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Natal Dispersal of Peregrine Falcons in Greenland

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Natal dispersal is female biased in most bird species in that proportionally more females than males disperse, or females disperse farther than males (Greenwood 1980). This pattern appears to be related to the amount of effort each sex spends in competing for territories or mates versus the amount of effort spent in raising young and choosing mates (Greenwood 1980). Presumably, males gain foraging and antipredator benefits that improve reproduction and survival when establishing territories in familiar areas. If males are philopatric, then females should disperse to avoid inbreeding (Pusey 1987) and to evaluate potential mates (Greenwood 1980). The effects of mating system and inbreeding avoidance on dispersal behavior are not mutually exclusive, and a combination of factors likely produces sex-biased dispersal.

Although some long-distance dispersers experience lower survival and reproductive success than their philopatric counterparts (Newton and Marquiss 1983, Nilsson 1989, Pärt 1990), others suffer no apparent costs (Arcese 1989, Plissner and Gowaty 1996, Miller and Smallwood 1997). Most investigations of natal dispersal have focused on species that breed at one year of age, have short lifespans, and nest in unpredictable environments. Few studies have examined dispersal in long-lived, long-distance migrants that nest in predictable environments. Individuals of these species typically spend several seasons exploiting different habitats over large spatial scales before settling to breed. Therefore, we might expect the benefits of short-distance dispersal

to males, such as higher productivity and lower mortality, to be less pronounced or absent, particularly if nesting habitat is not limiting.

We analyzed 20 years of Peregrine Falcon (*Falco peregrinus*) breeding data from Greenland to identify the proximate causes and consequences of natal dispersal associated with this long-lived, long-distance migrant. We determined if (1) sex ratio, survival, and population density affected natal dispersal; and (2) whether natal dispersal distance affected survival and subsequent productivity.

Study Area and Methods.—The study area encompassed approximately 6,000 km² in the widest part of ice-free land of western Greenland (66°45′N, 51°30′W). Most of the study area was rolling tundra (elevation up to 1,100 m) interspersed with nearly 1,000 lakes. Vegetation was dominated by willow (*Salix glauca*), dwarf birch (*Betula nana*), heaths (*Empetrum, Ledum, Cassiope*, spp.), and grasses (*Calamagrostis, Festuca, Poa*; see Burnham and Mattox [1984] for a more complete description of the study area).

From June to mid-August, 1978 to 1997, a variable number (two to five) of two-person teams backpacked across the tundra and visited cliffs that provided potential nesting habitat for Peregrine Falcons (Burnham and Mattox 1984). Teams observed cliffs for signs of breeding activity. If breeding activity was not evident after a minimum of 4 h of observation, the cliff was considered inactive. Observers recorded the presence of adult peregrines and attempted to classify individuals by sex at cliffs occupied by lone adults.

Banding teams either rappelled or climbed to eyries that contained young. Nestlings were individually marked with a Danish Zoological Museum num-

bered band on the left tarsus and an alpha-numeric color band on the right tarsus (except during 1982 to 1985). Nestling sex was determined based on size, and age was estimated during 1983 to 1997 following Moritsch (1983). Banding teams used spotting scopes and binoculars to note or read the alpha-numeric codes on the bands of attending adults. From 1983 to 1997, trapping teams captured adults at nest sites and banded each unmarked bird with a numbered band on the right tarsus and an alpha-numeric color band on the left tarsus (i.e. opposite the scheme used for nestlings).

Prior to using parametric statistics, we log-transformed data to satisfy assumptions of normality and homogeneity of variances. To determine the relationship between dispersal distance and productivity and lifespan (i.e. survivorship), we first calculated mean values of each parameter for each disperser. We calculated a productivity estimate for each disperser by dividing the total number of young produced (i.e. sum of brood sizes at banding) by the number of years of breeding. Most nestlings were banded when 20 to 25 days old, which is approximately 50 to 60% of the average age at which young leave the nest (40 days). Thus, productivity estimates were liberal because a few nestlings probably died before fledging, so we used these values only as an index to evaluate the relationship between productivity and dispersal distance. We used the number of years each disperser occupied a cliff as an estimate of breeding lifespan. These values were slightly conservative because we detected dispersers a mean $1.3 \pm$ SE of 0.3 years older than the mean age of first breeding (Ambrose and Riddle 1988), and a small proportion (3.9%) of the population exhibited breeding dispersal (Mattox and Seegar 1988). Therefore, we used these values only as an index to evaluate the relationship between dispersal distance and survivorship. We used simple linear regression to determine the relationship between dispersal distance and productivity and survival, but we also examined plots of the data for curvilinear relationships (see Nilsson 1989, Pärt 1990). Fledging dates of broods were estimated from mean nestling ages at banding, assuming young fledged when 40 days old. We report untransformed values in the Results.

