36.1	1,351	0.565	20.2	393	0.590	15.9	16.56	0.000

[a] Middle group includes all eggs laid 3 days before to 3 days after the mean laying date within each year; early group includes all eggs laid earlier, late group includes all eggs laid later.

[b] Proportion of chicks surviving to the mid- to late-chick stage.

[c] Residuals are observed − expected numbers of successful pairs in a 2 × 3 contingency table.

Effect of breeding experience.—Pairs thought to include at least one member with no breeding experience had consistently lower success than pairs with at least one year of experience, although the difference was significant only in 1978 (Table 3). Only a small sample of newly converted pairs was available each year, and the effect was highly significant when the data from all years were combined.

Phi (Table 3) measures the strength of relationship between two variables in a contingency analysis (Nie et al. 1975). In this instance it measures the association between breeding success in year i and nonbreeding in year $i - 1$. Although none of the five phi values calculated is large, there is a significant negative correlation between phi and annual breeding success (Fig. 1). That is, in years when the whole population had a high level of breeding success, the importance to individual pairs of prior experience was diminished.

Breeding experience had a small effect on laying date. Pairs newly converted from nonbreeding to breeding status laid 1.4 days later on average than pairs with known breeding experience ($F_{1,2155} = 20.9$, $P < 0.001$). A two-way ANOVA indicated a significant interaction between year and experience. That is, the effect of experience on laying date was greater in some years than in others ($F_{4,1958} = 5.1$, $P < 0.001$). The mean difference between new and experienced pairs ranged from 0.3 day in 1977 to 4.0 days in 1980.

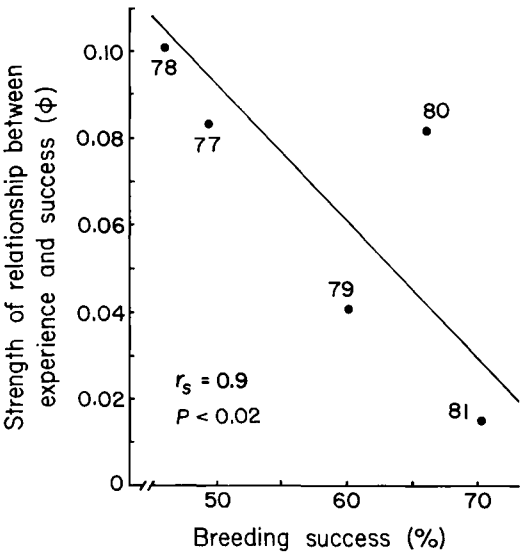

Fig. 1. Relation between overall breeding success of fulmars and the influence of breeding experience on individual success during 5 yr, 1977–1981.

Discussion

It is clear that differences in behavior among years accounted for most of variation I observed, but a sizable component of individual variation was present in some instances. Potentially, the relationships between breeding success and the two components of variation in behavior could take any of three forms: (1) within-year variation in behavior related to success, but no concordance between annual means of behavior and success, (2) annual variation in success correlated with annual means of behavior, but no relationship within years, or (3) both within-years and between-years variation in behavior predictably related to success. Laying date appeared to be an attribute of the first kind—a pair's position in the rank order of laying dates mattered, but annual differences in mean laying dates were unimportant. I expected most other variables to be in the third category—annual differences in time allocation re-

Table 3. Comparison of success rates in sites that were and were not used in the preceding year.

Year i	Overall breeding success	Breeding year $i - 1$ n	Breeding year $i - 1$ Success year i	Nonbreeding year $i - 1$ n	Nonbreeding year $i - 1$ Success year i	Difference	χ^2	P	Phi (ϕ)
1977	0.497	143	0.517	34	0.412	0.105	1.23	0.268	0.08
1978	0.461	340	0.482	57	0.333	0.149	4.36	0.037	0.10
1979	0.603	356	0.610	37	0.541	0.069	0.68	0.414	0.04
1980	0.661	352	0.673	37	0.541	0.132	2.63	0.105	0.08
1981	0.720	363	0.722	33	0.697	0.025	0.09	0.761	0.02
All yr	0.599	1,554	0.614	198	0.485	0.129	10.57	0.002	0.08

flecting variation in the food supply and the time budgets of individuals reflecting differences in foraging efficiency. In some instances (e.g. male prelaying attendance, pair attendance during incubation, mean shift lengths), I found consistent individual variation and a strong relation between annual means and success, but was unable to show the expected relations between individual scores and breeding success. To be sure, many individual behavior patterns (probably some important ones, such as rates of food provisioning during chick-rearing) were not considered in this study. Also, consistency per se may be important for all breeding activities if it helps to promote behavioral coordination within the pair (Coulson 1972, Coulson and Thomas 1983).

Most of the behavior I examined, such as patterns of incubation and attendance at the nest site before laying, have been rarely studied from the standpoint of individual variation. However, the tendency of females to lay at the same time each year relative to other females has been noted in other species (e.g. Serventy 1963, Nelson 1966, Brooke 1978). The higher breeding success of late-nesting fulmars was surprising in view of the opposite effect reported in most other studies of colonial birds (Burger 1981), including two studies of Northern Fulmars in Scotland (Macdonald 1975, Ollason and Dunnet 1988). Why fulmars in Atlantic colonies and the Semidis should differ in this respect is unclear, but in any case fledging rates could be a misleading indicator of reproductive success (number of young surviving to breed). Some studies reported a negative correlation between postfledging survival and hatching dates (Perrins 1966, Nisbet and Drury 1972, Parsons et al. 1976), whereas others have not (Hedgren 1981, Harris 1984).

Lack (1954) hypothesized that an optimal time for laying exists such that young are hatched when the food supply is at a seasonal maximum. On that hypothesis, the effect of laying date on breeding success should appear mainly in the chick stage, and both early- and late-hatched young should be disadvantaged relative to those in the middle. Neither condition was true in my study. Late layers were, if anything, more successful than middle layers, and the additional failure among early layers tended to occur early in incubation.

Certain features of the breeding biology of fulmars and other petrels suggest a different interpretation. When their egg is laid, fulmars abruptly switch from spending an average of 76% of their time foraging to spending only approximately 50% of their time foraging (Hatch 1990a). There can be no corresponding increase in the food supply for every pair, and the early failures found in early breeding pairs may result because foraging conditions are still marginal for maintaining incubation during the first part of the laying period. This would select for later nesting, but lower postfledging survival of late-hatched young would provide stabilizing selection. On this hypothesis, the survival of offspring from fledging to recruitment should be highest for the earliest breeders, but survival from laying to recruitment would be highest for birds near the center of the laying curve. Brooke (1978) expressed a similar view of selection acting on laying dates in the Manx Shearwater (*Puffinus puffinus*).

The roles of age and experience have received considerable attention in studies of seabird breeding biology (Ryder 1980), and the Northern Fulmar is no exception (Ollason and Dunnet 1978, 1988). The effect of experience seemed weak in my study, but my data illustrate one little-studied aspect. There is an interaction between annual and individual components of variation. The effect of breeding experience on success was strongest during years in which the whole population did relatively poorly. A similar interaction was indicated for the effect of breeding experience on laying dates. The study covered only portions of the two seasons with the lowest productivity (1976 and 1978), an unfortunate coincidence because those years might have revealed most clearly the behavioral difference among individuals.

