



Migration Patterns in Male Great Bustards (*Otis tarda*)

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The Great Bustard (*Otis tarda*) is distributed from Iberia and Morocco in the west to China in the east and has been considered sedentary in all but the northern and eastern parts of its range (Gewalt 1959, Glutz et al. 1973, Cramp and Simmons 1980). However, some studies have reported seasonal changes in population numbers in different areas in the Iberian Peninsula (Hidalgo and Carranza 1990, Alonso et al. 1995), suggesting that the species is a partial migrant (*sensu* Terrill and Able 1988) in this region.

We describe seasonal movements of marked adult male Great Bustards and discuss observed patterns in relation to the following questions: (1) Do migratory males display interannual fidelity to breeding and postbreeding areas? (2) Do males travel significantly farther than females in their seasonal movements? We also suggest several hypotheses that could explain patterns of partial and differential migration in male Great Bustards.

Methods.—Our study was carried out in the Wildlife Reserve of Villafáfila (41°50'N, 5°35'W; ca. 700 m elevation), which extends over 32,682 ha of dry, treeless and gently undulating farmland in the Province of Zamora, northwestern Spain. The land is almost entirely cultivated with wheat and barley. The remaining surface (ca. 9%) is occupied by natural grassland used for sheep grazing. The Reserve holds the world's densest population of Great Bustards (Alonso et al. 1995), which are ground-dwelling lekking birds that inhabit natural and cultivated grasslands. The Great Bustard is endangered in most of its range except for the Iberian Peninsula, which is the main stronghold for the species (Alonso and Alonso 1996). It exhibits one of the highest amounts of sexual size dimorphism of all vertebrates, and males and females generally occur in separate flocks. Between late winter and early spring, males concentrate at traditional arenas where they fight to establish rank and display in an exploded-lek mating system (see Höglund and Alatalo 1995). Juvenile males usually disperse after independence. From their third year on, they begin to establish territories at

leks 5 to 65 km from their natal sites, but generally they do not succeed in mating until they are at least four years old. Compared with males, females tend to remain closer to their natal site (0.5 to 5 km) and begin breeding earlier (Alonso et al. 1998).

Each summer from 1983 to 1993, we captured young Great Bustards (body mass 1 to 3.5 kg) by chasing them down while they were still being attended by the female parent. We marked a total of 105 juvenile males with patagial tags, and in the last three years of the study we attached backpack-mounted radio transmitters to 58 of these birds. Battery life of the transmitters averaged three to four years, which allowed us to track birds from ground vehicles or aircraft from the time they dispersed until they settled as breeding adults (and sometimes for longer periods). Only 15 males from the original pool survived long enough to settle in the study area and be studied during their adult life. Once established, these males could be located by sight (even when transmitters no longer functioned) during our surveys of the Reserve and its surroundings. In addition, in February and March 1993 and 1994, we captured 11 adult males using a rocket net and provided them with backpack transmitters and dorsal PVC tags for visual identification. During the three years after capture, we obtained locations for each of these males at least once per month. Therefore, the total sample of marked adults was 26, from which we gathered more than 800 locations on different days.

We located all radio-tagged individuals by triangulation and subsequent visual observation. Two of the 15 birds marked as juveniles settled as resident adults in the Reserve and could be located monthly. These two, plus the 11 marked as adults, resulted in 13 adult males for which we obtained data on monthly patterns of movement. The remaining 13 birds in the total sample of 26 were seasonal visitors to the Reserve and could be contacted only at leks during the breeding season, thus yielding information only on their presence or absence in the Reserve. Whenever a marked Great Bustard was found during surveys, we recorded its location to the nearest 100 m on 1:50,000 maps.

We conducted 50 censuses of Great Bustards in the Reserve between January 1987 and March 1998 with

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a frequency that varied from once per fortnight to one every four months. All parts of the Reserve were covered with equal effort to avoid biases in the probability of contact with individual birds. Some adjacent areas were also surveyed, although less intensively. Each survey was carried out by four people in two cars during two consecutive days. Surveys followed predetermined transects to cover the entire Reserve and always used the same starting location. Transects covered nearly 400 km in length and required 20 h per team to complete. Surveying was interrupted during midday hours (between 1000 to 1100 and 1500 to 1600 GMT, depending on the season), when birds usually were inactive and thus less detectable. Given the large size of Great Bustards, the generally flat terrain, and the fact that the maximum distance between roads in the Reserve was about 1 km, we assumed that we sighted nearly all of the birds in the study area (see Alonso and Alonso 1990). The census results that we present refer to males that were older than one year. Monthly variation in the number of male Great Bustards observed was analyzed by one-way ANOVA, and monthly differences were assessed with the LSD test using values based on more than three censuses. To account for interannual effects on the monthly variation in male numbers, we performed a two-factor ANOVA, adding the variable year to the original model.

To determine the central location of each male's lek, we plotted all sightings of a given male on 1:50,000 maps that contained the boundaries of all leks in the Reserve (Morales et al. 1996, Morales 1999). Sightings were plotted during the period when copulation rate is highest, which in our study area is between 25 March and 15 April (Carranza et al. 1989, Morales et al. 1996). For this analysis, data were pooled over the duration of the study, which yielded 17 to 45 locations for each male. The arithmetic mean of these coordinates was used as the coordinate of the lek that each male visited each year (this mean was calculated for every marked bird). All statistical analyses were conducted using STATISTICA 5.0 (Statsoft 1995).

For each of the 13 males for which we obtained the monthly pattern of movements (see above), we calculated the linear distance from its lek coordinates to every other sighting of that bird and obtained a monthly mean distance to the lek using all sightings of that bird over the study period. We analyzed the monthly variation of the mean distance to the lek for each of these males with a one-way ANOVA after log-transformation of the data.

