

SEXUAL SEGREGATION BY HABITAT IN AMERICAN KESTRELS WINTERING IN SOUTHCENTRAL FLORIDA: VEGETATIVE STRUCTURE AND RESPONSES TO DIFFERENTIAL PREY AVAILABILITY¹

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Abstract. Migrant American Kestrels (*Falco sparverius sparverius*) wintering in southcentral Florida showed marked segregation of the sexes due to differential habitat use. Females typically occupied territories in pastures, mowed hayfields, and recently planted citrus groves. Males were observed primarily along the margins of slash pine (*Pinus elliotii*) woodlots, eucalyptus (*Eucalyptus* spp.) plantations, and cypress (*Taxodium distichum*) sloughs, and within scrubby flatwoods, mature citrus groves, and residential areas. Although males were found in less open habitats, both sexes utilized the same type of hunting substrate: short grasses and weedy forbs <25 cm in height. Pellet analysis revealed that both sexes fed exclusively on arthropods. Male and female territories differed in the proportion of area covered by suitable hunting substrate (median values of 0.30 and 0.60, respectively). Additionally, the more numerous and larger trees or shrubs characteristic of male territories formed a visual barrier such that a smaller proportion of the available hunting substrate was visible from any one perch. Differential prey availability was evident from differences between male and female activity budgets; males allotted more time toward foraging and less time toward preening. In addition, males were more likely to attack novel prey items, and males experienced a greater loss of body mass during a period when ambient temperatures <0°C reduced arthropod prey availability. The evidence supports the hypothesis that female territories were of superior foraging quality.

Key words: American Kestrel; *Falco sparverius*; winter segregation; winter territoriality; habitat quality; activity budget; foraging.

INTRODUCTION

American Kestrels (*Falco sparverius*) commonly defend individual territories during winter (Cade 1955). Unbalanced winter sex ratios of kestrels have been attributed to differential habitat use in California (Koplin 1973), Arizona and Texas (Mills 1976), Georgia (Stinson et al. 1981), and Florida (Smallwood 1981, Bohall-Wood and Collopy 1986). The differences between habitats occupied by males and females have been described in terms of plant communities or land use (Koplin 1973, Mills 1976, Smallwood 1981, Bohall-Wood and Collopy 1986), vegetation density (Mills 1976), and vegetation height (Stinson et al. 1981).

In areas where sexual segregation of wintering kestrels by habitat has been reported, females consistently predominated in habitats characterized as being open and covered with short or sparse ground vegetation, while males were found primarily in woodland openings, along woodland

edges, or in other less open habitats. Mills (1976) tentatively suggested that females occupied "the best habitats." This suggestion was based on an apparently greater density of kestrels in open habitats, where females predominated. However, no quantitative measure of a habitat characteristic which may have been correlated with habitat quality was reported.

A principal objective of the present study was to examine the vegetative structure and land use characteristics of territories held by migrant American Kestrels (*F. s. sparverius*) wintering in southcentral Florida, a region in which there was a marked sexual segregation by habitat. No previous study has examined the relationship between specific habitat parameters and foraging quality in regard to winter segregation in kestrels. If the territories of male and female kestrels differ substantially in the availability of prey, then winter segregation may have a profound effect on the probability of winter survivorship of the sexes. Winter is the dry season in southcentral Florida, and during this period most prey resources of kestrels are probably nonrenewable.

¹ Received 17 December 1986. Final acceptance 8 April 1987.

It would be predicted that significant differences in foraging quality between territories held by males and those held by females would be accompanied by compensatory behavioral differences between the sexes. The second principal objective of this study was to examine the daily activity budgets of males and females for evidence of differential availability of prey.

STUDY AREA AND METHODS

STUDY AREA

The study area was located west of Lake Okeechobee in southcentral Florida, a region which supports a large population of migrant kestrels during winter (Layne 1980), and included portions of Highlands, Glades, and Hendry counties (Fig. 1). The characteristically flat topography was interrupted in Highlands County by the north-south oriented Lake Wales Ridge, a system composed of relict dunes and ancient coastlines. Within the study area the ridge was approximately 30 m above the surrounding flatlands.

