

## NATAL DISPERSAL AND PHILOPATRY OF SOUTHEASTERN AMERICAN KESTRELS IN FLORIDA

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**ABSTRACT.**—Sex-biased natal dispersal is common among many bird species, with females usually dispersing farthest. The relative dispersal distances of male and female American Kestrels (*Falco sparverius*) are unknown. We examined natal dispersal in Southeastern American Kestrels (*F. s. paulus*) in north-central Florida, observing birds marked as nestlings with either color bands or patagial tags. Natal dispersal distances of 34 kestrels ranged from 0.0 to 38.8 km. Mean natal dispersal distance of females (8.6 km) did not differ significantly from that of males (8.3 km) ( $P = 0.43$ ). We determined that no relationship existed for either sex between dispersal distance and subsequent reproductive success. However, the relationship between hatching date and dispersal distance was marginally significant ( $P = 0.071$ ); fledglings from earlier nests were more likely to breed close to their natal area than were those from late-season nests. Our results suggest that natal dispersal and site fidelity in Southeastern American Kestrels are determined, at least in part, by inter- and intra-sexual competition for breeding sites. Received 28 June 1996, accepted 11 Dec. 1996.

Sex-biased dispersal is common among many bird species, with females usually the sex which disperses farthest (Greenwood 1980). Females may disperse farther than males as a result of a resource-defense system, whereby males typically defend breeding territories and females choose among many males (Greenwood 1980, Greenwood and Harvey 1982, Pusey 1987). The resource-defense hypothesis assumes that males settle close to their natal area because prior familiarity with the area facilitates the establishment of territories. Social constraints may dictate that males continue to exhibit fidelity to breeding sites because of the importance of familiarity with their neighbors in establishing and defending territories (Payne and Payne 1993).

The relative dispersal distances of male and female American Kestrels (*Falco sparverius*) are unknown. However, given the fact that the male of the species establishes and defends the breeding territory (Balgooyen 1976), we might expect that dispersal would be female-biased. In migratory populations of American Kestrels (*F. s. sparverius*), males return to the breeding ground earlier than females (Bird and Palmer 1988), allowing them the opportunity to establish territories before females return. If females benefit from the opportunity to choose among many males and

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the resources they provide (e.g., through courtship feeding; Balgooyen 1976), we would then expect females to exhibit greater natal dispersal than males.

More studies are needed to examine the asymmetries in cost-benefits of dispersal in birds. Pusey (1987) suggested that by measuring breeding success of males and females at different distances from the natal area, hypotheses about the costs and benefits of natal dispersal could be tested.

We examined natal dispersal in nonmigratory Southeastern American Kestrels (*F. s. paulus*) in north-central Florida. The southeastern race, resident in Florida, has declined and is listed as threatened in Florida (Hoffman and Collopy 1988, Collopy 1996). We hypothesized that (1) natal dispersal distances would be greater for females than for males and that (2) female dispersal distance would be positively correlated with subsequent breeding success, whereas male dispersal distance would be negatively correlated with subsequent breeding success.

#### STUDY AREA AND METHODS

Nest boxes ( $N = 347$ ) were erected in north-central Florida in 1990 and 1991 as part of a population study (Smallwood and Collopy 1993). The study site was approximately 1200 km<sup>2</sup> in area and included portions of Alachua, Levy, and Marion counties. Nest boxes were mounted on live trees and on Florida Power Corporation utility poles in proximity to suitable foraging habitat (open areas with grasses and weedy forbs <25 cm in height; Smallwood 1988). Most nest boxes were located in remnant longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) sandhills or in pastures and agricultural habitats. Kestrel populations in these habitats were low prior to the initiation of the study due to a decline in the availability of natural nest-sites (Hoffman and Collopy 1988). Nearest-neighbor distances between nest boxes ranged from 1 to 2 km in most areas, which reflected the typical spacing between territories reported for kestrel populations elsewhere in North America (Bird and Palmer 1988).

Nest boxes were monitored throughout the breeding season (late March through mid-July). Nests were visited two or more times during incubation to determine clutch size and expected hatching date, and again before fledging to band the young. Each nestling surviving to banding age (14–24 days) was banded with a single U.S. National Biological Service aluminum band on one tarsus and either a combination of two colored plastic bands on the other tarsus or a unique patagial tag on one wing. Not all color-banded chicks received unique band combinations. Color band combinations denoted range and township locations during 1991 and individual nest boxes in 1992. Beginning in 1992, individuals banded as chicks in 1991 were observed using nest box territories as adults. During each visit to nest boxes in 1992–94, we also recorded the location, sex, behavior, and color markings of any adults present. When a banded adult was encountered on a nest box territory, we made repeated visits to confirm its identity.