We used the total sample of 26 males to measure interannual fidelity to leks and postbreeding areas by calculating the percentage of males that was seen displaying at the same lek or using the same postbreeding area, respectively. Any relocation of a male within 3 km of its average postbreeding coordinate was considered to be within that bird's postbreeding

area. To account for the total percentage of sedentary and dispersing males, we counted birds in this global sample that were sighted in the Reserve during the mating season only and birds that were detected in the vicinity of their leks throughout the year. We further used this sample to analyze the influence of age as a factor in the migratory behavior of the birds after dividing the sample into two age groups, <5 years and ≥ 5 years. Although the exact age was known only for birds that we caught as chicks ($n = 15$), males captured as adults ($n = 11$) were easily assigned to one or the other age category based on plumage characteristics (Glutz et al. 1973).

The degree of development of secondary sex traits such as male body mass or ornamental feathers can be used as an indirect measure of social status among males (Andersson 1994). Body mass and the degree of development of "moustache" feathers (see Gewalt 1959, Hidalgo and Carranza 1990) have been shown to play a role in determining social rank in male Great Bustards (Delgado et al. 1991, Carranza and Hidalgo 1993). We used these two traits to investigate the relationship between social dominance and migratory behavior among male bustards. Because adult body mass was not known for all birds in our global sample, we used only those marked as adults ($n = 11$). We divided this subsample into males that weighed less than 10 kg (median value) and males that weighed 10 kg or more to test the association between body mass and migratory status. With respect to moustache feathers, during three consecutive springs we classified birds visually in the field into three discrete categories of development: (1) poorly developed, (2) developed, and (3) highly developed (see Gewalt 1959, Morales 1999). It was possible to make such classification for 15 males in our global sample. We obtained a mean value for each of these males based on the value assigned to them each spring over the duration of the study. We then assigned each of these males into one of two groups based on the mean development of moustache feathers: (1) ≥ 2.5 , and (2) < 2.5 (2.5 was the median value for this sample of males).

To investigate the extent to which migration mirrors juvenile dispersal, we used a subsample of seven males for which enough data existed to determine the percentage of birds that revisited as migrant adults any of the areas where they had been located during their period of juvenile dispersal. We compared this value with the percentage of birds that did not visit such areas using a test of the difference between two percentages (Statsoft 1995). To test for sexual differences in migration distance, we compared data from marked females that were migratory ($n = 10$; Morales 1999) with data from our sample of nonsedentary males ($n = 6$).

Results.—Monthly variation in the number of male Great Bustards seen in the study area was significant ($F = 7.10$, $P < 0.05$), whereas the interannual effect

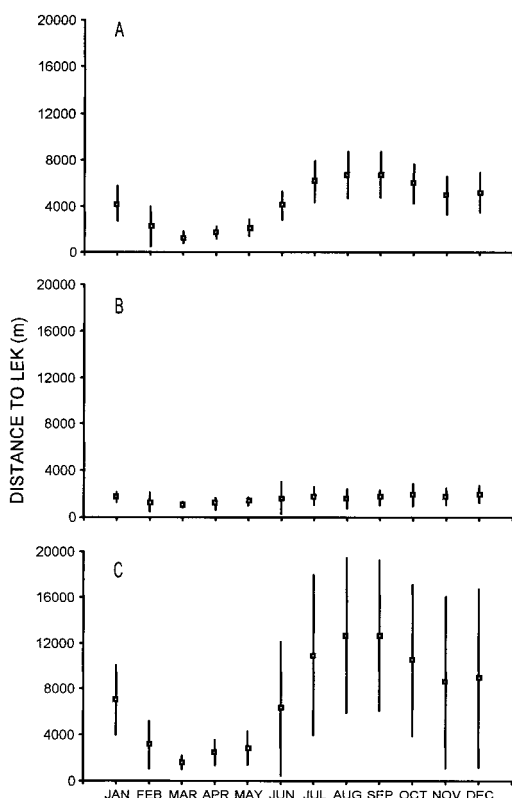


FIG. 1. Mean distance to lek (\pm SD) for male Great Bustards for which we had contacts in all months of the year. (A) Global pattern, all males ($F = 2.86$, $df = 11$ and 143 , $P = 0.002$); (B) sedentary males ($F = 1.22$, $df = 11$ and 70 , $n = 6$, $P = 0.29$); and (C) migratory males ($F = 3.87$, $df = 11$ and 60 , $n = 7$, $P < 0.001$).

was negligible ($F = 1.64$, $P > 0.05$). The highest average number of males occurred in March, and differences between March and all other months were significant ($P < 0.05$). Numbers decreased to a minimum during summer, representing 39% of the March population on average. The difference be-

tween the summer months combined versus all the other months was significant ($P < 0.05$).

A seasonal pattern of postbreeding dispersal from the lek was clearly distinguishable when we considered all 13 males that we radio tracked continuously (Fig. 1A). Moreover, by studying each individual separately, two distinct patterns emerged: (1) a sedentary pattern, corresponding to males that stayed close to their leks year-round and performed no significant monthly movements (< 3 km from their mating center; Fig. 1B); and (2) a migratory pattern. Males in the migratory group made significant seasonal movements between their breeding areas, which they attended from late January to early March through May (four males), or from October to May through June (two males), and their postbreeding areas, which they used during the rest of the year (Fig. 1C). Migrating individuals tended to abandon and return to the lekking areas at around the same dates each year (Table 1).

We observed no significant change of wintering area during the postbreeding period, but one male visited two leks that were more than 10 km apart and regularly repeated this pattern each year. The distances between lek and postbreeding areas varied from nearly 7 km to more than 20 km. Some birds with wing tags but no radio transmitter may have traveled longer distances.