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INCUBATION AS A REPRODUCTIVE COST IN FEMALE WOOD DUCKS

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ABSTRACT.—We investigated the effects of body mass of incubating female Wood Ducks (*Aix sponsa*) on aspects of their current and future reproduction, and we examined factors that affect length of the incubation period. During three breeding seasons, body mass of female Wood Ducks averaged 578.0 g early and 553.3 g late in the incubation period. Body mass at the start of incubation was not related to either hatching success or length of the incubation period. In one of three years, females that were heavy at the end of incubation survived better to the next breeding season than those that were light. Reduced survival of light females in one year coincided with a greater loss of body mass in that year relative to other years, which indicates that incubation can be an important reproductive cost to female Wood Ducks. There were no relationships between body mass at the end of incubation and date of nesting or clutch size in the next breeding season. Partial correlations between clutch mass and length of incubation that controlled for date of nesting indicated a positive association between clutch mass and incubation length in every year. This relationship was evident only for parasitic nests (i.e. nests in which more than one female was laying eggs). Increased length of the incubation period associated with larger clutch mass represents a potential cost of intraspecific nest parasitism not previously recognized. *Received 26 December 1989, accepted 17 June 1990.*

INCUBATING birds must provide the proper thermal environment for embryonic development. Simultaneously they must maintain their body condition so that survival and subsequent reproduction are not affected adversely. Time for feeding is restricted during incubation, which often makes it difficult for incubating individuals to meet daily metabolic costs (see Drent et al. 1985). Some avian species have adjusted to the demands of incubation by having biparental incubation (Eisner 1960, Feare 1984). In other species, males provide incubating females with food (Lyon and Montgomerie 1985, Nilsson and Smith 1988). In waterfowl (Anatidae), females of large-bodied species generally begin incubation with large energy reserves and are more attentive during incubation than females of small-bodied species, because large-bodied females spend less time feeding (review in Afton and Paulus 1990). Small anatids depend on exogenous foods to meet most metabolic demands during incubation and take two to three recesses each day to forage (Afton 1980, Hohman 1986).

Successful development of bird eggs occurs within a relatively narrow range of incubation temperatures (White and Kinney 1974). Cooling of eggs increases as ambient temperature decreases, and as time away from the nest by incubating individuals increases (Caldwell and Cornwell 1975, Afton 1979). Short-term declines in egg temperature, however, apparently have little effect on hatching success (Vleck 1981, Haftorn 1988). Nevertheless, a decrease in average egg temperature may lengthen the incubation period, which exposes the nest to greater risk of predation and increases the energy expended by developing embryos (Vleck et al. 1980, Booth 1987). Greater amounts of energy used by embryos of precocial species before hatching may decrease the size of residual yolk reserves that are important to newly hatched chicks for maintenance and growth (Peach and Thomas 1986).

Many species of birds modify activity patterns during incubation in response to variation in weather and food availability (Caldwell and Cornwell 1975, Cartar and Montgomerie 1985,

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Drent et al. 1985). Large-bodied species are affected less by environmental factors than small-bodied species (Afton 1980). Flexibility of incubation patterns within and among species suggests there is a tradeoff between maintaining body condition during incubation and providing eggs with a suitable environment for development. If time and energy constraints are important during incubation, then attentiveness at the nest should increase as body condition or food availability increases, assuming that greater attentiveness shortens the incubation period and increases hatching success (Martin 1987). Several studies support this idea. Aldrich and Raveling (1983) reported that female Canada Geese (*Branta canadensis moffitti*) that began incubation in good condition spent more time on the nest and had shorter incubation periods than females in poor condition. In years when food was abundant, European Starlings (*Sturnus vulgaris*) spent less time feeding, and some females were able to incubate without assistance from their mates (Drent et al. 1985). Female Blue Tits (*Parus caeruleus*) that were given a food supplement during incubation had shorter incubation periods and greater hatching success than females that were not provisioned (Nilsson and Smith 1988).

Loss of body mass during incubation may reflect the need to provide constant care for developing embryos (Sherry et al. 1980), or it may enable females to reduce wingloading and to conserve energy during brood rearing (Freed 1981). However, a critical body mass certainly exists for individuals during incubation. Below that threshold, birds either spend more time feeding (Aldrich and Raveling 1983) or they abandon the nest (Drent 1975, Ankney and MacInnes 1978, Jones 1987). Body mass of female waterfowl during the annual cycle typically is lowest at the end of incubation (Afton and Paulus 1990). Ability of individuals to balance the conflicting demands of incubation may influence current and future reproductive success.

Male Wood Ducks (*Aix sponsa*) do not take part in incubation. Females are relatively small (610 g) at the beginning of incubation (Afton and Paulus 1990) and have lipid reserves sufficient to meet energy demands for only five days of an average 30-day incubation period (Drobney 1980). Females typically take two incubation recesses each day to feed (Breckenridge 1956, Bellrose 1980). They lose an average of 1.3 g/day during incubation, but changes in body mass vary greatly within and among females (Harvey et al. 1989). Loss of body mass during incubation may influence the reproductive success of Wood Ducks. Kennamer and Hepp (1987), for example, reported that double-brooded females lost a smaller proportion of body mass during incubation of first nests than females that nested only once. In this study, we tested the effects of body mass of incubating female Wood Ducks on subsequent survival and on aspects of their current and future reproduction. We also examined factors that influence length of the incubation period.

Methods

The study was conducted from January to July, 1986–1989, on the U.S. Department of Energy's Savannah River Site (SRS) in west-central South Carolina (33.10°N, 81.30°W). Approximately 140 nest boxes were available to Wood Ducks each year, and boxes were checked weekly to provide information on nesting activity.

Nesting data.—Checking nest boxes weekly allowed us to find nests during the egg-laying stage. We estimated the date of nest initiation by subtracting the number of eggs in the nest when it was first found from the date that the nest box was checked (i.e. assumed laying rate of one egg per day [Bellrose 1980]). Female Wood Ducks frequently engage in intraspecific nest parasitism (dump or parasitic nests) where >1 female deposit eggs in a nest (Clawson et al. 1979, Semel and Sherman 1986). We classified nests as *dump nests* if egg deposition rates exceeded one egg per day or if clutch sizes were >16 eggs (Morse and Wight 1969). Nest initiation dates were estimated similarly for parasitic and nonparasitic nests. Dump nests occasionally contained more eggs than the elapsed time (days) between nest-box checks. These nests were estimated to have been initiated one day after the previous check of the nest box.

Length and breadth of eggs were measured (nearest 0.1 mm) with vernier calipers, and measurements were used to estimate fresh egg mass of each egg and clutch mass of every nest (Hepp et al. 1987b).

Duration of incubation.—The *incubation period* was defined as the number of days between the start of incubation and hatching of eggs. Day of hatching was known precisely in 1986 and 1987, because we marked newly hatched ducklings as part of another study (Hepp et al. 1989). In 1988, however, hatch dates were known only for nests (n = 19) that were visited on days when the eggs were pipping.

