A MECHANISM OF SEXUAL SEGREGATION BY HABITAT IN AMERICAN KESTRELS (FALCO SPARVERIUS) WINTERING IN SOUTH-CENTRAL FLORIDA

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ABSTRACT.—I observed the establishment of 240 winter territories by American Kestrels (*Falco sparverius*) on a 293-km census route in south-central Florida during autumn 1985. Most females arrived before males. Analysis of banding records revealed that immatures of both sexes and adult females preceded adult males in autumn migration in eastern North America; thus, the sex ratio of early arrivals was skewed toward females. In south Florida territorial kestrels occupied habitats in decreasing order of foraging quality, as measured by percentage cover of suitable hunting substrate (grasses or weedy forbs <25 cm in height) and woody canopy cover (which was correlated negatively with suitable hunting substrate and obstructed the view of hunting kestrels). Early-arriving males also occupied habitats of superior foraging quality and were as successful as females in defending territories against same-sex and opposite-sex kestrels as high-quality habitats became limited. Results of experiments in which free-flying intruder kestrels were released onto defended territories suggested that males defended winter territories more tenaciously than did females. Because there was no evidence of male submissiveness on the wintering grounds, the female-dominance hypothesis is not a plausible explanation for sexual segregation by habitat in wintering kestrels. Each kestrel's arrival date was apparently the principal determinant of the foraging quality of habitats still available for occupancy; foraging quality was correlated negatively with arrival date for the adult males and for the females and immatures. A delayed molt in adult males, associated with differential sex roles on the breeding grounds, may delay the migratory departure, resulting in the late arrival on the wintering grounds. *Received 20 March 1987, accepted 27 August 1987.*

DIFFERENTIAL habitat use by male and female American Kestrels (*Falco sparverius*) holding solitary winter territories has been observed in northern Mexico (J. Koplin pers. comm.) and in the southern United States (Koplin 1973, Mills 1976, Smallwood 1981, Stinson et al. 1981, Bohall-Wood and Callopy 1986). In these areas of winter segregation, females predominated in habitats characterized as 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) suggested tentatively that females occupied "the best habitats," although he did not measure quantitative habitat characteristics correlated with habitat quality.

South-central Florida is a region with a marked sexual segregation by habitat. I examined the relationship between specific habitat

parameters and foraging quality, and the implications with regard to winter segregation in kestrels (Smallwood 1987). Male and female habitats differed in two important ways. Males typically had access to less suitable hunting substrate. Because the more numerous and larger trees formed a visual barrier, a smaller proportion of the available hunting substrate was visible from any one perch. On average, therefore, male territories were inferior to female territories in terms of prey abundance and prey detection.

Several behavioral patterns were correlated with the differential foraging quality of territories. Males foraged actively for longer periods of time each day to catch a sufficient number of prey items, and males were less likely to reject an opportunity to capture prey, even when the prey item was unusual. During a period of cold weather that reduced the availability of arthropod prey, males experienced a greater relative and absolute loss in body mass, a loss that was too large to be attributed to size-related thermodynamics. Apparently, females were better

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able to establish and maintain winter territories with sufficient surpluses in prey resources to buffer against substantial reductions in prey availability.

The mechanism by which females come to inhabit most of the areas of superior foraging has been unclear. Stinson et al. (1981) observed winter segregation of male and female kestrels in coastal Georgia and listed three hypotheses: "(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." It is unlikely that males prevent females from occupying areas with less suitable hunting substrate and force them into areas of superior foraging quality (Smallwood 1987).

Female dominance on the wintering grounds commonly has been assumed to account for winter segregation in kestrels (Mills 1976, Smallwood 1981, H. Mueller pers. comm.; for a general model that predicts that dominants acquire winter territories in prime habitats, see Gauthreaux 1978: 30). In American Kestrels females average about 9% larger in body mass (Snyder and Wiley 1976), and female nestlings are more aggressive than their male siblings (Sherman 1913, Bent 1938, Roest 1957). Stinson et al. (1981) cited Cade's (1955) conclusion that "masculine submissiveness" was responsible for differential tendencies of male and female territory holders to strike a tethered female intruder, but they were unable to distinguish the possible effects of female dominance from differential habitat preferences.