We defined natal dispersal as the movement of individuals to a potential breeding site irrespective of whether they reproduced after dispersal (i.e., as in gross dispersal, Greenwood 1980). Natal dispersal was measured as the straight-line distance between the nest box where the kestrel hatched and the nest box where it was observed the following breeding season. In the two instances where color markings observed were not unique to a specific natal site, the median distance to all possible natal sites was used for analyses. Locations of all nest

TABLE 1  
NATAL DISPERSAL DISTANCES (KM) OF MALE (N = 13) AND FEMALE (N = 21) COLOR-MARKED SOUTHEASTERN AMERICAN KESTRELS IN NORTHCENTRAL FLORIDA, 1992–1994

|           | Male        | Female      |
|-----------|-------------|-------------|
| Range     | 0.00–32.45  | 2.14–38.79  |
| Mean (SE) | 8.28 (2.58) | 8.60 (1.76) |
| Median    | 4.38        | 5.06        |

boxes were determined with a portable global positioning system (Trimble Navigation, Sunnyvale, California). Locations were recorded in latitude/longitude and then converted to Universal Transverse Mercator coordinates. Dispersal distance was then calculated as the straight-line distance (hypotenuse) between the two points. Dispersal data were not normally distributed; therefore, non-parametric statistical treatments were used for all tests of significance.

Marked adults were considered to have bred at a particular nest box if they were observed making territorial displays (vocalizing, perching near, or flying close to the observers) while eggs or chicks were present in the nest box. The relationships between hatching date, dispersal distance, and the number of young fledged in their first breeding attempt were tested with Spearman's correlations.

## RESULTS

Fifty color-marked adult kestrels, including 34 one-year-old birds, were observed on nest box territories during the breeding seasons of 1992–1994. Natal dispersal distances of the 34 kestrels ranged from 0.0 km (a male that inherited his father's breeding territory as a yearling) to 38.8 km (Table 1). Most (71%) individuals dispersed <8 km (median distance = 4.9 km), while only a few dispersed much greater distances.

The distribution of male dispersal distances was similar to that of females (Fig. 1). Mean natal dispersal distance of males (8.3 km) did not differ significantly from that of females (8.6 km) (Wilcoxon rank-sum test,  $Z = -0.797$ ,  $P = 0.43$ ). When data were pooled into near (0–8 km) and far (>8 km) categories, no significant difference was detected between sex and distance (Fisher's exact test,  $P = 0.70$ ).

Egg-laying was confirmed for 28 (82%) of 34 one-year-old kestrels. The number of fledged young at these nests ranged from none to five and was not correlated significantly with natal dispersal distance for either males ( $r_s = 0.062$ ,  $P = 0.88$ ) or females ( $r_s = -0.049$ ,  $P = 0.84$ ). When data for both sexes were combined, the relationship between an individual's hatching date and its subsequent dispersal distance approached statistical significance ( $r_s = 0.323$ ,  $P = 0.071$ ).

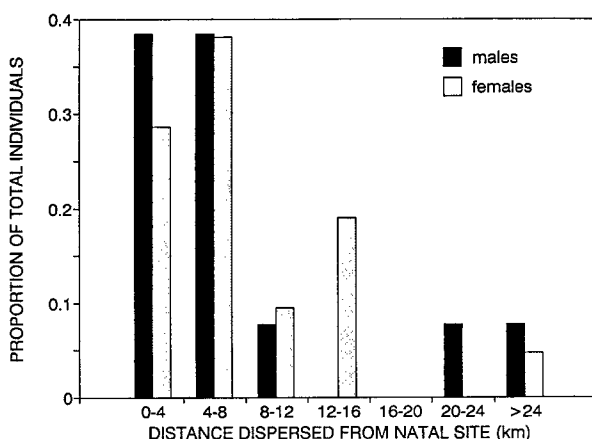


FIG. 1. Distribution of natal dispersal distances for Southeastern American Kestrels (N = 13 males and 21 females).

#### DISCUSSION

American Kestrels exhibited a skewed dispersal pattern, with most individuals dispersing relatively short distances, and a few dispersing much greater distances. A similar pattern has been reported for other raptor species, including Eurasian Sparrowhawks (*Accipiter nisus*) (Newton and Marquiss 1983, Newton 1986), Ospreys (*Pandion haliaetus*) (Doig 1989, Johnson and Melquist 1991), Eastern Screech-Owls (*Otus asio*) (Belthoff and Ritchison 1989), and Great Horned Owls (*Bubo virginianus*) (Adamcik and Keith 1978).