The day that females began incubation was esti-

mated in the following manner. For nonparasitic nests in 1986 and 1987, we assumed that females laid one egg per day and that incubation began on the day the clutch was completed (but see Arnold et al. 1987, Afton and Paulus 1990). It was assumed that females incubating dump nests (i.e. host females) in 1986 and 1987 laid a number of eggs similar to that of females of nonparasitic nests that nested at the same time. We also assumed that incubation began on the day the host laid her final egg. Clutch size of Wood Ducks declines seasonally (Hepp unpubl. data), as it does in other species of waterfowl (see Toft et al. 1984). Therefore, we regressed clutch size of normal nests with the date of nest initiation. Regression equations (**1986**: CLUTCH SIZE = 14.8 − 0.0399(DATE), $r^2 = 0.34$, $P = 0.0002$; **1987**: CLUTCH SIZE = 14.5 − 0.0358(DATE), $r^2 = 0.30$, $P = 0.0003$) were used to estimate the number of eggs deposited in dump nests by host females. Clutch sizes estimated in this manner were rounded to the nearest integer. To check the suitability of this regression approach for determining first day of incubation, we applied the method to 1988 data for which we also had accurate candling information (see below). A *t*-test for paired comparisons confirmed that the two methods were similar overall (mean difference = 0.31 days, df = 60, $P = 0.24$).

In 1988, most (75%) of the eggs in every clutch were candled (Weller 1957) in early incubation (before day 15) to determine the stage of embryo development (see Hanson 1954). From this information, we computed average number of days that eggs had been incubated for both parasitic and nonparasitic nests. We substracted the average day of incubation from the date that the eggs were candled to estimate the day that incubation began.

For analyses involving length of the incubation period, we tested parasitic and nonparasitic nests separately in 1986 and 1987 because of differences in the way the start of incubation was estimated in those years. In 1988 the method for estimating the day when incubation began was the same for all nests.

Body mass and the return of females.—We captured incubating females in nest boxes, banded them with USFWS leg bands, and measured body mass to the nearest 5 g with a 1,000-g Pesola scale. Some females were captured during both early (≤day 15; $\bar{x}$ = day 5) and late (>day 15; $\bar{x}$ = day 30) incubation. Most (88%) females were caught between 0800 and 1200 to minimize any diurnal variation in body mass. In 1987 and 1988, flattened wing length (mm) from the wrist to the end of the longest primary was measured also. Females were returned to the nest box after capture.

Body mass often is a good measure of nutrient reserves (e.g. lipids) in birds. However, adjusting body mass by a measure of structural size may improve this relationship (Johnson et al. 1985). We calculated and used a condition index (body mass/wing length) in analyses of 1987 and 1988 data. Inferences from tests using either body mass or the condition index did not differ. We, therefore, chose to use body mass for simplicity.

If body mass varies among females at the start of incubation, then changes in body mass expressed as grams per day may not assess accurately the relative costs of incubation. The following statistic was used to compare changes in body mass of incubating females:

$$\lambda = (\text{body mass}_{t+\Delta}/\text{body mass}_t)^{1/\Delta}, \quad (1)$$

where λ is the relative change in body mass, body $\text{mass}_{t+\Delta}$ is the body mass of females during late incubation, body mass_t is the body mass of females during early incubation, and Δ is the number of days between the two measurements of body mass. Values of 1.0 represent no change, <1.0 a loss, and >1.0 a gain in body mass.

Capture probabilities (p_i) of females were estimated with the Jolly-Seber capture-recapture model for open populations (Jolly 1965, Seber 1965). These estimates correspond to the probability that a female alive and in the population during breeding season i will be captured during that period. During the study, $\hat{p}_i$ averaged 0.89, which indicates that most females, if alive, returned to nest boxes and were captured (see Hepp et al. 1987a, 1989).

Analysis.—Return of breeding female Wood Ducks is a binary variable; a female either returns to nest and is recaptured, or she does not. Females were counted as returning if they were captured while incubating a clutch of eggs, regardless of whether the nest was successful. We used logistic regression analysis to examine the relationship between body mass at the end of incubation and return of females to breed in the subsequent year (Cox 1970). A number of ecological studies recently have used this method of analysis (see Haramis et al. 1986, Boyce and Perrins 1987, Hepp et al. 1989).

If θ_i is the probability of return for individual i, then the linear-logistic model provides a reasonable form of the relationship between θ_i and female body mass at the end of incubation (also see Martin 1987: 458):

$$\theta_i = \exp(B_0 + B_1 x_i)/[1 + \exp(B_0 + B_1 x_i)], \quad (2)$$

where B_0 and B_1 are the model parameters, and their estimates and standard errors are computed using maximum likelihood procedures. In model M_1 (Equation 2), x_i is the body mass of female i at the end of incubation.

We tested whether the body mass of females at the end of incubation influenced their return in the next breeding season by using a null model (M_0) that does not include body mass as an independent variable. In model M_0, θ_i is written:

$$\theta_i = \exp(B_0)/[1 + \exp(B_0)]. \quad (3)$$

TABLE 1. Means (±SD) of body mass (g) and the relative change in body mass (λ) of female Wood Ducks during incubation. Means in each column not followed by the same letter are significantly different (Duncan's multiple-range test, $P < 0.05$); relative change in body mass (λ) equals (body mass in late incubation/body mass in early incubation)$^{1/\Delta}$, where Δ is the number of days between the two measures of body mass.

Year	*n*	Early incubation	Late incubation	λ
1986	31	586.6 ± 47.1 A	546.1 ± 45.6 A	0.9970 ± 0.0022 A
1987	64	579.0 ± 43.2 A	548.0 ± 43.5 A	0.9980 ± 0.0020 B
1988	57	572.9 ± 43.7 A	564.5 ± 45.8 A	0.9994 ± 0.0018 C
Weighted average		578.0	553.3	0.9983

The null model assumes that each female has the same probability of return regardless of body mass at the end of incubation. Maximum likelihood estimates of B_0 were calculated, and likelihood ratio tests of model M_0 vs. M_1 provided a test of the hypothesized relationship. Likelihood-ratio test statistics are distributed as Chi-square. Test statistics were computed separately for each year, and composite statistics were calculated that also are distributed as Chi-square.

Wilcoxon rank sum tests provided another method to test the null hypothesis that females returning to nest were not heavier at the end of incubation than females that did not return to nest (Dietz 1985). Years were tested individually, and probabilities were combined to obtain a composite test (Sokal and Rohlf 1981: 780). Composite statistics are distributed as Chi-square with $2n$ degrees of freedom.

If body mass and return rate of females were age specific, then results and interpretation of these analyses might be affected. However, female age was not an important factor in these analyses, because annual return rates of yearling females were not different from adults (Chi-square tests, $P > 0.05$). These results agree with Nichols and Johnson (1990), who reported that survival rates of female Wood Ducks in the southeastern United States were not age-specific.