Of the total sample of 26 birds (including males with wing tags but no transmitter), 8 (31%) behaved as sedentary individuals, and the remaining 18 (69%) performed migratory movements, spending either the summer or the summer and winter away from their breeding ranges (generally outside the Reserve). We found no significant difference in the proportion of each migratory pattern between males younger than 5 years versus older than 5 years (Fisher's exact test, $P = 1.00$, $n = 26$), males weighing < 10 kg versus ≥ 10 kg ($P = 1.00$, $n = 11$), or males with poorly developed moustache feathers versus highly developed moustache feathers ($P = 1.00$, $n = 15$).

We observed all 26 males in our global sample on the same lek every year during the main copulation period. Even the "lek-shifting" male, referred to above, visited the same leks each year. All males that

TABLE 1. Months of return to and departure from leks for six migratory male Great Bustards that were equipped with radio transmitters.

Male	Month of return	Years	Month of departure	Years
A	January	1995, 1996	July	1994, 1995, 1996
B	February	1994, 1995, 1996	July	1994, 1995
C	March	1994, 1995, 1996, 1997	June	1994, 1995, 1996
D	March	1996, 1997	July	1996, 1997
E	October	1994, 1995, 1996, 1997	May	1994, 1995, 1996, 1997
F	October	1994, 1995	June	1994, 1995

made significant seasonal movements and could be radio tracked regularly or sighted during surveys visited the same areas during their postbreeding dispersal ($n = 6$). Moreover, no male changed its status from sedentary to migratory or vice versa during the study.

For seven males, we had enough data to compare the areas they visited as dispersing juveniles with those they regularly moved to as migrant adults. Both areas coincided in six cases (86%), and in only one case (14%) they did not ($P = 0.01$). Postbreeding dispersal distance from the lek was higher in males (median = 12,483 m, range 5,946 to 20,062 m, $n = 6$) than in females (median = 3,981 m, range 2,405 to 10,892 m, $n = 10$; Mann-Whitney U -test, $Z = 3.04$, $P = 0.002$).

Discussion.—We identified two well-differentiated patterns of seasonal movement with respect to leks in our sample of marked Great Bustard males: (1) sedentary males, which stayed within 2 to 3 km of their lek all year and did not exhibit a defined pattern of movement, and (2) migratory males, which moved yearly from leks to postbreeding areas 7 to 20 km away. This range of distances may underestimate the true distance moved by males, because birds without radio transmitters might have moved longer distances. The distinction between these two patterns was not arbitrarily based on a linear distance boundary but rather on the presence or absence of each bird during the postbreeding season in the area occupied by the exploded lek to which it belonged in spring. The two movement patterns agree with the seasonal variation in numbers of males censused in the Reserve of Villafáfila, which peaked in March, reflecting the arrival of individuals from outside the study area to concentrate at leks within the Reserve.

Although no other study based on marked individuals has been published, the few data available for other western populations of Great Bustards suggest that the pattern of seasonal movements described here is typical for the species, with average dispersal distances perhaps being dependent on local habitat characteristics (Alonso and Alonso 1990, Hidalgo and Carranza 1990). For example, in a study that is being conducted in central Spain, some radio-tagged males have traveled much greater distances from their leks to postbreeding areas (M. Morales et al. unpubl. data). Most reports of Great Bustard movements in other parts of Europe refer to observations of irruptive migrations into milder areas during harsh winters (Cramp and Simmons 1980). Whereas some populations from central and eastern Asia undertake long-distance movements from north to south, it is unclear whether these are total or partial migrations (Dementiev et al. 1969, Cramp and Simmons 1980).

All males showed year-to-year fidelity to leks and postbreeding areas, and none changed its status between years from migratory to sedentary or vice ver-

sa. Moreover, each male apparently showed constancy in departure and return dates, suggesting that seasonal movements are quite independent of the environmental conditions of particular years. The coexistence of sedentary and migratory individuals in the same population corresponds to a partial migration pattern as defined by Terrill and Able (1988). Partial migration has been reported in other lekking or polygynous birds, many of which were previously considered sedentary, such as several species of grouse (Schroeder 1985, Rolstad 1989, Cade and Hoffmann 1993, Schroeder and Braun 1993).

Partial migration may be regarded as a strategy with two condition-dependent states (migratory or sedentary) that are determined, for instance, by age, body condition, social status, or sex (Lundberg 1988). Two lines of evidence seem to reject age as a factor of the migratory status in our study: (1) we did not record any status change from migratory to sedentary or vice versa, and (2) the proportion of males that was migratory or sedentary did not change between age classes.

In polygynous, size-dimorphic species, male reproductive success is tied to social status, which often is determined through agonistic behavior in which body mass and other secondary sexual traits play an important role (Clutton-Brock et al. 1988, Andersson 1994). In partially migrant species, dominant individuals are expected to stay close to their breeding territories, whereas subordinate individuals should leave as a consequence of intraspecific competition (Gauthreaux 1982, Smith and Nilsson 1987). However, the lack of a significant association between migratory status and either male body mass or the development of moustache feathers does not seem to support this hypothesis.

Great Bustards exhibit partial migration among males (some males migrate, and some do not), and differential migration between sexes (females migrate shorter distances), which has also been described in other species such as Spruce Grouse (*Fallopennis canadensis*; Schroeder 1985) and Blue Grouse (*Dendragapus obscurus*; Cade and Hoffmann 1993). These sexual differences could give support to the arrival-time hypothesis for the evolution of differential migration between the sexes (Gauthreaux 1982, Ketterson and Nolan 1983, Smith and Nilsson 1987), because females seem to experience higher intrasexual competition for breeding territories and thus higher pressure for early arrival than do males (Morales et al. 1996, Morales 1999).

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What Happens to Old Nests in Natural Cavities?

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It is well known that old nest material accumulates in nest boxes and should be removed to keep the boxes usable. Perrins (1979) and Møller (1989) proposed that the removal of old material, via reduction of ectoparasites, could improve conditions in the boxes. This in turn could have profound effects on nest-site choice, mating success, and reproductive efficiency of the individuals that use the boxes.