Despite dispersing relatively short distances, most kestrels bred outside their natal home range. American Kestrel breeding territories are typically small (e.g., 0.24 km<sup>2</sup>, Bowman et al. 1987; 0.82 km<sup>2</sup>, Smith et al. 1972), with a diameter of usually no more than 1.0–2.5 km (Bird and Palmer 1988). Although we did not measure individual territory size in the present study, it is likely that nearly all individuals dispersed outside their natal home range (94% dispersed  $\geq 3$  km). One notable exception was a yearling male kestrel that successfully bred in the same nest box from which it fledged. It is not known whether he bred with his mother or an unrelated adult female because the adult female at the site was not color-marked. However, close inbreeding in kestrels has been recorded in a banding study in Canada, where a father-daughter pair bred and raised young successfully (D. Bird, pers. comm.).

We did not observe sex-biased natal dispersal. Much of the evidence for female-biased dispersal in raptors is from regional studies of eagles

or Ospreys. For example, in a study of Ospreys along the New England coast, Spitzer et al. (1983) found that 64% of females and 27% of males dispersed  $\geq 10$  km from their natal site; the maximum movement of females was 520 km in contrast to only 37 km for males. Comparisons of male and female dispersal distances in such a wide-ranging species would be biased if such a study were conducted in a restricted geographical area because the long distance movements of females would go undetected. However, it is unlikely that the spatial constraints of our study biased our comparison of male and female natal dispersal distances in kestrels because nest boxes were 1–2 km apart and the diameter of our study area was 30–50 km. Moreover, female-biased natal dispersal has been documented for raptors in study areas much smaller than ours, including a 36-km<sup>2</sup> study of Burrowing Owls (*Athene cunicularia*) (Millsap and Bear 1993) and a 122-km<sup>2</sup> study of Merlins (*Falco columbarius*) (James et al. 1987, but see James et al. 1989).

We determined that no significant relationship existed between dispersal distance and the subsequent number of young fledged. If we regard the number of offspring reared as an index of fitness, then our findings suggest no direct relationship between fitness and dispersal distance. The relationship between hatching date and dispersal distance approached statistical significance ( $P = 0.071$ ), lending more support to the alternative hypothesis that dispersal distance is a function of competition for available breeding sites. Waser (1985) suggested that early dispersers may settle closer to their natal territories because they are able to choose the closest vacant territories, whereas late dispersers must move farther away to find suitable sites. Village (1990) found late broods of Eurasian Kestrels (*Falco tinnunculus*) dispersed farther than earlier broods and were more likely to have reduced winter survival. He posited that juveniles move away from the nest until they locate a vacant territory where they are not driven away by adults or other juveniles. In contrast, there was no correlation between hatching date and dispersal distance in Eurasian Sparrowhawks (Newton and Marquiss 1983) or Boreal Owls (*Aegolius funereus*) (Korpimäki and Lagerström 1988), and no correlation between dispersal date and dispersal distance in Eastern Screech-Owls (Belthoff and Ritchison 1989). However, Eurasian Sparrowhawks that dispersed farthest from their natal site subsequently bred in poorer habitat, initiated nesting later in the season, and produced smaller clutches (Newton and Marquiss 1983), a result consistent with the hypothesis that subordinate or less competitive individuals are forced to move away from the natal area.

Shields (1982) defined philopatry as returning to an area within 10 home ranges of the natal site. Given this definition, philopatry of Amer-

ican Kestrels in our study area is probably quite high (71% if home range diameters are 1.0 km, 94% if home range diameters are 2.5 km). Similarly, in a Wisconsin study area supplemented with nest boxes, seven of 10 kestrels recaptured or recovered in subsequent breeding seasons were encountered within 35 km of their natal area (Jacobs 1995). Data from long-term banding projects in Canada suggest that migratory American Kestrels are "loosely philopatric," with most individuals returning to the same general area but rarely to the same nest site (Bowman et al. 1987). Our data show philopatry may be stronger for resident Southeastern American Kestrels in Florida. It is possible that the availability of nest boxes throughout the study area decreased the modal dispersal distance.

Our data also suggest that competition for nest sites may be more important than sex in determining the extent of natal dispersal in this population. Fledglings from late nests may be forced to disperse farther from their natal area than fledglings from early nests, regardless of sex. However, the timing of dispersal events in this nonmigratory population is not precisely known. More information on the seasonal timing of natal dispersal may further substantiate the relationship between hatching date, dispersal date, natal dispersal distance, and philopatry.

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