SAS (SAS Institute 1988) was used for statistical summaries and analyses. With the exception of logistic regressions and Wilcoxon rank sum tests, we used data from successful (i.e. that produced at least one duckling) first nests only. Second-nest attempts and nests that were unsuccessful were excluded. We used initiation date of first nests and clutch size of nonparasitic nests to test relationships between body mass at the end of incubation in year i and the nest initiation date and clutch size in year $i + 1$.

RESULTS

Body mass dynamics.—Body mass of female Wood Ducks early ($\bar{x}$ = 578.0 g) and late (553.3 g) in the incubation period did not differ among years (one-way ANOVAs, $P > 0.05$) (Table 1). Heavy females tended to nest earlier in the season than light females (Table 2). The relative change in body mass during incubation varied significantly among years ($F = 15.7$; df = 2, 149; $P < 0.001$) and was greatest in 1986 (Table 1). There was a decline in body mass for most incubating females in 1986 (87.1%, $n = 31$) and 1987 (81.2%, $n = 64$), but approximately 42% ($n = 57$) of the females in 1988 either gained body mass while incubating or there was no change.

Female return and future reproduction.—In 1986 the $\hat{B}_1$ value of the logistic regression was positive, indicating that heavy females were more likely to return to nest the following year than light females (Table 3). All tests of the relationship were marginally significant ($P < 0.10$) in 1986, but none of the tests were significant in 1987 or 1988.

Body mass of females at the end of incubation was not correlated in any year with either the date of nest initiation ($P > 0.30$) or clutch size ($P > 0.85$) in the next breeding season.

Hatching success and incubation length.—Body mass of females at the beginning of incubation was not correlated in any year with either hatching success ($P > 0.55$) or length of the incubation period ($P > 0.15$). The incubation period was longer in 1987 for females that nested early, but this relationship was absent in other years (Table 4). With the exception of nonparasitic nests in 1986, simple correlation anal-

TABLE 2. Correlations between the body mass of female Wood Ducks during early incubation (< day 15) and the date of nest initiation.

Year	*n*	r^a	*P*
1986	32	−0.30	0.10
1987	64	−0.45	0.0002
1988	58	−0.26	0.05

[a] Pearson's correlation coefficient.

TABLE 3. Logistic regression parameter estimates and test statistics of the relationship between body mass of female Wood Ducks at the end of incubation and the probability of returning to nest in the next breeding season.

Year of return	Model M_1 parameter estimates					M_1 vs. M_0			Rank sum test	
	$\hat{B}_0$	$\widehat{SE}(\hat{B}_0)$	$\hat{B}_1$	$\widehat{SE}(\hat{B}_1)$	P	χ^2	df	P	T	P
1987	−11.44	7.49	+0.024	0.014	0.09	3.67	1	<0.10	1.8	0.08
1988	0.54	3.16	−0.000	0.006	0.95	0.01	1	<0.90	0.4	0.68
1989	−0.09	3.31	−0.000	0.006	1.00	0.00	1	1.00	0.2	0.85
Means and totals	−3.66	7.45	+0.008	0.014	0.50	3.68	3	<0.50	$\chi^2 = 6.16$, df = 6, $P < 0.50$	

yses showed a positive association between length of incubation and clutch mass in all three years (Table 4). Results were significant ($P < 0.05$) in 1986 and 1987, and they were marginally significant ($P = 0.08$) in 1988. Clutch masses of parasitic and nonparasitic nests generally were larger early in the nesting season (Table 4), and this relationship may have contributed to the positive association between clutch mass and length of incubation. After controlling for date of nesting, partial correlation coefficients indicated a significant positive association between clutch mass and incubation length of parasitic nests in 1986 and 1987 (Table 4). This relationship was marginally significant ($P = 0.09$) in 1988 and not significant ($P > 0.20$) for nonparasitic nests in 1986 and 1987 (Table 4).

DISCUSSION

Body mass and incubation costs.—Studies of reproductive costs in birds have emphasized the effects of brood size on survival and future reproduction of the parents. Most research has been done on altricial species. In one of the few studies of a precocial species, Lessells (1986) manipulated brood size of Canada Geese (*Branta canadensis*), and demonstrated that body mass of females caring for large broods was lower during the molt period and that they molted later than females with small broods. Overwinter survival and clutch size in the next breeding season were not affected by brood size, but geese with larger broods nested later the next year. Care of precocial young after hatching generally is not considered a major cost to parents. Lessells' (1986) results emphasize that costs indeed are associated with rearing large broods in species that do not feed their young. The cost of parental care has been shown to increase with brood size in other precocial species (Walters 1982) and may play an important role in determining clutch size in these species (Winkler and Walters 1983).

In Blue Tits, where parents feed their young, increases in brood size resulted in greater loss of body mass for the adult females (Nur 1984, 1988). Females with low body mass had lower probabilities of surviving to the next breeding season, which suggests that loss of body mass is costly to females (Nur 1984, 1988). Similar results have been reported for male Pied Flycatchers (*Ficedula hypoleuca*) that care for large broods (Askenmo 1979). The basic idea is that parents that care for large broods have less time to devote to self maintenance; hence, they end the breeding period in poorer condition than parents of small broods.

Body mass of female Wood Ducks at the end of incubation had no effect on their date of nest initiation or clutch size in the next breeding season. In 1986, heavy females returned at higher rates than light females. There was no relationship in 1987 and 1988 between body mass of females and their survival to the next breeding season. Reduced survival of light females in 1986 coincided with a greater loss of body mass in that year relative to 1987 and 1988. Changes in body mass vary greatly within and among incubating female Wood Ducks (Harvey et al. 1989). Some females are better at balancing the various costs of incubation than others. Harvey et al. (1989) suggested that annual variation in the amount of local precipitation affected the availability of wetlands and influenced body-mass dynamics of incubating females. The positive relationship between body mass of females at the end of incubation and their survival to the next breeding season suggests that incubation can be an important reproductive cost for Wood Ducks during some years.

Female Wood Ducks that incubate clutches

TABLE 4. Correlations and partial correlations between the length of incubation, clutch mass, and date of nesting of female Wood Ducks.

Association	Nest type[a]				
	1986		1987		1988
	P (n = 20)	NP (n = 25)	P (n = 39)	NP (n = 22)	Combined (n = 19)
Correlation					
Length of incubation × clutch mass	0.44[b]	−0.11	0.63	0.54	0.41
	0.05[c]	0.59	0.0001	0.009	0.08
Length of incubation × nesting date	0.08	−0.03	−0.52	−0.59	−0.01
	0.75	0.87	0.0007	0.004	0.98
Clutch mass × nesting date	−0.43	−0.57	−0.35	−0.61	−0.18
	0.06	0.003	0.03	0.003	0.45
Partial correlation[d]					
Length of incubation × clutch mass	0.52	−0.16	0.56	0.29	0.42
	0.02	0.45	0.0003	0.21	0.09

[a] Nest type: P = parasitic; NP = nonparasitic; Combined = parasitic and nonparasitic nest types. See the Methods section for a description of nest types.

[b] Correlation coefficient, for $n < 20$ we used Spearman's correlation coefficient (r_s) and for $n \geq 20$ we used Pearson's correlation coefficient (r).

[c] Probability level.