The natural vegetation of the ridge was xeric woodlands dominated by pines (*Pinus* spp.) and oaks (*Quercus* spp.). Most of this vegetation had been replaced by citrus groves. The flatlands were used principally for cattle grazing and a relatively small portion of the study area was in sugar cane production. Scattered within the study area were numerous ponds, slash pine (*Pinus elliotii*) woodlots with saw-palmetto (*Serenoa repens*) ground cover, scrubby flatwoods, and cypress (*Taxodium distichum*) sloughs.

VEGETATION SAMPLING

Vegetative and land use characteristics of kestrel territories were sampled from 12 January to 15 February 1984 by means of 1-ha circular plots centered on observed hunting perches. This plot size was chosen because, in the study area, kestrel pounces generally occurred within a radius of approximately 56 m. Within each circle, 20 sampling points were uniformly distributed, but with a randomized orientation. At each sampling point, eight habitat parameters were categorically evaluated: (1) type of ground vegetation, (2) condition of ground vegetation (<33% dead, >33% but <67% dead, or >67% dead), (3) height of ground vegetation, (4) presence of tree or shrub canopy directly over sample point (no canopy, on edge of dense shrub/woodlot opening, under solitary tree or shrub, within dense shrub/wood-

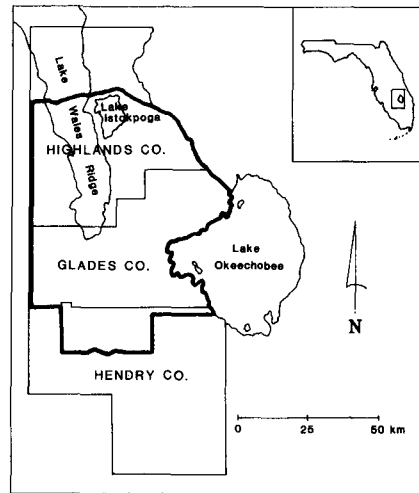


FIGURE 1. Study area in southcentral Florida.

lot with closed canopy), (5) type of canopy plant, (6) condition of canopy plant (see (2), above), (7) canopy height, and (8) land use. A single circular plot was evaluated within the territory of each kestrel.

KESTREL BEHAVIOR

The activity budgets of free-ranging kestrels were determined by observing the frequency and duration of kestrel behaviors during 20-min observation periods. The length of this sampling interval exceeded the duration of the longest observed behavior (see Altmann 1974:231-232). Data were collected from 20 December 1984 to 28 January 1985. All observations were made from a minimum distance of 100 m with the aid of a 20 to 45× spotting scope. In habitats containing a large number of visual obstructions (particularly the numerous trees typical of male habitats), two observers were stationed at different vantage points and both verbal accounts were simultaneously tape-recorded via two-way radios.

During each 20-min observation period, the frequency of occurrence for each of the following behavioral events was recorded: capturing prey, preening, engaging in nonpreening comfort movements (including scratching, stretching wing or tail, shaking body plumage, cleaning foot with bill, and yawning), and flying. The context in which flight occurred, including pounces on prey, and the duration of flights and of preening bouts were also recorded.

Time of day was standardized by designating local sunrise and local sunset as 06:00 and 18:00, respectively. Thus, standardized hours ranged from 52.25 min to 54.42 min, depending on date. Five kestrels of each sex were observed for a 20-min period (real time) during each of the 12 standardized daylight hours, forming a sexually and temporally balanced sample representing 120 individuals observed during a total of 40 hr.

To collect information on diets, trapping operations were conducted from 3 January to 23 February 1984, and from 18 December 1984 to 2 February 1985, using a modified bal-chatri trap (Berger and Mueller 1959) containing a single house mouse (*Mus musculus*) as a lure. Two strains of mice were used, wild-caught house mice and albino laboratory mice. Captured kestrels were weighed, held overnight to collect regurgitated pellets, and subsequently released at the capture sites.