Natural cavities are not cleaned by humans. Thus, by implication, conditions in them should deteriorate owing to the accumulation of old nest material. Indeed, Perrins (1979) stated that “. . . the nest material would slowly decompose within the chamber and presumably over a series of years the site might become filled with old nests.” I have tried to find support for this statement in the literature, but so far I have failed to find any information on this issue. Therefore, it seems that the information presented below, which indicates that old nest material disappears rapidly from natural cavities, constitutes the first data on this subject.

Study Area and Methods.—Data were gathered from 1992 to 1998 in the Białowieża National Park in eastern Poland, within which the last surviving fragments of European primeval lowland temperate forest are preserved. The tree stands of the park have never been cut, and the entire area has been strictly protected as a reserve since 1921. Hence, one can still observe cavities and cavity nesters in conditions free of direct anthropogenic disturbance. The forest consists of several types of old-growth stands (see Tomiałojć and Wesołowski 1990, Tomiałojć 1991, Wesołowski and Tomiałojć 1995), but most of the data were gathered in two types of chiefly deciduous stands. One was a stand of riparian trees composed mostly of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and Norway spruce (*Picea excelsa*); the other was a stand of upland deciduous forest composed of more than 12 species of trees, mainly hornbeam (*Carpinus betulus*), small-leaved linden (*Tilia cordata*), con-

tinental maple (*Acer platanoides*), pedunculate oak (*Quercus robur*), and spruce.

Since 1992, all cavities used by breeding birds within four large study plots (33 to 55 ha each; see Wesołowski 1998) and accessible from a ladder (up to 5 m above ground, in living trees) were marked and checked the following year (in the second half of April) to see whether old nest material was still present. For checking cavity contents, I used a small light bulb on a flexible wire and a small mirror.

The April inspections showed that cavities from previous years could be impossible for birds to use for several reasons (e.g. flooding, or being filled with rotten wood up to the cavity entrance). I have omitted these instances from the present analysis because they are irrelevant to the question at hand. If the cavity contained remnants of old material (e.g. moss and hair), it was classified as an “old nest.” If the cavity contained new material (e.g. fresh pieces of moss), it was classified as a “new nest” (the timing of the cavity inspections coincided with the nest-building phase of earliest breeding species in the study area; Wesołowski and Stawarczyk 1991, Wesołowski 1998). When a cavity contained no nest material and the bottom was covered with decayed material and rotten wood, or occasionally with a single fragment of leaf or piece of moss, it was classified as containing “no nest.”

Because the type of nest material could have influenced the rate of nest disappearance, I divided nests into two categories: (1) “tit” nests, which were constructed mostly of moss, wool, hair, or feathers and were made by *Parus major*, *P. caeruleus*, *P. palustris*, *P. ater*, and *Certhia familiaris*; and (2) “flycatcher” nests, which were composed mostly of dry leaves and other plant material and were made by *Ficedula albicollis*, *F. hypoleuca*, and *Erithacus rubecula*.

Results and Discussion.—No trace of the previous year’s nest was visible in two-thirds of the cavities (Table 1), nor did cavities with new nests (ca. 20%) contain remains from the previous year’s nest. As a rule, new nests were in the initial stages of construction, so any remains of old material would have been apparent. I found remnants of old nest material in

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TABLE 1. Contents of natural cavities in the second half of April in relation to the type of nest in the previous breeding season. Data are the number of cavities.

Previous nest	Cavity contents			Total
	Old nest (%) ^a	New nest (%) ^b	No nest (%)	
Tit ^c	5 (6.0)	19 (22.9)	59 (71.1)	83
Flycatcher ^d	24 (20.5)	20 (17.1)	73 (62.4)	117
Total	29 (14.5)	39 (19.5)	132 (66.0)	200

^a Remnants of old material still visible (e.g. moss and hair).

^b New material present (e.g. fresh pieces of moss).

^c Moss, wool, and hair or feathers; made by *Parus major*, *P. caeruleus*, *P. palustris*, *P. ater*, and *Certhia familiaris*.

^d Mostly dry leaves and other plant material; made by *Ficedula albicollis*, *F. hypoleuca*, and *Erithacus rubecula*.

only 6% of the cavities that originally had contained "tit" nests and in 20% of those that had contained "flycatcher" nests (Table 1). "Tit" nests vanished significantly more frequently from one year to the next than did "flycatcher" nests ($\chi^2 = 8.4$, $df = 2$, $P < 0.02$); consequently, dry leaves appeared to be more resistant to loss than did moss or substances of animal origin (see Table 1).

Causes of the disappearance of nest material are unknown. Nest material could have been removed by a non-human animal, or it could have decomposed *in situ*. In cavities that contained new nests, the remains could have been removed by the birds themselves; e.g. I commonly observed tits remove debris from nest cavities (Wesołowski 1998, 1999). Nest boxes in the managed part of the Białowieża Forest often contained nearly intact nests from the previous season. It is difficult to envisage why old material would be selectively removed from natural cavities but not from nest boxes. Therefore, I propose the alternative explanation that conditions in the cavities themselves, i.e. a favorable microclimate and a rich assemblage of decomposing organisms, result in high decay rates of old nest material.

Apart from cavities that were used for breeding in two consecutive years, numerous suitable but unused cavities were available in the study area (Wesołowski 1989, Walankiewicz 1991). Consequently, birds that were prospecting for new nest sites would have found traces of old material in cavities less frequently than the present data indicate, perhaps in less than 1 of 10 cavities.