[d] Date of nesting is held constant.

early in the breeding season generally are heavier than females that begin incubation later. Energy reserves of early-nesting females may provide them with an important buffer that can be used when energy expenditures increase or the ability of females to acquire energy decreases. Females that cannot begin incubation in good physical condition may postpone nesting, engage in intraspecific nest parasitism, or both. Clawson et al. (1979), for example, reported that some female Wood Ducks laid eggs parasitically before establishing their own nests later in the season. This type of "mixed reproductive strategy" may depend partly on female body condition (see Lank et al. 1989). Competition for limited nest sites certainly contributes to nest parasitism in the cavity-nesting Wood Duck. However, reproductive success may be improved if females pursue a "mixed strategy" when they cannot begin incubation in good condition. Wood Ducks have a lengthy breeding season (e.g. 122 days in South Carolina), which increases the opportunity for females that are parasitic early in the season to initiate their own nests at a later time.

Length of incubation.—Nest attentiveness during incubation is related positively to body mass within and among species of waterfowl (Afton and Paulus 1990). If Wood Duck response is similar to the response of other waterfowl, then low body mass should lead to reduced nest attentiveness with longer incubation periods and possibly lower hatching success. We found that body mass of female Wood Ducks at the beginning of incubation was not related to either duration of incubation or hatching success. These results contrast with those in Canada Geese where heavy females were at the nest longer than light females, and had shorter incubation periods (Aldrich and Raveling 1983). We have no data on the activity patterns of incubating Wood Ducks, and it is possible that body mass had no effect on nest attentiveness. However, heavy female Wood Ducks tended to nest earlier in the breeding season than light females. Even if small females were less attentive than large females, eggs would cool more slowly later in the season in response to warmer ambient temperatures (Caldwell and Cornwell 1975). Under these circumstances, females nesting later could spend less time at the nest without affecting egg temperature and thus hatching success and incubation duration.

We found that length of the incubation period was inversely related to nesting date in one of three years. Ambient temperatures are cooler early in the nesting season than they are later. Low temperatures cause eggs to cool faster when they are left unattended (Caldwell and Cornwell 1975), and temperature of eggs may decline as ambient temperature declines even with constant incubation (Haftorn and Reinert-

sen 1985). Low egg temperature during incubation may result in longer incubation periods (see Booth 1987). Beginning incubation in good condition, therefore, may be important for female Wood Ducks nesting early in the breeding season. Lipid reserves of female Wood Ducks can provide only a small part of the total energy demands of incubation (Drobney 1980). However, heavy females may be able to provide more constant care to eggs than light females, which is important when ambient temperatures are low. Female Wood Ducks that start incubating at higher body mass, for example, lose mass at a faster rate than light females (Harvey et al. 1989).

Length of the incubation period for Wood Ducks also increased as clutch mass of parasitic nests increased. Larger clutches can result in longer incubation periods (Jones 1987, Coleman and Whittall 1988), and energy expenditure is greater for birds that incubate at temperatures below the thermoneutral zone (Biebach 1984). All eggs in large clutches may not come in contact with the brood patch (Mertens 1977); consequently some eggs cool and need to be rewarmed, which causes a longer incubation period. In our study, the significant relationship between clutch mass and length of incubation for parasitic—but not for nonparasitic—nests suggests that disruption of nesting activity by nest parasites may also contribute to this relationship.

Clutch mass had no effect on the weight loss of incubating Wood Ducks (Harvey et al. 1989). This indicates either that energy expenditures of females were not dependent on clutch mass, or that they were able to adjust nutrient intake so that body mass was not affected. Jones (1987), for example, reported that swallows (*Hirundo rustica*) spent more time incubating experimentally enlarged clutches, but that body mass decreased only during periods when food availability was low.

Intraspecific nest parasitism (dump nesting) is common in Wood Ducks (Clawson et al. 1979, Heusmann et al. 1980, Semel and Sherman 1986), as well as in other species of birds (Rohwer and Freeman 1989). During a nine-year period in Missouri, clutch size of nonparasitic nests averaged 11.4 eggs, while clutch size of parasitic nests averaged 20.2 eggs (Clawson et al. 1979). Potential costs of nest parasitism to host females involve laying fewer of their own eggs (Andersson and Eriksson 1982, but see Rohwer 1984) and disruption or abandonment of nesting activity (Pienkowski and Evans 1982, Semel and Sherman 1986). A longer incubation period associated with larger clutch mass is also a potential cost of nest parasitism that has not been previously addressed. Nests taking longer to hatch are at greater risk from predation, and embryos may use more energy as a result of longer developmental time and hatch with smaller residual yolk reserves. Both factors have the potential to reduce the reproductive success of host females.

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FEMALE-BIASED SEX RATIO AT HATCHING IN THE GREEN WOODHOOPOE

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ABSTRACT.—In a population of Green Woodhoopoes (*Phoeniculus purpureus*) in the Rift Valley of Kenya, food abundance and breeding success varied greatly as a result of highly unpredictable patterns and abundance of rainfall. A given pair of woodhoopoes may breed successfully from zero to three times between May and December. We found a female-biased sex ratio in first nests of the year among those female breeders that had few (0–2) helpers. Apart from predation of entire broods, nestling mortality was extremely low (5%), and the bias was not based on differential starvation of male and female chicks. We examined several possible explanations for the female-biased sex ratio, and we suggest that production of female offspring by breeders in small groups is adaptive in that females are smaller and probably less expensive to rear than males. Young female nest helpers contributed significantly more feedings to subsequent broods than did their male siblings of the same age. The bias toward daughters could be effected either via nonrandom segregation of sex chromosomes or by differential mortality of eggs by sex. In several other bird species, larger eggs may give rise to males. This provides a possible means for the female parent to discriminate the sex of offspring before hatching. *Received 23 January 1990, accepted 12 May 1990.*

IN ANIMALS that reproduce sexually, each breeding individual should attempt to maximize its lifetime reproduction. One way parents might enhance their own reproductive advantage is through facultative control of the sex of their offspring. For vertebrates, this is a controversial and poorly understood subject. Although numerous explanations exist for why individuals should control the sex of offspring under specific conditions (Trivers and Willard 1973, Myers 1978, Williams 1979, Burley 1982, Charnov 1982, Clutton-Brock and Albon 1982, Clutton-Brock 1986), evidence for adaptive control of offspring gender in birds is scanty (Howe 1977, Williams 1979, Fiala 1981, Richter 1983, Clutton-Brock 1986, Breitwisch 1989) and usually ambiguous (cf. Ankney 1982 and Cooke and Harmsen 1983, and Blank and Nolan 1983 and Weatherhead 1985). In his review of sex ratio variation in birds, Clutton-Brock (1986: 326) concluded that "Sound evidence for sex ratio variation at hatching is thus scarce."

We report data that imply that in a cooperatively breeding bird (the Green Woodhoopoe, *Phoeniculus purpureus*), a female-biased sex ratio at hatching may occur under certain ecological and social conditions.