DATA ANALYSES

Each character value generated by a 1-ha circular plot sample was expressed as a proportion of the 20 sampling points of the plot. For example, the ground vegetation of a plot may have been 0.75 grasses, 0.25 water, and 0.00 for all other ground vegetation categories. All 58 proportion variables thus generated were used in a discriminant function analysis with sex as the single independent variable. The classification criterion used to characterize male and female territories was determined by a measure of generalized squared distance (Rao 1973:574–577). Those variables which were most important in discriminating between male and female territories were determined by a stepwise discriminant analysis by forward selection with an entry significance level of 0.25 (Costanza and Afifi 1979). Although the synthesis of a classification criterion was conducted with parametric procedures, the performance of this criterion in assigning sample observations as being from male or female territories was distribution free. Suitable hunting substrate is herein defined as ground vegetation consisting of grasses and/or weedy forbs <25 cm in height (see "kestrel behavior," below).

Analyses of temporal patterns of behavior were performed on six blocks of two standardized hours, herein referred to as early morning, mid-morning, late morning, early afternoon, mid-afternoon, and late afternoon. Behavioral differences among blocks were tested for significance

separately for males and females. Differences between males and females over the combination of all six blocks were also tested for significance. Although results are presented below in units of events/day and events/hour, all statistical tests were performed on raw data (e.g., events/20 min).

Tendencies for males and females, upon first exposure, to strike a trap containing either an albino laboratory mouse or a wild-strain house mouse were examined, and the interrelation among prey type, kestrel gender, and the tendency to strike a trap was tested for significance. Kestrels usually cannot be captured by the same trapping technique more than once during a season (Tabb 1977; pers. observ.). Due to this constraint, unpaired tests were used to examine the differences between the body mass of kestrels captured before and after a period of severe cold weather.

RESULTS

VEGETATION CHARACTERISTICS

Female kestrels were observed primarily in pastures, hayfields, and other open areas extensively covered by short ground vegetation, including recently planted citrus groves. Males were most common along the perimeters of slash pine woodlots, eucalyptus (*Eucalyptus* spp.) plantations, and cypress sloughs, and within scrubby flatwoods, mature citrus groves, and residential areas. A circular plot was sampled in each of 170 kestrel territories (54 males, 116 females). Discriminant function analysis generated a classification criterion which correctly identified 112 (96.55%) sample plots from females and 44 (81.48%) sample plots from males. Variables which made significant contributions to the discrimination of male and female territories are shown in Table 1.

The proportion of the territory covered by suitable hunting substrate differed significantly between males and females (median values of 0.30 and 0.60, respectively; two-tailed Wilcoxon's rank sum test, $Z = 5.962$, $P < 0.0001$; Fig. 2). Male territories were covered more extensively by woody canopies (median proportions: male, 0.35, female, 0.05; two-tailed Wilcoxon's rank sum test, $Z = 7.894$, $P < 0.0001$; Fig. 3). In addition, the trees or shrubs found in male territories were significantly taller than those found in female territories (median size categories of 10 to 20 m and 5 to 10 m, respectively;

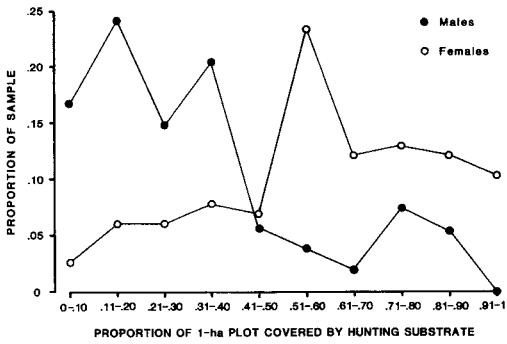


FIGURE 2. Proportion of American Kestrel winter territory covered by suitable hunting substrate (grasses and/or weedy forbs <25 cm in height), southcentral Florida, 1983 to 1984. Data represent territories of 54 males and 116 females.

two-tailed Wilcoxon's rank sum test, $Z = 2.437$, $P = 0.015$). The proportion of suitable hunting substrate was inversely proportional to canopy coverage ($n = 170$, Spearman's rho [r_s] = 0.322, $P = 0.0001$).