Results.—During the 1978 to 1997 breeding seasons, we banded 1,702 nestlings from 583 broods. The number of nestlings banded each year ranged from 17 to 190 (6 to 69 broods per year). At least one nestling in 56 broods could not be identified to sex during banding, so we calculated nestling sex ratio from the sample of 527 broods (1,566 nestlings) in which sex was determined for all nestlings. The overall sex ratio (774 males, 792 females) did not differ from parity ($\chi^2 = 0.10$, df = 1, $P = 0.75$).

We documented 42 (2.6%) banded nestlings that were recruited into the study population. Nestlings banded in 1996 and 1997 were not included in this calculation because they had not reached sexual maturity by 1997. Broods that produced recruits tended to fledge earlier (median = 16 August) than other broods (median = 18 August; one-tailed t-test, $t = 1.52$, df = 386, $P = 0.065$). The direction of dispersal averaged 83°, although the distribution of directions did not differ from random (Rayleigh test, $z = 2.24$, $n = 27$, $P = 0.097$).

More males ($n = 35$) than females ($n = 7$) were recruited into the study area population than expected from the nestling sex ratio ($\chi^2 = 18.78$, df = 1, $P < 0.001$; test conducted for years 1978 to 1995). We identified recruits by either observation (74%) or capture (26%), and each method yielded equal success for males and females (Fisher's exact test, $P = 0.23$). Dispersal distances within the study area for banded recruits were similar for males ($\bar{x} = 28.1 \pm 4.4$ km, $n = 21$) and females ($\bar{x} = 27.1 \pm 4.4$ km, $n = 6$; Mann-Whitney test, $P = 0.60$; Fig. 1). However, the only long-distance dispersal that we documented was a female that was banded in 1990 and captured at her breeding cliff in 1997, approximately 690 km south of her natal site (not shown in Fig. 1).

We checked an average of 56 ± 6 cliffs each year, but determining the effect of population density on dispersal distance was difficult because the number of individual cliffs visited each year varied. Seventeen cliffs were checked annually from 1983 to 1995. The period 1978 to 1983 was not used in the analysis because so few cliffs were checked repeatedly during the early years of study. The percentage occupancy of these 17 cliffs by adult peregrines, a measure of breeding density, was unrelated to dispersal distance ($R^2 = 0.06$, $n = 26$, $P = 0.12$). We observed lone adult peregrines at 71 of the 1,112 cliffs visited from 1978 to 1997. Of the 71 adults, 58 could be identified to sex: 27 (46.6%) males and 31 (53.4%) females, a proportion similar to that expected from the nestling sex ratio ($\chi^2 = 0.18$, df = 1, $P = 0.67$).

To date, we have received information of 45 recoveries (i.e. dead birds) of the 1,702 banded nestlings: 12 males (26.7%) and 33 females (73.3%), which is a higher proportion of females than expected from the nestling sex ratio ($\chi^2 = 8.41$, df = 1, $P = 0.004$). Of these 45 birds, the proportion of males (58.3%) and females (63.6%) that died before reaching the mean age of first breeding was similar ($\chi^2 = 0.11$, df = 1, $P = 0.75$). Although females were recovered more often in populated regions (east coast of the United States and the Caribbean vs. elsewhere; $\chi^2 = 2.78$, df = 1, $P = 0.095$), both sexes were killed by humans with similar frequency ($\chi^2 = 1.58$, df = 1, $P = 0.21$). Males ($\bar{x} = 10,692 \pm 384$ km, $n = 7$) wintered (November to April) farther south of the study area than did females ($\bar{x} = 5,661 \pm 233$ km, $n = 15$; Mann-Whitney test, $P < 0.001$). Males wintered in South America, whereas females, with one exception, wintered in Central America or the Caribbean.