My objective was to determine the mechanism by which male and female kestrels occupy different habitats during winter. For this purpose I observed the migration of kestrels into south Florida and the acquisition of winter territories.

STUDY AREA AND METHODS

Study area.—The study area was west of Lake Okeechobee in south-central Florida (27°00′N, 81°20′W) and has been described previously (Smallwood 1987).

Census techniques.—I established a 293-km census route in the study area. The route was divided into three sections, surveyed in the same order, one section per day. A census was usually completed over three consecutive days. I conducted 12 complete censuses between 30 September and 10 November 1985, the period in which kestrels arrive on the study area

(Layne 1980, 1982). I included a kestrel in a survey if it was sighted within 250 m of the road and was perching, hovering, or engaged in agonistic behavior. I excluded kestrels that simply flew over the census area, for which there was no evidence of foraging or territorial behavior. For each kestrel included in a census, a 1-ha circular plot centered on the kestrel's location was evaluated for percentage coverage by suitable hunting substrate (grasses or weedy forbs <25 cm in height) and woody canopy, and its location was recorded.

To determine age and to color-mark individuals, I captured kestrels with a modified bal-chatri trap (Berger and Mueller 1959). Retained secondaries are diagnostic in determining adulthood in kestrels (Smallwood and Clark unpubl. data). An interrupted flight feather molt may indicate a relatively early fall migration (see Discussion); consequently, I examined the relationship between the presence of retained secondaries and gender of kestrels known to be adults (by criteria other than retained flight feathers, such as fault-bar patterns or unworn flight feathers; see Parkes 1955).

Because only 41 kestrels were uniquely color-marked and only 10 others were recognized individually by unusual plumage characteristics, I determined territory establishment by an individual when (1) a kestrel of the same sex had been seen on at least two censuses, (2) the most recent sighting had occurred during the second half of the season (seventh to twelfth census), (3) the kestrel had not been missed on more than five consecutive censuses, and (4) all sightings had occurred within a maximum range of 0.56 km along the route (the maximum observed distance traveled by a marked kestrel). The midpoint of each 3-day census period was considered to be the date of territory establishment. Each individual territory holder thus identified had been sighted 2–11 times, and, therefore, an equal number of 1-ha circular plots had been evaluated. Values for coverage by suitable hunting substrate and woody canopy were proportions (area covered/total area) ranging from 0 to 1, and multiple 1-ha plot samples usually consisted of two or three values (e.g. five estimates of suitable hunting substrate might have been 0.9, 0.9, 0.9, 0.7, 0.7). Because of this distribution, means were chosen as the measure of central tendency. Thus, for each territory holder I used mean values for coverage by suitable hunting substrate and woody canopy in all analyses.

I determined the availability of habitats of various foraging quality by dividing the route into 293 sections varying in length from 0.1 to 1.9 km, chosen from a random-numbers table. I evaluated each random location in terms of suitable hunting substrate and woody canopy coverage with a 1-ha plot at the location's midpoint. The side of the road to be sampled was determined at each location by a coin toss, and the plot was centered on the nearest potential kestrel hunting perch.
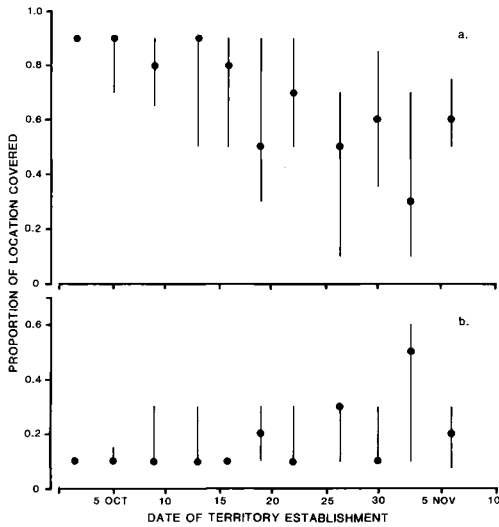
Fig. 1. Foraging quality of random locations occupied by American Kestrels during winter and date of territory establishment in south-central Florida, 1985. (a) Percentage coverage by suitable hunting substrate (grasses or weedy forbs <25 cm in height. (b) Percentage coverage by woody canopy. Median date of territory establishment in each random location ($n = 140$) was determined; the medians (of medians) and the upper and lower quartiles for each date are shown.
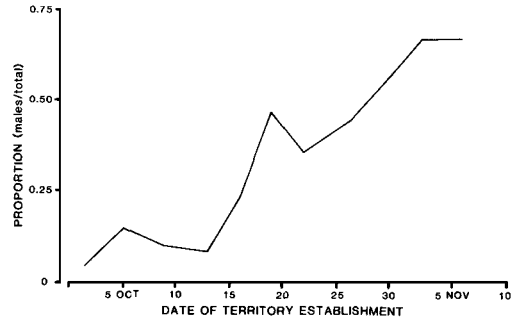