Rates of disappearance of old material were similar in all study plots ($\chi^2 = 0.74$, $df = 3$, $P = 0.86$) and did not vary substantially among years ($\chi^2 = 3.37$, $df = 4$, $P = 0.49$). Given that the species concerned accounted for more than 80% by number of all secondary cavity nesters in the Białowieża Forest (Tomiałojć and Wesołowski 1990, 1996; Wesołowski and Tomiałojć 1997), my results are likely to be representative for the situation in this primaeval forest. However, it

is not known whether the rapid disappearance of old material is typical of most natural cavities, or whether it is only a local phenomenon. Nevertheless, my data indicate that contrary to the suggestions of Perrins (1979) and Møller (1989), it is the accumulation of old nest material, rather than the removal of such material, that distinguishes nest boxes from natural cavities.

The removal of old nests from boxes can reduce the load of ectoparasites whose survival depends on nest material (Rendell and Verbeek 1996). Whether parasite numbers would decline if nest material disappeared from decay is unknown. Clearly, additional information is needed on the relationship between parasite loads and the presence of old nest material in natural cavities.

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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 eeries that contained young. Nestlings were individually marked with a Danish Zoological Museum num-

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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 $1.3 \pm \text{SE of } 0.3$ 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-

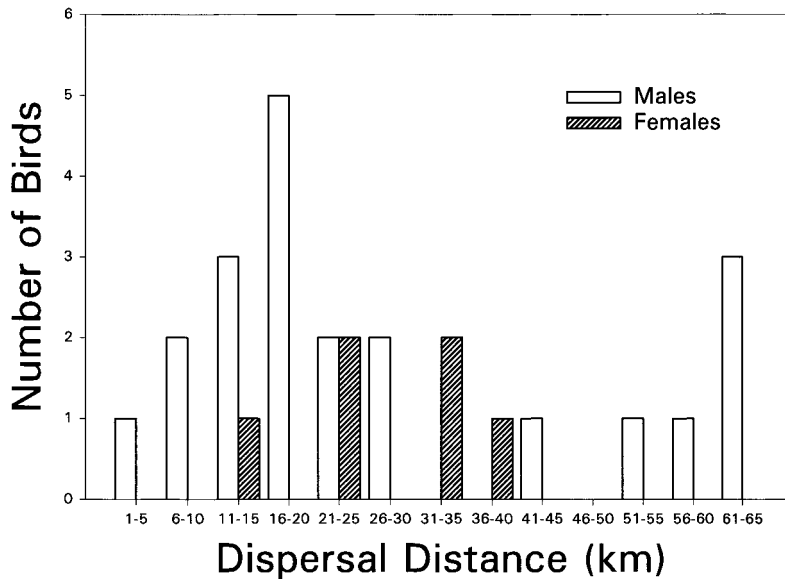


FIG. 1. Natal dispersal distance of Peregrine Falcons produced and recruited in the study area in western Greenland.

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values of Avian Blood: Implications for Trophic Studies

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The use of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) 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 ^{15}N (up to 4‰) and ^{13}C (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 ^{13}C 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 ^{15}N enrichment occurs is largely due to the excretion of isotopically light nitrogen (^{14}N) 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 ^{15}N . 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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In this paper, we compare the isotope signatures measured in whole blood of Great Skua (*Catharacta skua*) adults and chicks (more than 28 days old) with those of the same samples after they have been subjected to an aggressive lipid and uric acid/urea extraction technique. As top predators in many marine ecosystems, seabirds frequently have been used in isotopic studies (Hobson 1987, 1990; Hobson et al. 1994; Thompson and Furness 1995). Seabirds tend to share a number of life-history characteristics, so the Great Skua should be a good model for seabirds in general. Moreover, because elevated levels of uric acid have been reported in the blood of chicks from a wide range of taxa (including pelecaniforms [Wolf et al. 1985], ciconiiforms [Alfonso et al. 1991], and galliforms [Featherston 1969]), it might be expected that this phenomenon would apply to a great many species.

Methods.—Great Skuas were sampled on Foula, Shetland (60°08'N, 2°05'W), during summer 1996 and on St. Kilda, Western Isles (57°49'N, 8°35'W), during summer 1997. Blood was collected from the tarsal vein using a 23-gauge needle and transferred to a glass vial, where it was stored frozen until analysis. Prior to analysis, samples of whole blood were freeze dried and powdered. Part of each dried sample was subjected to a standard technique for the extraction of lipids using a soxhlet apparatus with refluxing chloroform for 4 to 6 h. Unfortunately, the samples were not weighed.

All $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses were carried out by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Europa Anca 20-20 C/N/S apparatus. Samples were loaded into miniature tin cups (4 × 6 mm) for combustion. A typical run consisted of a reference sample, duplicate analyses of two standards (internal laboratory carbon standard and IAEA-N-2), and then 8 to 10 samples. This sequence was repeated throughout the run, allowing a correction to be made for drift, if necessary. Isotope ratios are expressed in parts per thousand (‰) according to the following equation:

$$\delta X = \left[\left(\frac{r_{\text{sample}}}{r_{\text{standard}}} \right) - 1 \right] \times 1,000, \quad (1)$$

where X is ^{15}N or ^{13}C and r is the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. The r_{standard} for ^{13}C is Pee Dee belemnite and for ^{15}N is atmospheric nitrogen. Measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are precise and accurate to $\pm 0.2\text{‰}$ and $\pm 0.4\text{‰}$, respectively. To adjust for test-wise error, we applied a sequential Bonferroni adjustment for α ($\alpha = 0.006$ for 8 statistical tests).

