

SEX DIFFERENCES IN WINTER HABITAT OF AMERICAN KESTRELS IN GEORGIA

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Most North American hawks are sexually dimorphic in body size (Snyder and Wiley 1976), and this difference is often associated with differences in behavior and ecology (Newton 1979). Koplín (1973) and Mills (1976) have documented such differences in habitat use by male and female American Kestrels (*Falco sparverius*) wintering in the western United States. We report similar behaviors for American Kestrels wintering in the southeastern United States and discuss hypotheses possibly explaining these differences in habitat use.

METHODS

We studied American Kestrels on St. Catherine's Island, Georgia, from 19 October–25 December 1978, 6 September–29 October 1979, and 4–21 December 1979. St. Catherine's Island is a barrier island of about 5665 ha (exclusive of salt marsh) approximately 6.5 km east of the Georgia mainland. Thomas et al. (1978) provide a general description of the island.

When a kestrel was sighted, we recorded its sex and qualitatively described the vegetation within 40 m of the kestrel (see below). We did not record subsequent observations of a particular sex at a site on the same day unless 2 or more birds of the same sex were observed simultaneously. Vegetation was described as "low" in fields and dunes where all vegetation was <1 m high, as "intermediate" in a savannah at the north end of the island where long-leaf pines (*Pinus palustris*) were scattered through otherwise low vegetation (Fig. 13 in Thomas et al. 1978), and as "high" in woodlands and woodland-marsh ecotones where the vegetation was >1 m high. Throughout this study, we visited the different habitats approximately in proportion to their occurrence on the island. We occasionally recorded the duration of observed hunting flights, the number of hovers made during the flights, intended prey, and whether or not the flight resulted in prey capture.

The multiway frequency table was analyzed with the Biomedical Computer Program BMDP3F (Dixon 1977) at the University of Washington Academic Computer Center. All other nonparametric tests were calculated after Sokal and Rohlf (1969) and Hollander and Wolfe (1973).

RESULTS

The occurrence of male and female kestrels in 3 habitats during early and late fall on St. Catherine's Island is presented in Table 1. We observed males 99 times and females 75 times (exclusive of same-day resightings of birds of the same sex). In 1978, both sexes were present when we arrived at the island on 19 October. In 1979, the first female and male kestrels were sighted 16 and 22 September, respectively. We

TABLE 1. Sightings of male and female American Kestrels by habitat and time of year on St. Catherine's Island, Ga.

Time of year	Sex	Vegetation			Total
		Low	Inter- mediate	High	
16 Sept-15 Nov	Male	7	16	27	50
	Female	17	30	1	48
16 Nov-25 Dec	Male	4	11	34	49
	Female	10	17	0	<u>27</u>
					174

estimate that about 8 males and 6 females held winter territories on the island in late fall of both years.

Statistical analysis of the 3-way frequency table (Table 1) is summarized in Table 2. Multiway frequency table analysis not only tests the hypothesis that each variable is independent of all other variables, but also tests whether or not various subsets (i.e., "models") of the total set of variables are interdependent (Bishop *et al.* 1975, Fienberg 1978; also see Jenkins 1975). Each model can generate a table of expected values, which is compared to the observed values. Significant differences between expected and observed values imply the model in question does not adequately describe interactions within the total set of variables. The model which provides the best description of Table 1 is VS,ST ($0.54 > P > 0.53$; Table 2), indicating kestrel sex (S) and surrounding vegetation (V) as well as sex and time of year (T) are interdependent, but all other combinations of variables (e.g., VT) are independent. Male kestrels were sighted most frequently in high vegetation, while females were sighted most frequently in low and intermediate vegetation; females were relatively less common in late fall than in early fall (Table 1).

The significance of differences between various models can be evaluated by computing the difference between the log-likelihood-ratios of the models and comparing it with appropriate χ^2 values (the difference between each model's degrees of freedom is the degree of freedom for this comparison) (Fienberg 1978). For example, although the model VS is simpler than the model VS,ST, the model VS,ST provides a significantly better fit to the observed data (log-likelihood-ratio = 5.97, $df = 2$, $P < 0.052$).

