Sex-related Differences in Habitat Use in Wintering American Kestrels

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ABSTRACT.—We investigated sex-related differences in habitat use in wintering American Kestrels (*Falco sparverius*) at two scales: within a 10 m radius and within a 100 m radius of perch sites. Female kestrels used areas containing a higher percentage of short vegetation (<0.25 m high) suitable for foraging than did males at both scales (100 m radius females 80%, males 69%; 10 m radius females 80%, males 73%). At both scales, females had more pasture (a high-quality foraging substrate) available than did males; areas within a 100 m radius of male perch sites contained more woodlot than did female perch sites. Logistic regression models indicated greater overlap between male and female habitat use on a 10 m radius scale than on a 100 m radius scale, suggesting that males may preferentially select smaller areas devoid of woody vegetation relative to what is available within 100 m radius of perch sites. Our results suggest that males may be constrained to winter in areas with lower overall foraging opportunities and possibly higher predation risk than areas used by females. Our work supports the hypothesis that males and female kestrels prefer open areas as wintering habitat.

Sex-related differences in habitat use occur in many taxa. Such differences can occur by competitive exclusion (Grubb and Woodrey 1990, Marra and Holberton 1998) or by each sex maintaining separate habitat preferences that result from sex-specific selection pressures (Power 1980, Masman et al. 1988, Bleich et al. 1997). American Kestrels (*Falco sparverius*) show geographic variation in both winter sex ratio and sex-related habitat use (Smallwood 1988, Arnold 1991). Females often are observed in open areas devoid of woody vegetation, whereas males often are observed in semiopen areas that contain some woody vegetation (Koplin 1973, Mills 1975, Smallwood 1987). Open areas used by female kestrels contain a larger proportion of short vegetation suitable for hunting than do semiopen areas used by males, leading some researchers to suggest that open areas are higher in quality to both sexes than are the semiopen areas often used by male kestrels (Mills 1976,

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Smallwood 1988). Other researchers contend that sexual habitat segregation is not caused by exclusion but by the maintenance of separate habitat preferences because of higher relative survival and body condition in the habitats where each sex is observed (Koplin 1973, Meyer and Balgooyen 1987).

Experimental and observational studies support the hypothesis that males and females both prefer open areas in the nonbreeding season. In a previous study, we experimentally removed wintering kestrels and observed that both males and females use vacated open areas (Ardia and Bildstein 1997). Sex-related differences in habitat use have been reported only in the southern part of the wintering range (below the $-7°C$ minimum winter temperature line, approximately 39°50′N latitude; Root 1988) where wintering densities are high (Root 1988), and presumably, competition for preferred sites is also high. Arnold and Martin (1991), working in Ontario (latitude 43°19′N), observed no differences in habitat use between males and females and hypothesized that low wintering densities (0.13 kestrels·km^{-1}) reduced competition for open areas.

The goal of this study was to test the hypothesis that American Kestrels exhibit sex-related differences in habitat use at an intermediate latitude site (latitude 40°55′N) in southeastern Pennsylvania. Our study site is just north of the $-7°C$ minimum winter temperature line (minimum temperature $-8°C$, National Climatic Data Center 1994, 1995) and has a low density of kestrels, 0.14 kestrels·km^{-1} (Ardia 1997). If Arnold and Martin (1991) are correct that low densities lead to minimal overlap in habitat use between males and females, we predicted that we would observe no sex-related differences in habitat use, or at minimum, that males would be found using more open areas than reported from locations with high densities of kestrels. If the converse is true, that males do maintain a preference for semiopen areas, then we would expect to find a clear difference in habitat use between males and females, with males using areas similar to those reported in other studies. As a further test of whether males use open areas, we predicted that if males do prefer open areas in which to forage, but have lower availability within their winter-use areas, then males might be more selective in their foraging locations relative to what is available around perches due to a lower proportion of suitable areas. To assess that possibility, we tested

TABLE 1.   Vegetation types recorded on 10 and 100 m radius plots centered on American Kestrel perches in southeastern Pennsylvania.