KESTREL BEHAVIOR

All observed pounces by kestrels directed toward naturally occurring prey ($n = 529$) occurred in open areas; 97.5% were made onto substrates of grasses and weedy forbs <25 cm in height (thus, the operational definition of suitable hunting

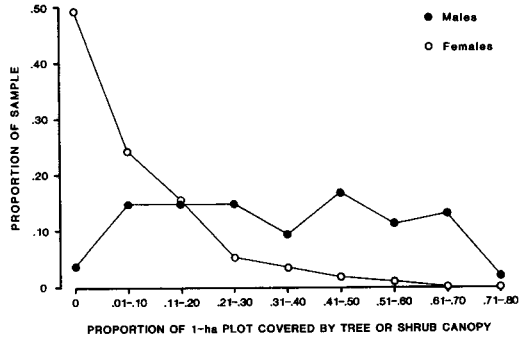


FIGURE 3. Proportion of American Kestrel winter territory covered by woody canopy, southcentral Florida, 1983 to 1984. Data represent territories of 54 males and 116 females.

substrate), 2.3% onto bare soil or sand, and, in a single instance, onto the road surface. Examination of pellets collected from kestrels captured and held overnight ($n = 169$) suggested no sexual differences in diets. Prey remains in these pellets were exclusively from arthropods, primarily grasshoppers, beetles, and spiders. Diurnal rodent prey of appropriate size (e.g., *Microtus* spp.) was not available in the study area (Hamilton and Whitaker 1979).

Behaviors of 60 male and 60 female kestrels were documented during the 20-min observation periods. The total number of attempted prey cap-

TABLE 1. Habitat variables important in the discrimination between territories of male and female American Kestrels in southcentral Florida during winter, 1983-1984.^a

Variable	Proportion ^b		Partial r^2	F	P
	Male	Female			
Canopy characteristics					
Absence of tree or shrub canopy	0.646	0.919	0.396	109.91	0.0001
Canopy plant <33% living	0.002	0.003	0.057	9.97	0.002
Canopy height between 5 and 10 m	0.112	0.014	0.036	6.14	0.014
Canopy plant >67% living	0.336	0.077	0.011	1.71	0.19
Canopy height between 0 and 2.5 m	0.001	0.003	0.011	1.67	0.20
Ground vegetation characteristics					
Plant height >2 m	0.074	0.029	0.028	4.55	0.035
Type: grasses and woody growth	0.013	0.007	0.022	3.57	0.061
Type: emergent vegetation	0.024	0.013	0.014	2.23	0.14
Plant height between 1 m and 2 m	0.215	0.087	0.010	1.58	0.21
Categories of land use					
Fallow field	0.226	0.101	0.143	27.77	0.0001
Plowed field	0.019	0.000	0.070	12.44	0.0005
Water	0.040	0.032	0.060	10.52	0.001
Maintained lawn, other than roadside berm	0.053	0.017	0.032	5.28	0.023
Woodlot	0.234	0.022	0.032	5.21	0.024

^a Stepwise discriminant analysis by forward selection, with an entry significance level of 0.25.

^b Mean proportion of 1-ha circular plot. See text for explanation.

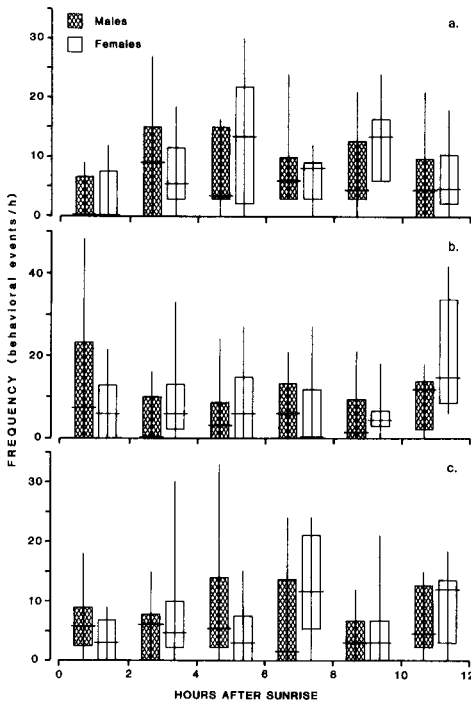


FIGURE 4. Temporal patterns in American Kestrel activity budgets during winter in southcentral Florida, 1984 to 1985. Median rates and quartile deviations are shown for (a) attempted prey captures, (b) preening bouts, and (c) bouts of nonpreening comfort movements, including scratching, stretching wing or tail, shaking body plumage, cleaning foot with bill, and yawning. Data were collected from 60 males and 60 females.