Aspects of the hunting behavior of kestrels in different habitats are summarized in Table 3. The flight times of females hunting over low vegetation where no high perches were available were significantly greater than flight times of either sex hunting over intermediate vegetation and of males hunting in high vegetation (Mann-Whitney U test, $P < 0.006$). Females hunting over low vegetation also hovered significantly more often during hunting flights than either sex over intermediate vegetation and than males in high vegetation (Mann-Whitney U

TABLE 2. Results of analysis of Table 1. See text for discussion of analysis of multiway frequency tables. Models incorporate effects of vegetation (V), sex of kestrel (S), and time of year (T).

Model	Degrees of freedom	Log-likelihood ratio	Probability
V	9	97.57	<0.0001
S	10	106.43	<0.0001
T	10	106.97	<0.0001
V,S	8	94.25	<0.0001
V,T	8	94.78	<0.0001
S,T	9	103.65	<0.0001
V,S,T	7	91.46	<0.0001
VS	6	9.43	>0.1507
VT	6	89.90	<0.0001
ST	8	100.47	<0.0001
VS,T	5	6.64	>0.2486
VT,S	5	86.58	<0.0001
ST,V	6	88.28	<0.0001
VS,VT	3	1.76	>0.6229
VS,ST	4	3.46	>0.4838
VT,ST	4	83.40	<0.0001

test, $P < 0.006$). No other paired comparisons were significantly different (Mann-Whitney U test, $P > 0.15$). Individual hovers by females hunting over low vegetation ranged from 2.4–12.6 sec in duration (median = 6.0 s; $n = 22$).

In 1979, males in intermediate vegetation were successful in 4 of 6 hunting attempts for which the outcome was observed; females in intermediate vegetation were successful in 18 of 36 attempts. These differences are not significant (G-test, $P > 0.75$). In 1979, during hunting flights in intermediate vegetation when the intended prey was visible to us, males pursued 2 birds and 4 insects; females pursued 1 bird and 18 insects. These differences are not significant (G-test, $0.09 > P > 0.05$).

TABLE 3. Duration of hunting flights (s) and number of hovers per flight for male and female American Kestrels in several habitats on St. Catherine's Island, Ga.

Sex	Vegetation type	No. of observations	Flight time (s)		No. hovers/flight	
			Median	Range	Median	Range
Female	Low	33	66.0	4.0–296.0	3	0–12
Female	Intermediate	54	5.05	2.0–30.0	0	0–1
Male	Intermediate	12	3.5	2.0–45.0	0	0
Male	High	16	9.0	1.5–102.4	0	0–4

DISCUSSION

On St. Catherine's Island, female American Kestrels occur more often in open habitats with low vegetation, while males occur more often in brushier habitats with a high understory. This different use of local habitat is a common pattern of behavior wherever male and female kestrels winter together (northern California: Koplín 1973; southwestern USA: Mills 1976). In addition to these within-locality differences between the sexes in wintering kestrel populations, other differences also apparently exist. Broun (1949) and Heintzelman and Nagy (1968) report a preponderance of male kestrels sighted at observation stations during fall migration, suggesting male and female kestrels have different migration behaviors. Males tend to be more common than females at sites in the northern part of the wintering range (Roest 1957, Enderson 1960, Johnson and Enderson 1972) and females tend to be more common than males at sites in the southern part of the wintering range (Koplín 1973, Mills 1976, Tabb 1977). As discussed by Mills (1976), the local differences in habitat use will complicate attempts to study regional differences in sex ratios of wintering kestrel populations. For example, our observation of an overall sex ratio biased towards males is probably a consequence of the local availability of habitats, rather than an indication of a regional preponderance of males. Layne (1980) interpreted a preponderance of males at a locality in southcentral Florida similarly.

Three hypotheses potentially explain the observed sex differences in habitat use by wintering kestrels: (1) males aggressively exclude females from preferred winter habitats, (2) females aggressively exclude males from preferred winter habitats, and (3) each sex selects different habitats because of different winter habitat preferences. We know of no evidence supporting the first hypothesis and, in fact, Cade (1955) suggests female kestrels are more aggressive than males (see below).