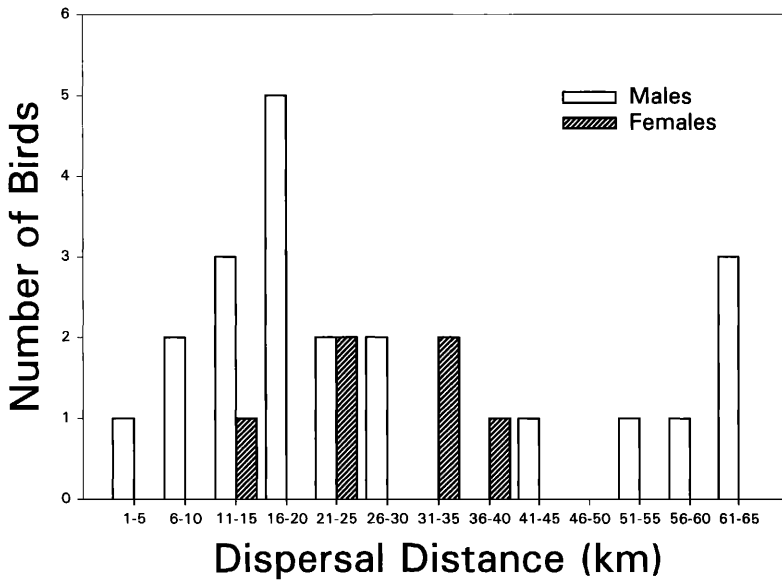We examined two consequences of dispersal dis-

FIG. 1. Natal dispersal distance of Peregrine Falcons produced and recruited in the study area in western Greenland.

tance. Breeding lifespan, the mean minimum number of years occupying a cliff, was similar for male (2.2 ± 0.3 years, $n = 31$) and female (2.0 ± 0.3 years, $n = 6$) dispersers (Mann-Whitney test, $P = 0.97$). Lifespan was unrelated to dispersal distance (males, $R^2 < 0.01$, $n = 16$, $P = 0.94$; females, $R^2 = 0.27$, $n = 5$, $P = 0.21$). Productivity, the mean number of young raised to fledging each year, was similar for male (2.4 ± 0.2 young, $n = 35$) and female (2.7 ± 0.3 $n = 7$) dispersers (Mann-Whitney test, $P = 0.76$). Productivity was unrelated to dispersal distance (males, $R^2 < 0.01$, $n = 21$, $P = 0.98$; females, $R^2 = 0.05$, $n = 6$, $P = 0.33$). The sample size of female recruits was small, so these data should be interpreted with caution. We did not observe close inbreeding (i.e. parent-offspring or sibling-sibling mating).

Discussion.—Natal dispersal of Peregrine Falcons in Greenland was female biased. We have discounted two proximate factors that could have produced sex-biased dispersal. First, the sex ratio of nestlings was equal, so an overproduction of males did not increase the probability that they, rather than females, recruited into the local population. Second, sex-specific breeding opportunity did not influence dispersal because the sex ratio of lone adults occupying cliffs was equal, and adult males and females had similar breeding lifespans. Therefore, turnover rates and the availability of territories were similar between the sexes (see Court et al. 1989).

Recoveries of banded nestlings (12 males, 33 females) suggested that females have lower survivorship than males, a factor that could have caused female-biased dispersal by reducing the number of fe-

males available for recruitment. Evaluating the implications of these data was difficult because male and female peregrines produced in Greenland wintered in different areas (W. Mattox unpubl. data). Males wintered in South America, whereas females wintered in Central America and the Caribbean. Females simply may have died in areas frequented by humans, which would have increased the probability of their discovery and given a false impression of low survival. For example, significantly more females than males (50% vs. 16%) were recovered in the populated regions of the United States (i.e. East Coast) and the Caribbean compared with remote regions of Greenland and South America, yet both sexes were equally likely to be killed by humans. Moreover, if differential survival contributed to females-biased dispersal, then we should have seen more lone males than females at breeding cliffs, but we did not. When these findings were combined with the observation that survivorship of juvenile male and female peregrines, based on sightings rather than recoveries, was similar in the midwestern United States (Tordoff and Redig 1997), we believe that differential survivorship probably did not occur or contribute to sex-biased dispersal.

Density of the breeding population did not affect dispersal distance of peregrines (see also Newton and Marquiss 1983, Pärt 1990). However, population density has influenced dispersal distances in other species (Nilsson 1989, Negro et al. 1997), and this effect was related to availability of breeding habitat. The nesting population of Peregrine Falcons in Greenland has increased each year during the past

26 years (Burnham and Mattox 1984, Mattox and Seegar 1988). Apparently, breeding habitat within the core study area remained available, which probably prevented the expression of density-dependent effects on settling patterns.