Fig. 2. Sex ratios of American Kestrels establishing winter territories in south-central Florida, 1985. Spearman's rank correlation coefficient, $r_s = 0.934, P = 0.0001, n = 11$.

Analysis of North American banding records.—I obtained from the Bird Banding Laboratory, U.S. Fish and Wildlife Service, records of all kestrels of known age and sex banded in North America east of 100°W, between 38° and 44°N (hereafter east-central North America), during September through November, 1960–1984. The median dates of banding for adult males, adult females, immature males, immature females, pooled males (adults and immatures), and pooled females were determined separately for each year. Analyses were performed using median banding dates from each of the 25 yr as replicates.

Territory-defense experiments.—Twenty-six male and 26 female kestrels were captured and marked by imping uniquely colored rectrices, between 13 and 27 January 1985. Each marked bird was transported at least 25 km and released onto a defended territory within 100 m and within sight of the territory holder. In this way I tested the responses of 52 individual territory holders to same-sex or opposite-sex intruders. All defending kestrels were observed to face the intruder. I defined operationally four levels of response intensity. (1) An *approach* by the territory holder was any flight toward the intruder, other than an attempted prey capture that may have occurred in the same general direction of the intruder. All approaches resulted in the displacement of a perching intruder,

the chasing of a flying intruder, or both. (2) A *chase* occurred when a defending kestrel concurrently flew behind and along the same flight path of an intruder. Chasing behavior was unambiguous in these trials. (3) A *stoop* was a diving flight directed toward the intruder, and (4) a *strike* was physical contact with the intruder. A response at any one level was preceded by each of the lower-level responses, often in quick succession. In each test I recorded the time from release of the intruder until the territory holder approached the intruder, and the time from release until the defender either discontinued chasing a displaced intruder or the intruder left the area.

RESULTS

A total of 240 territories was established along the census route between 1 October and 7 November 1985. The linear abundance of kestrels holding winter territories was 0.82 kestrels/km for the entire route, with a range of 0/km (0 kestrels/12.24 km) to 3.89/km (15 kestrels/3.86 km) for arbitrarily chosen segments of the route.

One or more kestrel territories were established on 140 of the 293 random locations along the census route. Percentage coverage by suitable hunting substrate was correlated negatively with date of territory establishment with regard to the first kestrel to arrive in a random location (Spearman's rank correlation coefficient, $r_s = -0.384, P = 0.0001$), the last kestrel to arrive ($r_s = -0.273, P = 0.001$), and the median arrival date ($r_s = 0.332, P = 0.0001$; Fig. 1a). Percentage coverage by woody canopy was correlated positively with date of territory establishment (date of first arrival: $r_s = 0.225, P = 0.007$; date of last arrival: $r_s = 0.176, P = 0.037$; median arrival date: $r_s = 0.191, P = 0.023$; Fig. 1b).
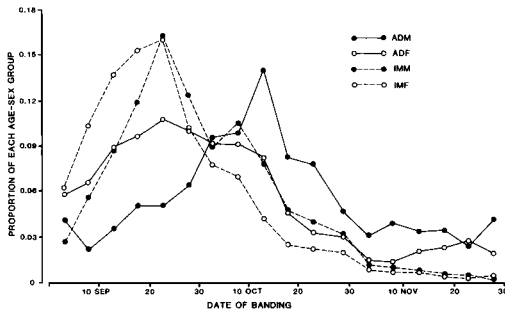
Fig. 3. Temporal pattern of fall migration of American Kestrels in the United States east of 100°W, between 38° and 44°N. ADM = adult males, ADF = adult females, IMM = immature males, IMF = immature females. Data from U.S. Fish and Wildlife Service, 1960-1984.