The second hypothesis, that females are forcing males into inferior habitats, has been previously proposed by Mills (1976). Cade's (1955) observations, that free-ranging female kestrels attack tethered female kestrels placed in their winter territories more aggressively than do free-ranging males, whereas both males and females aggressively attack tethered males placed in their winter territories, are consistent with this hypothesis (Cade 1955). Two observations suggest female kestrels are not invariably excluding males from habitats where males would experience the highest net energy gain per time. First, males do not increase their use of female-dominated habitats when females leave the island in late fall (Table 1). Second, although both males and females capture prey from hovering flight (Jenkins 1970, pers. obs.), only females in low vegetation regularly hunted from hovering flight on St. Catherine's Island (Table 3). Because attacks from hovering flight tend to be less successful than attacks from perches (Sparrowe 1972, Collopy 1973), it is not obvious that female kestrels hunting over low vegetation where perches were unavailable were in fact hunting where net energy gain per time is highest. The greater energy expenditure required for attacks

from hovering flight relative to attacks from perches (cf. Grubb 1977) would only exacerbate this problem. Possibly, these females were excluded from the intermediate vegetation by other females and did not hunt in the high vegetation because of size-related agility-constraints. Although net energy gain per time is determined by an aggregate of factors (many not measured in this study, e.g., availability of different-sized prey in different habitats), these considerations suggest further study is needed before the second hypothesis can be accepted as the sole explanation for the observed differential habitat use.

The third hypothesis which could explain differential habitat use is that individuals of each sex select habitats based on different habitat preferences. Different habitat preferences presumably would reflect size-related differences in preferred prey species and hunting methods. Even if sexual dimorphism in body size, as occurs in American Kestrels (Snyder and Wiley 1976), is selected for principally by breeding season factors (Reynolds 1972, Snyder and Wiley 1976), differential winter habitat use could occur if hunting success or winter survival in different habitats varied with body size. The third hypothesis would be discredited if no sex differences exist in hunting behavior or preferred prey. On St. Catherine's Island, we observed no significant differences in measured aspects of male and female hunting behavior when hunting was from perches in intermediate and high vegetation (Table 3). However, male kestrels eat more birds (Mills 1976) than do females, suggesting differential habitat use may reflect sex differences in prey preferences. If we assume sex differences in habitat use are widespread (see above), Tabb's (1977) report that both males and females return to winter at the same sites over a period of several years is also consistent with the hypothesis that individuals of each sex have distinct winter habitat preferences. Hence, we tentatively conclude that sex differences in habitat use reflect sex differences in preferred habitats, although female exclusion of males from jointly preferred habitats may also cause differential habitat use.

Local and regional differences in habitat use have been documented for many birds (e.g., Koplín 1973, Mills 1976, Pitelka 1979, Williamson 1971). Such differences are generally thought to enhance breeding success (e.g., Williamson 1971) or longterm survival (e.g., Koplín 1973). In contrast, Jehl (1979:180) argues differential habitat use by species with sexual size dimorphism (as occurs in most cases cited above) "would only increase the frequency of similar morphs in one area, and the expected result would be to *increase* intraspecific competition." Jehl concludes differential habitat use is not ecologically advantageous to individuals. However, although differential habitat use increases within-habitat intraspecific overlap in resource use, overlap does not necessarily imply competition (Abrams 1980), and an individual's winter survival (or breeding success) is not simply a consequence of the amount of intraspecific competition experienced. For an extreme case, consider an individual wintering away from conspecifics in an area where prey are

scarce; both intraspecific competition for food and probability of long-term survival are low. Conversely, individuals wintering with many conspecifics in an area where prey are super-abundant will experience much overlap (but little competition) with conspecifics in resource use and a high probability of winter survival. In general, motile organisms are expected to select habitats where survival or breeding success will be highest, and these factors can vary with number of competitors, prey availability, and predation intensity. In species with differences in foraging habits (due to size dimorphism or to sex-related behavioral differences), each sex is expected to select portions of the environment where individual survival (or breeding success) is highest. Due to sex differences in preferred prey and habitat differences in availability of different prey, sex differences in local habitat use reported here for American Kestrels possibly generate higher individual winter survival rates than would random use of habitats.

SUMMARY

Habitat use of wintering American Kestrels was studied on St. Catherine's Island, Ga. Females occurred significantly more often in habitats where most vegetation was less than 1 m high, while males occurred significantly more often in habitats where vegetation was over 1 m high. Females were more common in early fall than in late fall. These sex differences in habitat use may reflect sex differences in preferred winter habitats, possibly due to differences in preferred prey of males and females, and habitat differences in availability of such prey.

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