Vegetation type	Description
Low agricultural field	Cultivated field; crop stubble; height <0.25 m
Pasture	Grazed grassy vegetation; height <0.25 m
Fallow field	Unused agricultural field or pasture; height <0.25 m
Shoulder	Vegetation adjacent to road shoulder; height <0.25 m
Lawn	Mowed grass; height <0.25 m
Road	Pavement or gravel; no vegetation present
Building	Human structure
Woodlot	Woody vegetation; often with canopy; area >50 m²; height >2 m
Windbreak/orchard	Woody vegetation arrayed linearly; canopy no wider than 5 m; height >2 m
High agricultural field	Cultivated field; standing crop remains; height >2 m

the hypothesis that patterns of habitat use differ between males and females at different scales of measurement.

Methods.—We conducted this study in Berks and Lehigh counties, southeastern Pennsylvania (centered on 40°55′N, 75°75′W). The study area (~800 km²) is a patchwork of rolling hills and farmlands, which consists primarily of open agricultural land (pasture, corn, soybean, and alfalfa) separated by small woodlots and orchards. Between 70–100 pairs of American Kestrels nest in the area each year in nest boxes (Apanius 1991, Rohrbaugh and Yahner 1997). We designated winter as November–February because that is a period of limited migratory movement (Smallwood 1988).

We measured habitat use of wintering kestrels using an automobile strip-survey (Craighead and Craighead 1956) along 153 km of survey route on secondary roads. We traveled a total of 2,749 km (53 surveys) between November 1994 and February 1995. We drove at speeds of 15–30 km·h⁻¹ and used 8 × binoculars and a 15–45 × spotting scope to locate kestrels within 0.4 km of the road. We sexed kestrels by plumage. Prior to habitat data collection, we developed a visual estimation technique (Arnold and Martin 1991) by practicing visual estimation and measuring actual vegetation composition with a meter tape and grid mapping. That technique was accurate and repeatable (e.g. for suitable vegetation ±7.5% root mean squared error difference between estimates and actual measurements, for pasture 6.7%, for woodlot 5.4% N = 15; correct classification of vegetation height 29 of 30 attempts, 97% accuracy).

For data collection, we then visually estimated the percentage composition of each vegetation type within a 10 and 100 m radius of each initial sighting location (see Table 1 for vegetation classification). For birds first observed while perching, we recorded vegetation at the location when first observed; for hovering birds, we measured the area directly below the bird; and for flying birds, we waited until the bird landed and measured vegetation around the first perch. Flying birds that did not perch were not included in the analysis.

We chose 10 m radius circles (0.31 ha area) because we believed that size would reflect hunting opportunities surrounding the bird, and 100 m radius circles (3.14 ha area) because kestrel territories in that area are on average 3.3 ha in size (range 1.5–4.0, N = 20, size based on territory mapping; Ardia 1997). However, because we have no knowledge of the center of each bird's territory, this 100 m measure invariably includes some habitat not used for foraging. We did not differentiate between kestrels in hunting posture (head bobbing, scanning) and not in hunting posture because we have observed kestrels not in hunting posture make predation attempts and also frequent switching between postures.

Statistical comparisons were made among 28 female and 31 male color-banded solitary kestrels. We used average values for each individual (3–20 data points per individual, average 5.3 observations/individual). We compared male perch-site areas and female perch-site areas using logistic regression. Vegetation composition within 10 and 100 m radius areas was compared between males and females for each vegetation type and within two super-categories: vegetation suitable for foraging (≤0.25 m high) and vegetation unsuitable for foraging (>0.25 m high). We chose the height of 0.25 m because at our study site, 114 of 117 (97.5%) of foraging attempts were on vegetation ≤0.25 m high and because this height was used in other studies on kestrel non-breeding habitat use (Smallwood 1987, 1998; Arnold and Martin 1991). All tests were considered significant at $P < 0.05$.

Logistic regression is considered the most appropriate method to model the relationship between a binary response (i.e. male vs. female) and multiple explanatory variables (Press and Wilson 1978). To determine which habitat features were most important to differentiating male from female perch areas, we conducted stepwise logistic regression on habitat types using $\alpha = 0.10$ as entry and exit probabilities (PROC LOGISTIC, SAS Institute 1988). Because cor-

relation among variables was low ($\rho < 0.55$), we report results using habitat types, rather than principal components, to test our hypothesis. Concordance was based on success of classifying each observation as female. We tested the global hypothesis ($\chi^2 = 0$) of no covariate effect using likelihood ratio (-2 log likelihood). Individual parameter estimates were tested using a Wald χ^2 test. We present regression coefficients (β_i) for each significant variable to indicate direction and strength of response.