Peregrine Falcons have a resource-based breeding system whereby males obtain and defend territories to attract females. This mating system should produce female-biased dispersal, which it does, and also should exert a cost on males who disperse farthest (Greenwood 1980). However, male peregrines in Greenland do not suffer reduced productivity or survivorship when dispersing greater distances, at least within our study area. This finding is not unique among birds (Arcese 1989, Plissner and Gowaty 1996, Miller and Smallwood 1997). When a negative relationship occurs between dispersal distance and productivity and survivorship (Newton and Marquiss 1983, Nilsson 1989, Pärt 1990), it is attributed to benefits accrued from familiarity with the natal area (Pärt 1995), knowledge gained either from early arrival after spring migration (Pärt 1994) or from explorations prior to autumn migration (Morton 1992). Knowledge of natal areas probably is poorly developed in high-latitude peregrines because they migrate soon after they leave the nest (Mearns and Newton 1984). However, most peregrines first breed when two or three years old (Mearns and Newton 1984, Ambrose and Riddle 1988, Tordoff and Redig 1997), so individuals have several summers to explore and become familiar with an area before they secure a territory.

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Influence of Lipid and Uric Acid on δ¹³C and δ¹⁵N Values of Avian Blood: Implications for Trophic Studies

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The use of nitrogen (¹⁵N / ¹⁴N) and carbon (¹³C / ¹²C) stable isotopes to infer trophic relationships in food webs has become a common and widely accepted technique (see Michener and Schell 1994). Stable-isotope ratios in the tissues of consumers reflect those in their diets in a predictable fashion, being isotopically enriched in ¹⁵N (up to 4‰) and ¹³C (usually ca. 1‰; DeNiro and Epstein 1981, Peterson and Fry 1987). Thus, unlike conventional dietary studies, stable-isotope analyses reflect assimilated (vs. merely ingested) foodstuffs. In addition, depending on the tissue chosen, dietary information spanning different temporal scales can be obtained (Hobson and Clark 1992a). Typical proteins used in such analyses are bone collagen and muscle (e.g. Hobson 1987, 1990; Hobson et al. 1994), which usually require the sacrifice of live animals or the opportunistic sampling of carcasses.

Isotopic analyses can also be performed on tissues that can be sampled nondestructively, such as blood, feathers, and hair (Hobson and Clark 1993, Thompson and Furness 1995, Bearhop et al. 1999). Nondestructive sampling is desirable when dealing with rare species, when individuals are part of ongoing studies, and when investigating variation within individuals over time. However, there are consistent differences in isotopic signatures among tissue types (e.g. Tieszen et al. 1983). Some of this variation can be linked to differences in tissue metabolic rates, but some reflects differences among tissues in biochemical composition (e.g. Hobson and Clark 1992a). Lip-

id presents a particular problem. The lipid component of a given tissue type can be quite variable among individuals and generally is depleted in ¹³C compared with whole tissues (e.g. Tieszen et al. 1983). For these reasons, it is common practice to remove lipids from tissue samples where they may be present (Hobson 1987, 1990; Hobson and Clark 1992b; Thompson and Furness 1995).

One of the most obvious ways to take nondestructive samples from animals is to obtain blood. The lipid component of blood generally is very low and is carried mostly in the plasma (Deuel 1955). Researchers have either analyzed whole blood (Hobson and Clark 1993, Hobson et al. 1997) or removed the serum fraction and analyzed the cells (Ben-David et al. 1997). However, the concentration of uric acid and urea (the end products of protein catabolism) reach substantial levels in blood plasma, particularly in times of high protein turnover such as during growth (Skadhauge 1983, Wolf et al. 1985, Alonso et al. 1991). Indeed, the concentration of uric acid in blood plasma is close to its solubility limit, and in avian urine, it grossly exceeds this limit and is present in colloid suspension (Skadhauge 1983). The mechanism by which ¹⁵N enrichment occurs is largely due to the excretion of isotopically light nitrogen (¹⁴N) in nitrogenous waste (Peterson and Fry 1987). Thus, if blood levels of urea or uric acid are elevated, then whole blood measurements will appear to be depleted in ¹⁵N. To date, no workers have assessed the influence that the lipid component and the uric acid / urea content may have on the isotopic signature of whole blood.

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