Results.—The $\delta^{13}\text{C}$ signatures of blood from adult Great Skuas did not change significantly after washing in hot chloroform (before, $\bar{x} = -17.1 \pm \text{SD}$ of 0.6‰ , $n = 23$; after, $\bar{x} = -17.2 \pm 0.8\text{‰}$, $n = 23$; paired $t = 1.61$, $P = 0.122$). The same was true of $\delta^{15}\text{N}$ values in adult blood (before, $\bar{x} = 12.6 \pm 0.9\text{‰}$, $n = 21$; after,

$\bar{x} = 12.6 \pm 0.9\text{‰}$, $n = 21$; paired $t = 0.76$, $P = 0.94$). The $\delta^{13}\text{C}$ values of chick blood also remained unaffected by the treatment (before, $\bar{x} = -17.6 \pm 0.6\text{‰}$, $n = 30$; after, $\bar{x} = -17.7 \pm 0.9\text{‰}$, $n = 30$; paired $t = 0.43$, $P = 0.43$). However, the mean $\delta^{15}\text{N}$ value of chick blood increased significantly after treatment (before, $\bar{x} = 11.6 \pm 0.5\text{‰}$, $n = 30$; after, $\bar{x} = 12.8 \pm 0.7\text{‰}$, $n = 30$; paired $t = 11.5$, $P < 0.001$). Before extraction with hot chloroform, the mean $\delta^{13}\text{C}$ value of adult whole blood was lower than that of chicks ($t = 2.9$, $\text{df} = 51$, $P = 0.005$), as was the mean $\delta^{15}\text{N}$ value ($t = 4.3$, $\text{df} = 29$, $P < 0.001$). However, after treatment with hot chloroform, we detected no significant differences between blood from adults and chicks ($\delta^{13}\text{C}$, $t = 1.9$, $\text{df} = 51$, $P = 0.052$; $\delta^{15}\text{N}$, $t = 1.1$, $\text{df} = 49$, $P = 0.27$).

Discussion.—Given that other researchers have measured the ^{13}C content of lipid as being depleted relative to whole tissues (e.g. Tieszen et al. 1983), carbon-isotope ratios suggest that the lipid component of adult blood is so small that it does not significantly affect the whole-tissue isotope signatures. These findings are supported by studies that determined that the lipid component of avian blood is less than 1% of the total wet mass (e.g. Wolf et al. 1985, Rosa et al. 1993, Sartori et al. 1995); hence, it is unlikely to be of sufficient magnitude to influence the overall $\delta^{13}\text{C}$ value. The pattern for skua chicks appears to be similar, which is somewhat surprising because young birds tend to have larger stores of lipid than adults (see Blem 1990), and one might have expected to detect a similar pattern in blood. However, even if lipid levels in chick blood were much higher than those in adult blood, they would still comprise only a small proportion of the whole tissue and as such would probably not be substantial enough to affect the $\delta^{13}\text{C}$ ratio significantly.

The results for ^{15}N were different than those for ^{13}C . After washing in hot chloroform, $\delta^{15}\text{N}$ values in chick blood were significantly higher than those of whole tissue, whereas no such difference was detected in adult blood. Moreover, after the aggressive extraction procedure, the mean $\delta^{15}\text{N}$ signature of chick blood did not differ significantly from that of adult blood. These observations suggest that washing whole blood with hot chloroform results in the removal of isotopically light nitrogenous compounds, which are present in high concentrations in chick blood but in low amounts in adult blood.

Excreted nitrogenous compounds, such as urea and uric acid, are isotopically depleted in ^{15}N (Peteresen and Fry 1987). Assessment of plasma concentrations of these components in adults and chicks of the White Stork (*Ciconia ciconia*) yielded higher overall concentrations in chicks (Alfonso et al. 1991). Furthermore, in Brown Pelicans (*Pelecanus occidentalis*) and domestic fowl (*Gallus gallus*), large chicks tend to have elevated levels of uric acid in blood due to their large daily food intake (Featherston 1969, Wolf

et al. 1985). Uric acid is the end product of protein catabolism and is produced mostly in the kidney and liver, and the serum concentration of uric acid is employed as an indicator of rates of protein catabolism (Stevens 1996). Rates of protein turnover are substantially higher during growth periods, with muscle protein turnover of 30% per day in chicks versus 5% per day in adults (Swick 1982).

We suggest that the aggressive extraction technique using refluxing hot chloroform removes uric acid from whole blood. The solubility of uric acid in chloroform increases substantially with temperature from ca. 0.11 mM at 25°C to more than 0.25 at 50°C (M. Teece unpubl. data). Furthermore, in a study of mono- and dimethyl uric acids in incubation media, a mixture of chloroform and 2-propanol (85:15 v/v) was used to extract the compounds of interest (Benchekroun et al. 1990). Because uric acid is assumed to be isotopically light (Petersen and Fry 1987) and is present in substantially higher concentrations in chicks than in adults (Alfonso et al. 1991), removal of this compound during the extraction procedure would account for the observed results.

Our results indicate that there is no need to extract lipids prior to isotopic analysis of avian blood. However, if protein turnover in the individuals being studied is thought to be high, then the possibility of elevated uric acid levels should be considered, particularly when comparing the diets of adults and young. It is worth noting that adult birds also can experience periods of high protein turnover, for example during rapid molt or egg formation (Blem 1990), at which time they also may have high levels of uric acid in their blood. Therefore, the influence of elevated concentrations of nitrogenous waste on the $\delta^{15}\text{N}$ of blood must be considered when assessing trophic status based solely on the measurement of bulk tissue.

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Dive Depth and Diet of the Black-vented Shearwater (*Puffinus opisthomelas*)

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In general, procellariiforms have been considered to be surface and shallow-dive foragers (Brooke 1990, Warham 1990). This view has persisted despite Kuroda's (1954) demonstration that Short-tailed Shearwaters (*Puffinus tenuirostris*) and Sooty Shearwaters (*P. griseus*) have streamlined tarsi and a narrow pelvis that should make them more proficient divers than some other procellariiforms. Weimerskirch and Sagar (1996) deployed maximum depth gauges and found that Sooty Shearwaters dive to 67 m. These depths are surprising for such a proficient flier. Weimerskirch and Sagar's data corroborate Kuroda's predictions from his morphological data and challenge previous assumptions about shearwater foraging ecology. However, it is difficult to determine whether diving is widespread in shearwaters because no studies have been published on the diving capabilities of species other than the Sooty Shearwater. Here, we examine maximum dive depths and diet of the Black-vented Shearwater (*Puffinus opisthomelas*).