tures between sunrise and sunset by males was not significantly different than that by females (estimated mean values of 70.7 and 85.6, respectively, based on the observed median day length of 10 hr 31 min; two-tailed Wilcoxon's rank sum test, $Z = 1.131$, $P = 0.26$). Also, the proportions of pounces which were successful were nearly identical for males and females (0.76 and 0.73, respectively; two-tailed Wilcoxon's rank sum test, $Z = 0.656$, $P = 0.51$). No significant temporal differences in pounce success ratios were detected for either males or females (Kruskal-Wallis chi-square approximations, $\chi^2 = 9.40$, $df = 5$, $P = 0.094$, and $\chi^2 = 6.30$, $df = 5$, $P = 0.28$, respectively). However, although female pounce rates exhibited significant temporal differences (Kruskal-Wallis, $\chi^2 = 12.80$, $df = 5$, $P = 0.025$), male pounce rates did not (Kruskal-Wallis, $\chi^2 = 7.03$, $df = 5$, $P = 0.22$; Fig. 4a). The duration of flights from perch to prey item was greater for

TABLE 2. Responses of American Kestrels upon first experimental exposure to rodent prey,^a southcentral Florida, December to February, 1983 to 1984 and 1984 to 1985. Two Chi-square contingency tables are shown.

Prey type	Kestrel gender	Responses ^b		χ^2	P
		Struck trap	Did not strike trap		
Wild	Male	32	9	0.011	0.91
	Female	45	12		
Albino	Male	34	5	6.110	0.013
	Female	69	35		

^a *Mus musculus*.

^b Significantly associated with the relationship between kestrel gender and response, Mantel-Haenszel test, $MH = 1.82$, $df = 1$, $P < 0.036$.

females than for males (median values of 3.6 and 3.0 sec, respectively; two-tailed Wilcoxon's rank sum test, $Z = 2.108$, $P = 0.035$). However, males and females did not differ significantly in the total amount of time engaged in foraging-related flight (flying from perch to prey item, hovering, returning to hunting perch, and flying between alternate hunting perches; two-tailed Wilcoxon's rank sum test, $Z = 1.657$, $P = 0.10$).

Females spent more time engaged in preening than did males (two-tailed Wilcoxon's rank sum test, $Z = 2.019$, $P = 0.044$). Females also exhibited significant temporal differences in the frequency of preening bouts (Kruskal-Wallis test, $\chi^2 = 12.38$, $df = 5$, $P = 0.030$; Fig. 4b) and bouts of nonpreening comfort behaviors (Kruskal-Wallis test, $\chi^2 = 11.56$, $df = 5$, $P = 0.041$; Fig. 4c). No significant temporal differences in either preening or other comfort movements were detected in males (Kruskal-Wallis tests, $\chi^2 = 5.03$, $df = 5$, $P = 0.41$, and $\chi^2 = 2.26$, $df = 5$, $P = 0.81$, respectively). Pounce rate was inversely proportional to the frequency of preening bouts for both males and females ($r_s = -0.374$, $P = 0.003$, and $r_s = -0.284$, $P = 0.028$, respectively).

The responses of 241 individual kestrels (80 males, 161 females) to an initial presentation of a house mouse in a bal-chatri trap are presented in Table 2. Although the responses toward a wild-strain mouse were nearly identical (attacks were made by 78.0% of the males and 78.9% of the females; test of homogeneity, $\chi^2 = 0.01$, $df = 1$, $P = 0.91$), males were more likely than females to attack a white laboratory mouse (attacks were made by 87.2% of the males and 66.3% of the females; test of homogeneity, $\chi^2 = 6.11$, $df = 1$, $P = 0.013$). Thus, prey type was significantly as-

sociated with the relationship between kestrel gender and the response toward rodent prey (Mantel-Haenszel test, $MH = 1.82$, $df = 1$, $P < 0.036$).