Results.—We recorded habitat data from 59 American Kestrel territories (28 female, 31 male). For both 10 and 100 m radius areas, we rejected the null hypothesis of no predictor effect of habitat variables (10 m radius: Wald $\chi^2 = 10.3$, df $= 1$, $P = 0.001$; 100 m radius: Wald $\chi^2 = 11.1$, df $= 1$, $P < 0.001$). Within both a 10 and 100 m radius of perch sites, female kestrels had more habitat suitable for foraging available (see above for definition of suitable habitat) than did male kestrels (10 m radius, 80% to 73%, $P < 0.05$ Fig. 1A; 100 m radius, 80% to 69%, $P < 0.05$; Fig. 1B).

Differences in amount of suitable vegetation available to males and females were due to differences in amounts of pasture and woodlot in male-use versus female-use areas (Fig. 1). Within a 10 m radius of perch sites, only percent composition of pasture discriminated between male-use versus female-use areas ($\beta_i = 0.03$, $\chi^2 = 10.3$, df $= 1$, $P < 0.01$). On a 100 m scale, the percentage composition of pasture and woodlot discriminated between male-use versus female-use areas (pasture $\beta_i = 0.05$, $\chi^2 = 8.2$, df $= 1$, $P < 0.01$; woodlot $\beta_i = -0.11$, $\chi^2 = 3.0$, df $= 1$, $P < 0.05$). For both scales, as percentage composition of pasture increased, probability increased that the bird observed was female. Conversely, within a 100 m radius of perch sites, as percentage composition of woodlot increased, probability that the occupant was female decreased. Woodlot, due to its larger β_i, exerted slightly more predictive influence than did pasture in determining whether each 100 m radius use area was used by a female or male; however, due to its larger area, pasture exerts more biological influence.

Patterns of sex-related habitat use differed between 10 and 100 m radius areas. Low concordance for both logistic models suggests substantial overlap in habitat use between males and females (100 m radius: concordance 78%, disconcordant 21%, tied 1%; 10 m radius: concordant 66%, disconcordant 23%, tied 11%). Males and females showed greater differentiation, and our logistic model was more successful in predicting the sex of each observation on a 100 m scale than on a 10 m scale, suggesting more similarity between male and female at smaller scales than larger.

Discussion.—This study provides support for the hypothesis that sex-related habitat segregation occurs even when American Kestrels occur at low winter population densities. We found that males and fe-
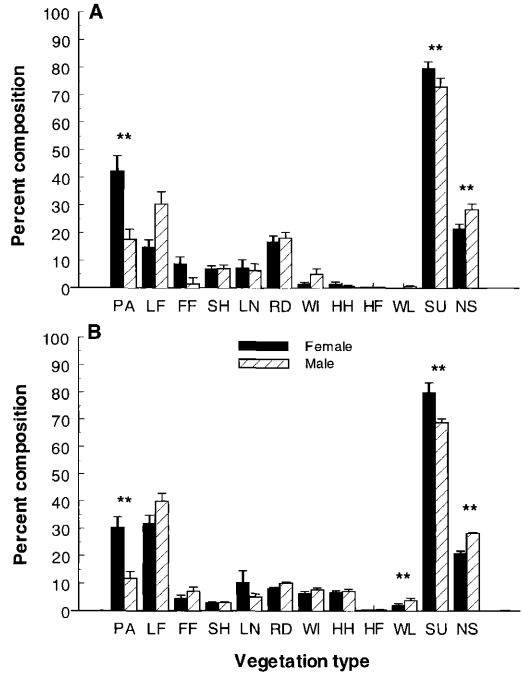

FIG 1. Habitat use of male and female American Kestrels wintering in southeastern Pennsylvania shown by individual vegetation type and supercategories around perch sites for a 10 m radius area (A) and 100 m radius area (B). Individual vegetation type: PA = pasture; LF = agricultural field <25 cm high; FF = fallow field, SH = roadside shoulder; LN = lawn; RD = roadway; WI = windbreak/orchard; HH = buildings; HF = agricultural vegetation > 25 cm high; WL = woodlot. Supercategories: SU = suitable for foraging; NS = nonsuitable for foraging. Female $N = 28$, Male $N = 31$. ** $= P < 0.05$. Data are means ±SE.

males differed in amount of vegetation suitable for foraging found within their use-areas, especially in the availability of pasture, a preferred vegetation type. Kestrels, regardless of sex, had higher prey-capture rates and greatest number of overall captures when foraging over pasture (Ardia 1997). Females used areas that contained a greater percentage of pasture, on average, than did males.