The Black-vented Shearwater is endemic to islands off the Pacific coast of Mexico and is the only shearwater that breeds on islands in the California Current (Everett 1988). Anecdotal observations of this species began at the turn of the century (Anthony 1896), but only recently have detailed studies been conducted on the biology of this species (Keitt 1998). Natividad Island, Baja California, Mexico, with a breeding population of about 150,000 pairs, supports most of the world population. The Black-vented Shearwater is a summer breeder with a four-month reproductive cycle that is very similar to that of the well-studied Manx Shearwater (*Puffinus puffinus*; Harris 1965, Perrins et al. 1973, Brooke 1990). At-sea observations indicate that the Black-vented Shearwater, unlike many other procellariiforms, is a near-shore forager that does not regularly make extended pelagic foraging trips (Ainley 1976).

Methods.—Maximum depth gauges (MDG) were deployed at Natividad Island between 13 May and 30 June 1998. The MDGs were constructed similar to those described in Croll et al. (1992). Briefly, lengths of Tygon tubing (15 to 18 cm) were lined with a soluble indicator (confectioner's sugar), and one end was securely tied to allow water entry only at the

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open end. Following Boyle's law, when the MDG is submerged, water enters the open end of the tube and dissolves the confectioner's sugar to a length proportional to the maximum pressure encountered, providing a measure of the maximum depth of the dive (see Falk et al. 2000).

Breeding adults were captured at their nest burrows, marked with United States Fish and Wildlife Service leg bands, and fitted with a depth recorder attached to the contour feathers between the scapulars with a cable tie. The mass of the tube and tie was approximately 2 g (<0.6% of body mass). Depth recorders were recovered after one foraging trip (24 to 120 h after deployment), and the length of Tygon tubing with undissolved confectioner's sugar (L_d) and the total length of the tube (L_s) were measured to the nearest millimeter. Maximum depth attained during the foraging trip (D_{max} , in meters) was calculated as:

$$D_{max} = 10.08 (L_s/L_d - 1), \quad (1)$$

where 10.08 is a constant in meters reflecting atmospheric pressure at sea level (Burger and Wilson 1988).

We recovered 11 depth gauges during incubation and 19 during the chick-rearing stage. We obtained multiple measurements of maximum dive depth from 10 birds. Because a comparison of all maximum dive depths and dives recorded from the same birds showed the pooled variances to be similar (103.5 and 104, respectively), we treated each dive depth as an independent measurement.

We collected 20 regurgitation samples opportunistically from adult Black-vented Shearwaters during the chick-rearing period in 1997 and 1998. The birds regurgitate when handled, and samples were collected from birds caught at the colony for banding and morphological measurements. We assumed that most samples came from adults that were preparing to feed chicks, but we do not know for certain whether the birds were breeders or nonbreeders. Samples were weighed, preserved in 10% formalin, and stored in alcohol. In addition, gizzards from seven shearwaters that were killed by house cats were collected from April to June 1998. These were stored in alcohol and the contents inspected in the lab.

Regurgitation samples were sieved and all hard parts saved. Fish vertebrae were identified by comparison with known specimens by Tom Wake, Director of the Zooarchaeology Laboratory, Institute of Archaeology, University of California at Los Angeles. Contents of the gizzards were separated into otoliths and squid beaks. Otoliths were sent to Mark Lowry at the Southwest Fisheries Science Center for identification. Eric Hochberg from the Santa Barbara Museum of Natural History identified the squid beaks.

We estimated the length (mm) and wet mass (g) for the largest squid in our sample using the allometric

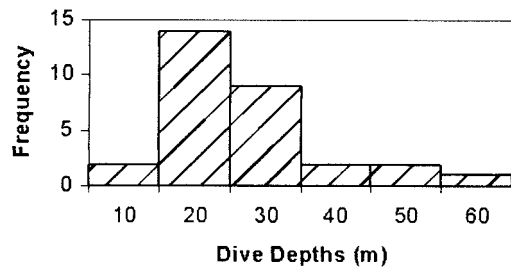


FIG. 1. Frequency distribution of maximum dive depths ($n = 30$) by Black-vented Shearwaters on Natividad Island, Mexico.

equations from Clarke (1986) for mastigoteuthid squids:

$$\ln(\text{wet mass}) = 0.184 + 2.88 \times \ln(\text{lower rostral length}), \quad (2)$$

and

$$\text{mantle length} = -1.8 + 29.08 \times \text{lower rostral length}. \quad (3)$$

Results.—We recovered 30 depth gauges from 18 shearwaters; eight birds were sampled once, nine twice, and one four times. MDGs were deployed for a mean of $3.4 \pm \text{SD of } 1.9$ days ($n = 30$). The mean maximum dive depth was 21 ± 11 m ($n = 30$), and the shallowest and deepest maximum dives recorded were 8 m and 52 m, respectively. The distribution of the 30 maximum depths showed that most of the dives were much shallower than the maximum dive potential for the species (Fig. 1). Dive depth and duration of MDG deployment were not significantly correlated ($r_s = 0.04$, $P = 0.82$). Birds dived deeper during the chick-provisioning period ($\bar{x} = 24.3 \pm 12.3$ m, $n = 19$) than during incubation ($\bar{x} = 16.3 \pm 4.2$ m, $n = 11$; Behrens-Fisher $t = 0.23$, $df = 18$, $P = 0.02$; Fig. 2).