The study area experienced severe cold temperatures in January 1985. Measurements of the body mass of kestrels captured on the third (last) consecutive day of ambient temperatures $<0^{\circ}\text{C}$ were compared to those of kestrels captured prior to the onset of cold weather (Fig. 5). The decline in female body mass was not significant (4 g; one-tailed Wilcoxon's rank sum test, $Z = -1.237$, $P = 0.11$). During the same time, male body mass declined by 13 g (one-tailed Wilcoxon's rank sum test, $Z = 2.847$, $P = 0.002$).

DISCUSSION

Both male and female kestrels fed exclusively on arthropods, capturing them on the ground in open patches of a mutually preferred type of hunting substrate. Similar diets for male and female kestrels have been reported previously (Cade 1960: 243, Balgooyen 1976:47-48). The preference for open patches of ground covered by short grasses and weedy forbs as hunting substrate was consistent with previous accounts (e.g., Roest 1957, Balgooyen 1976:54-55). Male territories differed from female territories in two important ways: (1) males controlled access to habitats covered by a lesser proportion of suitable hunting substrate, and (2) because the more dense and larger trees and shrubs formed a visual barrier, a smaller proportion of the available hunting substrate was visible from any one perch. Patches of a particular type of ground vegetation, i.e., suitable hunting substrate, probably contained similar prey densities, regardless of whether those patches were used by males or females. Therefore, male territories, on average, were inferior to female territories in terms of the rate of encounters with prey.

Differences in the foraging quality of habitats, although difficult to measure directly, were evident in the differences in kestrel predatory behavior. Males hunted at a statistically constant rate throughout the day. The pounce rates of females, however, increased during the morning, reaching a peak before noon. Hunting activity of females was markedly lower during early afternoon, increased in mid-afternoon, then waned toward evening.

A study designed to determine the importance of prey characteristics in eliciting attacks by wild

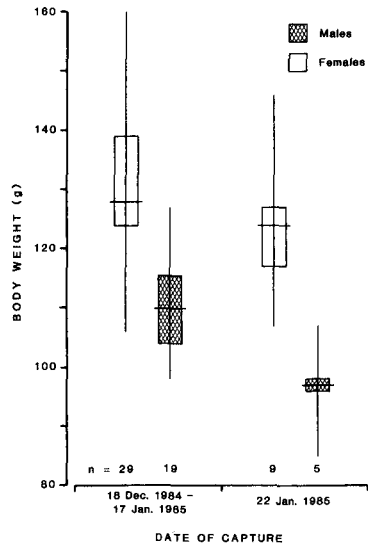


FIGURE 5. Body mass of American Kestrels in southcentral Florida before and after three consecutive days of ambient temperatures $<0^{\circ}\text{C}$, 20 to 22 January 1985. Medians and quartile deviations are shown.

kestrels (Smallwood, unpubl.) showed that rate of movement of prey was the best predictor of an attack response. The importance of movement as a prey selection factor has been demonstrated in captive studies of kestrels (Ruggiero and Cheney 1979), Eastern Screech-Owls (*Otus asio*; Metzgar 1967, Kaufman 1974), Common Barn-Owls (*Tyto alba*; Kaufman 1974), and Red-tailed Hawks (*Buteo jamaicensis*; Snyder 1975).

During morning and early afternoon, the arthropod prey in the study area probably increased their rate of movement as ambient temperature increased (see Balgooyen 1976:63). Thus, the lower rate of female hunting activity in early afternoon, in contrast to the expected behavior, may have occurred during a period of increasing prey vulnerability. An alternative prediction states that prey conspicuousness, due to movement, may have decreased during the hottest part of the day (mid-afternoon). However, a second peak in pounce rates by females occurred at this time, again in contrast to the expected behavior. Therefore, the pattern of hunting activity in females was probably not the result of tracking daily fluctuations in prey vulnerability.

The rhythm of female hunting activity would be predicted for a predator in an area containing abundant food resources, i.e., feeding until satiation, followed by reduced foraging activity,

and then another foraging bout later in the day. Male pounce rates did not change. Males appeared to be constrained to forage actively for longer periods of time to capture a similar number of prey items.