METHODS AND PERTINENT NATURAL HISTORY

We studied the social behavior and ecology of a marked population of Green Woodhoopoes near Lake Naivasha, Kenya, from mid-1975 through January 1982, and in June–July 1984 (Ligon and Ligon 1978, 1983, 1988, 1989a, b). Briefly, social units consist of 2–16 birds that contain no more than a single breeding pair, regardless of flock size. Each group defends a territory year-round, and territory size often is related positively to group size.

In each year breeding normally begins in late May or early June, following the "long rains" of March to May, and generally terminates in December or earlier. The number of successful nesting efforts per year appears to be controlled by food availability, which in turn is determined largely by patterns of rainfall. Two broods during the period June to December are common, and if environmental conditions are extremely favorable, three broods can be produced by one pair during this interval. When conditions are poor, breeding activity is limited, and only one or even no nesting attempt may occur. In such years, there is a lot of territory-to-territory variation both in the time of breeding and in the number of nests attempted.

Moth larvae make up the vast majority of food items of nestlings and adults during the six- or seven-month nesting season (unpubl. data), and numbers of these caterpillars through the year are related most directly to the amount of precipitation during the putative dry season, January to March. During this period, the moth caterpillars pupate in the ground and survive well only if the soil remains dry. If extensive rain falls during the "dry" season, mortality of the pupae is high, and few adults emerge to give rise to the generation of caterpillars that appears following the long rains. There is a significant inverse relationship between dry-season rainfall and subsequent repro-

ductive success in this population of woodhoopoes (Ligon and Ligon 1989a, b).

Nests are placed in tree cavities. We used an adjustable mirror and flashlight to inspect nest cavities after the eggs were laid. After determining clutch size, we generally did not inspect the nest again until the young began to hatch. This was indicated by changes in the behavior of the breeding female and helpers. After one or more eggs had hatched, the breeding female continued to eat large food items brought to her, but carried very small items into the nest cavity. As the eggs hatched, the helpers increased greatly the frequency of feeding visits and the number of minute food items brought to the nest. Unhatched eggs remained in the nest.

Clutch size in Green Woodhoopoes varied little; 88% were either three- or four-egg clutches. Despite this conservatism in clutch size variation, one third of the eggs in clutches of all sizes failed to hatch (see Ligon and Ligon 1988: table V). Separation of the data by year revealed a similar pattern: one third of all eggs laid in each year did not hatch (Ligon and Ligon 1988: table VI). Ligon and Ligon (1988) attribute this high rate of hatching failure to inbreeding depression.

In contrast to the high rate of hatching failure, starvation of nestlings was extremely rare (Ligon and Ligon 1988: table VI). Excluding losses of entire broods to predators, 95% (71/75) of the young woodhoopoes that hatched survived to fledge. The rarity of nestling starvation is probably related to the high hatching failure (i.e. a small number of nestlings initially may mean that each receives a larger proportion of the total food delivered than would be the case with a larger brood). The rarity of nestling mortality is important in that the number and sex of chicks fledged is 95% of the number and sex hatched (i.e. a sex ratio bias at fledging reflects the same bias at hatching).

RESULTS

Sex ratios of fledglings from first broods.—In small social units (i.e. a breeding pair with 0–2 helpers), more daughters are produced than sons in early (June to August) first broods of the year and in June to August broods of one (Table 1). Early broods are inevitably first broods, whereas first broods of the year are not necessarily produced early. Depending on the timing and amount of previous rainfall, first broods can appear either early (June–August) or late (after August) in the breeding season. In addition, the two "broods of one" categories (Table 1) are subsets of the two "all fledglings" categories. Broods of one are treated separately because if adaptive prehatching brood reduction occurs in conjunction with adaptive sex ratio manipulation (see Discussion), such broods represent the extreme limit of adaptive reduction. The sex of single-chick broods thus is critical for evaluation of these ideas. The data for small flocks suggest that significantly more female than male offspring are produced in early first broods, regardless of size, and that the same is true for broods of one. When early and late broods of small flocks are combined, this sex bias disappears. In groups with more than two helpers, early broods were not significantly biased towards females.

This general pattern is illustrated in detail in the subset of data for 1981 (Table 2). These data are instructive because environmental conditions were unusually favorable: every mated pair in the study population initiated nesting in May or June (i.e. food resources were adequate to permit early breeding in all territories), most groups were small, and fledging success was high. Although the 1981 data are too few for statistical significance, they illustrate for one year the pattern of interest. Note that in the small groups three times as many daughters as sons were produced in first broods, and that broods of one also are strongly biased toward females. Second broods of those same breeding groups later in 1981 were not female-biased.

Female-biased sex ratio.—At least two possibilities should be considered to explain why breeding female Green Woodhoopoes in small flocks preferentially produce female offspring early in the June–December breeding period.

1. Trivers and Willard (1973: footnote 21) suggest that under some circumstances parents should produce the more "altruistic" sex, to help in the parents' subsequent reproductive efforts. To test this idea we compared young (≤2 yr of age), same-age, male and female full siblings with regard to the aid they provided to nestlings. Females made significantly ($P < 0.001$) more feeding visits than did their male siblings (Table 3), and females also tended to deliver more insect biomass per hour (Ligon and Ligon in prep.) than did males (not significant). This greater visitation effort by female helpers was apparent only in birds ≤2 yr of age. Among older helpers, males apparently contribute as much as females (Ligon and Ligon 1978).

Young female helpers often brought extremely small food items to nestlings at very high rates of delivery (Ligon and Ligon in prep.), a pattern not exhibited by their male counterparts. Thus a significant sexual difference exists

TABLE 1. Sex ratios of fledgling Green Woodhoopoes in small (0–2 helpers) and large (>2 helpers) groups, 1975–1981.

	Nests (*n*)	Females	Males	*P*[a]
Small flocks				
All Fledglings	55	57	43	NS
All fledglings from early (June–Aug.) first broods	27	30	12	<0.005
Fledglings from all broods of one	20	14	6	NS
Broods of one, June–Aug. nesting	14	11	3	<0.05
Large flocks				
All Fledglings	73	70	63	NS
All fledglings from early (June–Aug.) first broods	59	30	28	NS
Fledglings from all broods of one	30	16	14	NS
Broods of one, June–Aug. nesting	16	6	10	NS

[a] Chi-square test; NS = not significant.

in the behavior of young helpers that could account, at least in part, for preferential production of daughters under the conditions we described. This suggestion is related to Fisher's (1930) hypothesis concerning cost of offspring of a particular sex (i.e. if young females are better helpers than males are, this in effect reduces the cost of producing daughters).

2. Adult male woodhoopoes weigh almost 20% more than females (Ligon and Ligon 1978), and this size difference is apparent well before fledging. Presumably females are less expensive to produce than males and thus are more likely to be reared successfully when food is scarce (also see Richter 1983), or when nest helpers are few. In addition, brood sizes of early nests in small flocks are significantly smaller ($P = 0.0516$) than in later nests (1.64 [28 broods] versus 2.04 [27 broods]), which further suggests that food early in the nesting season may be scarcer than later in the year.