Gizzard samples revealed that Black-vented Shearwaters fed on mastigoteuthid squid and northern anchovies (*Engraulis mordax*). Of the seven gizzards collected, three (43%) were empty and four (57%) contained squid beaks. Two of these latter four also contained fish otoliths. Most of the materials were unidentifiable fragments of squid beaks. Three of the gizzards contained a squid species in the Mastigoteuthidae. A fourth gizzard contained two identifiable specimens of *Mastigoteuthis pyrodes*, which is another species of mastigoteuthid. We calculated the wet mass of the squid with the largest intact beak to be 1.6 g and the length to be 30 mm. Additional beaks in this gizzard were too small to identify. We found nine otoliths from at least five northern anchovies in two gizzards.

We were able to weigh 9 of the 20 regurgitation

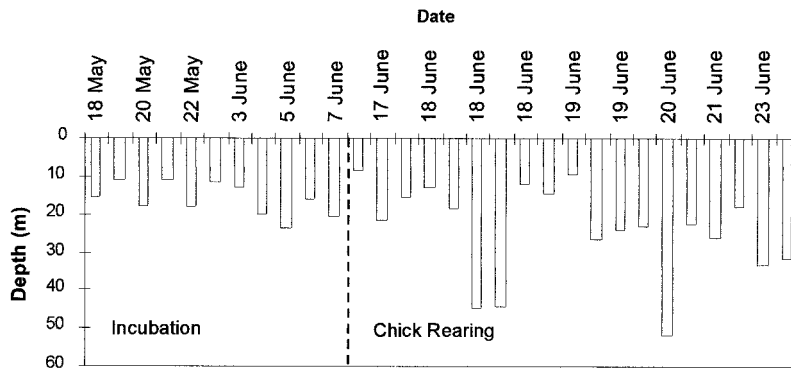


FIG. 2. Changes in maximum dive depths by Black-vented Shearwaters during the breeding season on Natividad Island, Mexico.

samples collected in the 1997 and 1998 breeding seasons ($\bar{x} = 43 \pm 16.4$ g). Twelve (60%) of the 20 samples contained almost no hard parts to aid in identification of the contents. Eight (40%) samples contained partially digested fish without heads, and six contained northern anchovies with estimated total lengths of 6 to 10 cm. Two samples contained Pacific sardines (*Sardinops sagax*) with estimated total lengths of 8 to 10 cm. One of the samples contained vertebrae from a chub mackerel (*Scomber japonicus*).

Discussion.—The first application of MDGs on procellariids revealed that Sooty Shearwaters reached depths of 67 m (Weimerskirch and Sagar 1996). Our data on maximum dive depths of Black-vented Shearwaters, a species with very different ecology than the Sooty Shearwater, further supports the morphological evidence provided by Kuroda (1954) that shearwaters are accomplished divers.

Some seabirds have much more specialized diving morphology than shearwaters. Using the allometric equation for maximum dive depth for penguins and alcids (Burger 1991; $D_{\max} = 75.905 M^{0.316}$, where M is the mass of the bird in kg), a 406-g bird like the Black-vented Shearwater would be expected to dive to 57 m. This is remarkably similar to the observed maximum dive depth of 52 m in our study, a surprising result considering that shearwaters do not share the same specialized diving morphology of alcids and penguins. A Sooty Shearwater, at 850 g, would be expected to dive to 72 m, again very close to the maximum observed depth of 67 m for this species (Weimerskirch and Sagar 1996).

It is possible that Black-vented Shearwaters maximize their diving capability by minimizing wing-surface area through molting, as proposed for Common Murres (*Uria aalge*; Croll 1990, Thompson 1998). Decreased wing-surface area results in increased wing loading and decreased flight efficiency. Unlike most species of procellariiforms, which molt outside of the breeding season (Warham 1996), Black-vented Shearwaters begin primary molt when their chicks

hatch, and they continue to molt throughout the chick-rearing period (B. Keitt unpubl. data). Because the colony on Natividad Island is located close to a productive upwelling center at Punta Eugenia (Huyer 1983), Black-vented Shearwaters, which are known to forage near the coast (Ainley 1976), may encounter relatively high prey abundance close to the breeding colony (Tyler et al. 1993). Thus, unlike Sooty Shearwaters, which travel 1,500 to 2,000 km to forage during the chick-rearing period (Weimerskirch et al. 1994), Black-vented Shearwaters may have less need for efficient flight when foraging. Although primary molt may decrease flight efficiency, it is also likely to increase diving efficiency by decreasing wing drag. Thompson et al. (1998) examined remigial molt in Common Murres and suggested that primary molt in the larger alcids "reduces their wing-surface area to a size that is probably close to the optimal for underwater flight." The timing of molt in Black-vented Shearwaters also may serve to increase diving efficiency during the chick-provisioning period.

Northern anchovies and Pacific sardines were the main items found in the Black-vented Shearwater diet samples. The location of Natividad Island in an area of strong upwelling provides a highly productive foraging area within 30 km of shore (Huyer 1983, Tyler et al. 1993). Northern anchovies and Pacific sardines are the most common schooling fish in this region (Luch-Belda et al. 1989), and it is likely that Black-vented Shearwaters are feeding on prey items with the highest availability near the colony.

In conclusion, we found that Black-vented Shearwaters, like Sooty Shearwaters, are able to forage down to 50 m in the water column. This provides support for Kuroda's anatomical evidence for diving adaptations in shearwaters. Our limited data on diet are the only data available for this poorly studied species, and they show that Black-vented Shearwaters feed on locally abundant schooling fish and mesopelagic squid. We found distinct temporal

changes in maximum dive depths during the shearwater's breeding season. These may translate into temporal differences in prey consumption; however, we were not able to collect diet samples and diving data on the same birds at the same time. Further studies should examine these important factors simultaneously.

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