Although distances were not measured directly, the average duration of a flight from perch to prey item was greater for females than for males. This is consistent with the hypothesis that hunting females commanded unobstructed views of larger patches of suitable hunting substrate from any one perch (see Bohall-Wood and Collopy 1986:560). The increased metabolic cost of this longer flight does not appear to be important; the total amount of time engaged in foraging-related flight, which included flights to alternate hunting perches, did not differ significantly between males and females.

Females spent more time engaged in preening behavior. Perhaps males could not afford to allocate as much time to certain maintenance behaviors because of a greater amount of time devoted to foraging. This conclusion is supported by the inverse relationship between pounce rate and frequency of preening bouts in both males and females. As expected, hunting bouts were often interspersed with preening, but kestrels did not actively forage while actually engaged in preening.

Males were similar to females in capture success, once a prey item was detected, and in the total number of prey items captured per day. However, on average, males were constrained to forage actively throughout the day while females were able to meet their foraging needs and still have a substantial amount of time remaining to allot toward nonforaging activities.

Other behavioral evidence supports the hypothesis that male territories were of inferior foraging quality. Although the responses of male and female kestrels toward a wild-strain mouse did not differ (it is highly probable that these migrant kestrels had previous experience with rodent prey on the breeding grounds), a greater proportion of males attacked white laboratory mice, which certainly provided an unfamiliar prey stimulus in terms of behavior and coloration. Neophobia, in regard to foraging, has been documented in several species of birds, including kestrels (Ruggiero and Cheney 1979), Blue Jays (*Cyanocitta cristata*; Coppinger 1970), and Chestnut-sided Warblers (*Dendroica pensylvanica*; Greenberg 1983). One would predict that a

predator inhabiting an area of lower prey availability would be less likely to reject an opportunity to capture prey, even if the prey item were unusual.

Perhaps the strongest evidence for differential foraging quality of male and female territories was the difference in loss of body mass associated with a period of severe cold weather, a time when arthropod prey availability was certainly reduced. Because kestrels are only moderately sexually dimorphic with respect to body mass, differences in responses to thermal stress were probably minimal. Body mass corresponds to a cubic function and the median body mass of male kestrels prior to cold temperatures (110 g) was 0.951³ times that of females (128 g). The surface area/volume ratio of males was therefore approximately 0.951²/0.951³ or 1.052 times that of females. The metabolic rate of nonpasserine birds is described by the regression equation:

$$V_{\text{oxygen}}/M_b = 0.679 \times M_b^{-0.277},$$

where V_{oxygen}/M_b is the specific oxygen consumption in liters O₂ per kg body mass per hr, and M_b is body mass in kg (Schmidt-Nielsen 1979:189). Substituting initial measurements of body mass, male metabolic rates would be expected to be 1.043 times that of females. Given that females lost 3.125% body mass during the period of cold temperatures, males would be expected to lose 3.125% × 1.052 × 1.043, or 3.429% body mass (i.e., assuming equal net caloric intakes, males produced heat at a rate of 1.043 times that of females, and then lost that heat 1.052 times faster). The observed value, 11.818%, represented more than 28 times the increased percent body mass loss of males over females attributable to scaling effects.

Differential prey availability (i.e., unequal net caloric intake) was the likely cause of differential loss of body mass. Male and female kestrels undergo similar losses in percent body mass during short-term (79 hr) food deprivation (Shapiro and Weathers 1981). Female kestrels wintering in southcentral Florida evidently were more successful than males in establishing and maintaining territories with sufficient surpluses of prey resources to buffer against substantial reductions in prey availability.

ACKNOWLEDGMENTS

I am grateful to T. C. Grubb, Jr., and T. A. Waite for the many valuable contributions they have made to-

ward this study, including suggestions on statistical analyses, interpretation, and critical reviews of various drafts. Suggestions by T. A. Bookhout also substantially improved this manuscript. Field assistance was provided by M. A. Smallwood, N. J. Smallwood, M. S. Woodrey, and S. L. Morgan. This study was supported by funds from The Ohio State University, Archbold Biological Station, Hawk Mountain Sanctuary Association, and Sigma Xi. This study represents a portion of the dissertation research conducted in partial fulfillment of the requirements for a doctoral degree in zoology at The Ohio State University.

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