However, absolute differences in habitat use between males and females were not large, and overall our study provides support for the hypothesis that both female and male kestrels will use open areas as nonbreeding habitat, in contrast to hypotheses that suggest different habitat preferences for each sex. Females and males perched in areas composed predominantly of short vegetation (<0.25 m high) and exhibited considerable overlap in habitat use. Relative to what is available within 100 m of a perch, male

kestrels appeared to use areas in which to perch that contained less woody vegetation and more grassy vegetation. Woody vegetation, at least at our study site, is not suitable for hunting and may increase predation risk (Ardia and Bildstein 1997).

The proportion of suitable foraging habitat within male use-areas (69%) is considerably higher in our Pennsylvania study site than in Florida (30%), where females excluded males from open areas (Smallwood 1987, 1988), but is similar to Ontario (77%), where no sex segregation was observed (Arnold and Martin 1991). Along a geographic gradient from south to north (Florida to Pennsylvania to Ontario), male kestrels demonstrate large differences in the percentage of open area found within territories. That males use physiognomically different areas across their winter range demonstrates little support for the hypothesis that males maintain a distinct preference for semi-open areas.

The main factor that varies across this north–south gradient is ability of males to occupy preferred sites. In northern locations where density of conspecifics, and thus site competition, is low, males occupy preferred open areas (Arnold and Martin 1991). When density of conspecifics is high, such as in the lower latitudes, males appear to be forced to use less-preferred semiopen areas (Mills 1976, Smallwood 1987, 1988). At our site in Pennsylvania, males and females differ in use, but not to the extent reported in locations farther south, likely because densities are somewhat intermediate and habitat availability may be lower.

Sex-related differences in habitat use can have important life-history and population regulation consequences (Morton et al. 1987, Marra et al. 1998, Marra and Holberton 1998). For example, male kestrels show a decrease in monthly mean body condition whereas females do not, and males maintain smaller energy surpluses relative to females (Ardia 1997). The differences in competitive ability that underlie that ecological interaction can result from sex-related differences in behavior and ecology. Exclusion, the mechanism likely responsible for sex-related differences in habitat use in American Kestrels, is most likely an integration of pressures during an entire life cycle. Spatial and temporal interactions of those pressures affect the quality of winter habitat used both within and between sexes.

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Female Hematozoan Infection Reduces Hatching Success but not Fledging Success in Pied Flycatchers *Ficedula hypoleuca*

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ABSTRACT.—We report association between female blood parasite prevalence (percentage of infected birds) just after egg laying and reproductive success in two successive breeding seasons, in a breeding population of Pied Flycatcher *Ficedula hypoleuca* in central Spain. Females infected with *Trypanosoma* spp. had a higher probability of deserting their clutches during the incubation period than noninfected females. Females infected with *Haemoproteus balmorali* hatched proportionally fewer eggs than noninfected females. Female infected with *H. balmorali* during the incubation period may have a decreased ability to thermoregulate which may affect their incubation capacity. Fledging success, breeding success, fledgling mass, and tarsus length were not associated with infection of the mother by blood par- asites during the incubation period, suggesting that females and their mates may compensate during the nestling period for the negative effect of blood par- asites during the incubation period.

Most parasites exert an intense selective pressure on their hosts by reducing their condition, survival prospects, mating, or reproductive performances (Loye and Zuk 1991, Møller 1997). That detrimental effect may vary in relation to parasite virulence. In order to understand evolutionary interactions occur- ring between parasites and their hosts, it is necessary to know the extent to which parasites have a detri- mental effect on their hosts' reproduction and sur- vival in wild populations. Reproductive success has been the target of many field studies of birds, be- cause it is expected to relate closely to fitness (Stearns 1992). Blood parasites have been shown to negatively affect reproductive success of their hosts

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