This explanation agrees with the hypothesis that disproportionate production of the less expensive sex (here, smaller females) occurs when resources required for rearing offspring are potentially or actually limited (Myers 1978). It is supported by the fact that in flocks with few or no helpers, female nestlings are significantly more common than males in early broods of one (Table 1). Trivers and Willard (1973) also predict decreased production of the more expensive sex, generally males, under conditions of food limitation. However, the focus of selec-

TABLE 2. First-brood reproduction in social units of Green Woodhoopoes 1981.

	Helpers		Experience of female breeders[a]	Offspring sex		
	Male (*n*)	Female (*n*)		Male (*n*)	Female (*n*)	? (*n*)
Small Flocks[b]						
DD	1	1	E	0	1	
MSG	0	0	N	0	1	
NLP	0	0	N	0	1	
3ST	0	1	N	0	1	
CR5	0	0	E	1	1	
WWH	1	0	E	1	2	
RFM	1	1	E	1	2	
Large Flocks[c]						
BRF	1	5	N	2	2	
AD	3	1	N	0	1	1
ST	1	2	E	1	0	
BF	1	3	E	1	2	
CF	1	2	E	1	1	
MM	1	1	E	0	2	

[a] Novice (N) or experienced (E) at first nesting of 1981.
[b] 0–2 helpers.
[c] 3–6 helpers.

TABLE 3. Feeding visits (per hour of observation) by same age, full sibling novice helpers of opposite sex. Subscript indicates first or second nest of that year; where two sibling helpers of the same age and sex were present, their values were averaged.

Flock-Yr	Male helper(s)	Female helper(s)	Age (mo)
DD-1978	0.98	2.64 (2)	12
AD-1977	1.90	6.00	9
AD-1979$_1$	1.14 (2)	1.08	24
AD-1979$_2$	0.59 (2)	1.14	26
3ST-1979$_1$	1.73	0.87 (2)	20
3ST-1979$_2$	0.77	1.91 (2)	22
ST-1977	1.42	2.83	21
MS4-1978	0.34	5.25	20
HS-1978	1.67	1.93	12
3ST-1979	1.51	4.12	19

tion in the two hypotheses is not the same. Trivers and Willard suggest that a female in poor condition should produce offspring of the sex which, upon maturation, has the better chance of breeding successfully relative to others of its sex, when in suboptimal physical condition (generally females). In contrast, Myers emphasizes the overall reproductive success of the parent rather than that of the offspring.

DISCUSSION

We have addressed two possible adaptive explanations for the female-biased sex ratio: rearing the more helpful sex and rearing the less expensive sex. In addition, because Green Woodhoopoes are so dependent on allies of the same sex to maintain control of their territory (Ligon and Ligon 1983, 1989a), a female breeder with a few or no subordinate female flock mates might prefer to produce daughters before sons. That is, if a female woodhoopoe produces a daughter as soon as possible, her security relative to groups of females in neighboring flocks would be enhanced. Because the female breeder lays and incubates the eggs alone (Ligon and Ligon 1978), and therefore controls events within the nest, such a strategy could potentially be employed by a breeding female, even if this conflicted with the interests of her mate.

Females of simple pairs sometimes produce first offspring that are male, which is counter to the expectations of both the ally and more helpful sex hypotheses, and (assuming that female breeders never make mistakes) suggests that the "cheaper sex" explanation may be of most importance (i.e. when food on the territory is abundant, rearing a male nestling may be no more costly than rearing a daughter). In contrast, according to the other two hypotheses, in small groups, daughters should always be produced before sons, regardless of environmental conditions at the time of nesting.

In several species of cooperatively breeding birds, males are more likely than females to serve as helpers (Brown 1987), but until recently there has been no evidence that production of male offspring is favored. In the Red-cockaded Woodpecker (*Picoides borealis*), virtually all helpers are male. A significant bias toward producing males occurs in groups in which the breeding female is a newcomer to the territory (i.e. has not previously bred there), whether or not she is helped (Gowaty and Lennartz 1985). This situation resembles that of the woodhoopoes: in both species a female breeder with few or no helpers (typically a new arrival to the territory or a novice breeder) produces significantly more offspring of the more helpful sex (daughters in the woodhoopoes, sons in the woodpeckers). However, in these woodpeckers, unlike the woodhoopoes, males and females are similar in size (Ligon 1968, Ligon and Ligon 1978).

Proximate causes of the biased sex ratio in Green Woodhoopoes.—We have considered four possible mechanisms responsible for the female-biased sex ratio described here.

1. *Sex-biased mortality of nestlings.* In general, biased sex ratios of nestlings are a result of post-hatch nestling mortality (Clutton-Brock 1986). However, in the woodhoopoes, post-hatch starvation of nestlings is so rare that it cannot be the mechanism producing the female bias.

2. *Age of female breeder.* Blank and Nolan (1983) found that older female Red-winged Blackbirds (*Agelaius phoeniceus*) produced a preponderance of sons. We have no record of any female woodhoopoe breeding successfully at <3 yr of age. We examined the numbers of sons and daughters produced by females of ages 3–4, 5–6, and 7–9 yr, and we found no relationship between sex of offspring and age of the female breeder.

3. *Females are the heterogametic sex.* In birds, females are the heterogametic sex and it is possible that the sex-ratio bias described here is based on a modification of the primary sex ratio. We have not been able to investigate this possibility.

4. *Differential mortality of one sex in the egg stage.* Sex of hatchlings possibly could be determined by the female parent during the incubation period, as she alone incubates the eggs. In some species of birds, egg size apparently correlates with sex; either those eggs that produce males are larger than those that produce females (Howe 1976, Ankney 1982, Ryder 1983, Mead et al. 1987) or vice versa (Fiala 1981; but cf. Blank and Nolan 1983 and Weatherhead 1985). In the woodhoopoes, considerable intraclutch variation exists in egg size and shape (See Ligon and Ligon 1978: fig. 7). Either the size or shape of eggs could provide the incubating female with a simple means of "choosing" offspring sex (i.e. by selectively denying incubation to some eggs).

Several observations of single eggs off to one side of the nest cavity suggested to us that this might occur, but we were unable to obtain sufficient data (based on marked and measured eggs that hatched) to investigate this notion. In short, we speculate that if inbreeding depression is not the sole cause of the high level of embryonic mortality (Ligon and Ligon 1988), both it and the biased sex ratio may be interrelated, as previously suggested for birds (Charnov 1982: 111).

Other evidence for parental control of offspring sex in birds.—In addition to the sex ratio manipulation of offspring in Red-cockaded Woodpeckers (Gowaty and Lennartz 1985), some of the findings of Patterson et al. (1980) appear to parallel the pattern for Green Woodhoopoes described here. Patterson et al. found a significant male bias in first broods of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), but not in the second or third broods. Conditions of food availability are better early in the season, and in the blackbirds the male feeds only first broods. Here it appears that under the optimal conditions of abundant food and paternal provisioning, the more costly male offspring are favored. Similarly, when food availability and assistance are limited, female woodhoopoes produce an excess of females, the less expensive sex to rear. In each case it appears that the sex of offspring produced is gauged to the availability both of food and the amount of provisioning assistance the female parent is likely to receive.

In a population of Common Grackles (*Quiscalus quiscula*), five-egg clutches (the most common clutch size) showed a decreasing proportion of females as the breeding season progressed, and presumably as the dependability of the food supply increased (Howe 1977). Howe suggested that this reflected a seasonal change in primary sex ratio probably controlled by nonrandom segregation of the sex chromosomes. Fiala (1981) also described a seasonal pattern of variation in sex ratio in Red-winged Blackbirds, with the proportion of females rather than males increasing for a time as the season progressed. Fiala (1981) surmised that young female Red-winged Blackbirds, which typically initiate nesting later than older birds, might produce an excess of female offspring and that this could account for the significant portion of the seasonal trend he observed. Blank and Nolan (1983), in part confirming Fiala's suggestion, demonstrated that young females do indeed produce a majority of daughters, but via differential nestling starvation. In addition, Blank and Nolan showed that the progeny of old females is biased toward sons, probably as the result of differential hatching of the sexes. As mentioned earlier, Patterson et al. (1980) found a male-biased sex ratio in first broods of the season in Yellow-headed Blackbirds. In this species male breeders help to provision only first broods. All of these temporal trends suggest maternal control of nestling sex ratio.

Other possible means of controlling offspring sex are related to correlations between laying sequence and sex, and between egg size and sex. Within Common Grackle clutches, egg weight increases with laying sequence, and mortality from last-laid eggs is less for females (Howe 1976). Fiala (1981) discovered a female bias in last eggs among the Red-winged Blackbirds he studied, and last eggs were largest in clutches of four (cf. Weatherhead 1985). In both of these North American blackbirds, significant trends have been described between increasing egg size and laying sequence, and with sex of last-laid eggs. However, Blank and Nolan (1983) found no indication that position in the laying sequence was associated with sex or that eggs from which males and females hatched differed in their energy content (also see Weatherhead 1985). In four-egg clutches of the Lesser Snow Goose (*Chen c. caerulescens*), Ankney (1982) reported that the first two eggs laid were larger than the last two, and that first eggs gave rise to males significantly more often than to females, but Cooke and Harmsen (1983) were unable to confirm this. Ryder (1983) described a relationship between egg sequence and sex in the Ring-billed Gull (*Larus delawarensis*). Like Ankney (1982), Ryder found more males produced by first-laid eggs than by last-laid eggs. Mead et al. (1987) determined that in White-crowned Sparrows (*Zonotrichia leucophrys*), egg size correlates with sex: male eggs are larger. (See Mead et al. [1987] for additional discussion of the relationship between egg size and sex.) All of these studies taken together (Table 4) suggest that sex-ratio adjustment does occur in birds and that the mechanism we have suggested for woodhoopoes, although not previously described, is plausible. They also point out that at the population level sex ratios usu-

TABLE 4. Possible factors involved with sex-ratio adjustment in the Green Woodhoopoe and in some other avian species (sources listed).

Green Woodhoopoe (this study)	Other Studies
1. Population nestling sex ratio not significantly biased.	Howe (1977), Fiala (1981), Ankney (1982), Ryder (1983), Blank and Nolan (1983), Richter (1983), Weatherhead (1985)
2. Seasonal variation in sex ratio.	Howe (1977), Fiala (1981)
3. Sex ratio biased when female breeder novice or with little or no help at the nest.	Gowaty and Lennartz (1985), Blank and Nolan (1983), Patterson et al. (1980)[a]
4. Smaller sex (female) produced when food less abundant.	Howe (1977), Blank and Nolan (1983), Patterson et al. (1980)[b]
5. Sex produced that will contribute more help at subsequent nests.	Gowaty and Lennartz (1985)
6. Suggestion that variation in egg size may be related to offspring sex.	Howe (1977), Fiala (1981), Ankney (1982), Mead et al. 1987

[a] Sex ratio biased when help (male parent) is present.
[b] Sex ratio biased when food is more abundant.

ally will not be biased (Fisher 1930, Richter 1983).

Finally, four species for which a sex-ratio bias has been described (i.e. Common Grackle, Red-winged Blackbird, Yellow-headed Blackbird, and Green Woodhoopoe) share certain important features which, taken together, strengthen the likelihood that adaptive manipulation of the hatching sex ratio occurs under certain conditions. First, all exhibit strong sexual dimorphism; male nestlings are considerably larger and thus more costly to feed than females. Second, there is seasonal or temporal variation in food abundance, which changes the costs of rearing offspring over time. Third, there is variation in the amount of provisioning assistance the female breeder will receive. In the grackle and blackbirds, the male parent may or may not feed nestlings, whereas in the woodhoopoes the variation in provisioning appears to be related in large part to number of helpers.

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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 must be submitted no later than 15 January, with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192 USA.**

Three postdoctoral fellowships were awarded for the 1989 year: Jean-Louis Martin, Avian geographic variation and speciation in the Palearctic: Are there general rules? Richard O. Prum, Phylogeny and behavioral diversification of the cotingas (Cotingidae); and C. Jeffery Woodbury, A taxonomic study of the avian spinal cord.

Three collection study grants for the 1989 year were awarded: Timothy Crowe, for a study of supra-generic phylogenetic relationships within the gamebirds (Order: Galliformes); Nedra Klein, for a study of speciation in the Yellow Warbler (*Dendroica petechia*); and Miguel Lentino Rosciano, for a study of the systematics of *Crypturellus erythropus* and *Tyto alba*.

Chapman grants for 1988, totaling $40,066, with a mean of $598, were awarded: Craig W. Benkman, The ecology and status of the Hispaniolan Crossbill; William L. Benner, How does House Finch color variation affect female choice? James V. Briskie, Dynamics and consequences of copulation patterns in Smith's Longspurs; Kevin J. Burns, The geography of Fox Sparrow ontogeny; Alice L. E. V. Cassidy, Song variation and learning in Song Sparrows (*Melospiza melodia*); Luis M. Chiappe, Continental birds from the Late Cretaceous of Patagonia; Carla Cicero, Stucture and variation in the song of the Lincoln's Sparrow (*Melospiza lincolnii*) in California; David A. Cimprich, Effect of flocking with dominant heterospecifics on nutritional status; Evan G. Cooch, Effect of growth rate on adult body size and fecundity in Snow Geese; Barbara Diehl, Structure and functioning of a bird community in a patchy and changing habitat; Andrea Dinep, The development of social behavior in White Ibis chicks; Keith L. Dixon, Investigation of the Crested Titmouse hybrid zone in Texas; David Eastzer, Allozyme frequencies across a song transition zone; Scott V. Edwards, Molecular evolution in cooperatively breeding Australo-Papuan babblers (*Pomatostomus*); Bruce A. Eichhorst, Genetic variation in the Western and Clark's grebes: color-morphs or species? Lisa M. Ellis, Interaction of testosterone and delayed plumage maturation in Black-headed Grosbeaks; David Enstrom, Mate choice and delayed plumage maturation in Orchard Orioles; Patricia Escalante, Evolutionary relationships of *Geothlypis* warblers; Charles M. Francis, Survival rates of Lesser Snow Geese; Renee D. Godard, Individual discrimination by two wood

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