TABLE 1. Median dates for all American Kestrels of known age and sex banded in North America east of 100°W, between 38° and 44°N, September through November of 1960-1984.

Age-sex[a]	n	Median banding date	Pairwise comparisons[b]		
			IMM	ADF	ADM
IMF	7,846	23 Sept	NS	**	***
IMM	8,366	28 Sept	—	NS	***
ADF	903	1 Oct	—	—	**
ADM	1,252	13 Oct	—	—	—

[a] IMF = immature females, IMM = immature males, ADF = adult females, ADM = adult males.

[b] Two-tailed Wilcoxon's rank sum tests. NS = $P > 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$. P-values were adjusted to control for the experimental error rate using Bonferroni's probabilities (Snedecor and Cochran 1980).

The proportion of males for all kestrels of known sex (sex was determined in 1,268 of 1,283 sightings) sighted on a census (n = 12 censuses) was correlated positively with census date (r_s = 0.909, P = 0.0001); the proportion of males ranged from 0.029 on the first census to 0.352 on the penultimate census. The median date of territory establishment (Fig. 2) was 13 October for females (n = 175) and 22 October for males (n = 65) (2-tailed Wilcoxon's rank sum test, Z = 6.111, P < 0.0001).

The median banding dates (Table 1) for all females (n = 8,749) and males (n = 9,618) during fall in east-central North America were 23 and 28 September, respectively (2-tailed Wilcoxon's rank sum test, Z = 3.666, P = 0.0002). Adult females and immatures of both sexes preceded adult males (2-tailed Wilcoxon's rank sum test, Z = 4.831, P < 0.0001; Fig. 3).

In the study area the median dates of territory establishment of known-age kestrels were: adult females and immatures (n = 25), 13 October; adult males (n = 7), 19 October (1-tailed Wilcoxon's rank sum test, Z = 1.514, P = 0.065; Fig. 4). Eighteen adult kestrels (12 females, 6 males) were examined soon after they established territories. Half of the females but none of the males carried one or more pairs of retained secondaries (Fisher's exact test, P < 0.05).

For territories of known-age kestrels, the median percentage coverage by suitable hunting substrate was 77% for adult females and immatures and 55% for adult males (2-tailed Wilcoxon's rank sum test, Z = 2.214, P = 0.027). The coverage by woody canopy was 10% for adult females and immatures, and 22% for adult males (2-tailed Wilcoxon's rank sum test, Z = 2.224, P = 0.026). Percentage coverage by suitable hunting substrate was correlated negatively with date of territory establishment (Fig. 5a) for adult females and immatures (r_s = −0.435, P = 0.030; a reduction of 0.8%/day) and for adult males (r_s = −0.807, P = 0.028; a reduction of 2.2%/day). Coverage by woody canopy was correlated positively with date of territory establishment (Fig. 5b) for adult females and immatures (r_s = 0.399, P = 0.048; an increase of 0.5%/day), but not significantly so for adult males (r_s = 0.436, P = 0.33; an increase of 0.9%/day).

Of 1,283 kestrel sightings recorded during fall censusing, I observed 43 agonistic encounters involving 85 individuals. Of these, 10 were between opposite-sex kestrels. Four females known to have established territories before the encounters successfully defended those territories against male intruders. Three established males were successful against female intruders, and an additional 3 males were first sighted successfully defending against females. There was no evidence that an intruder of either sex displaced a territory holder of the opposite sex.

Males were more likely than females to respond with territorial defense behavior (response rates of 96% and 73%, respectively) during intruder-release experiments (n = 52 trials: 13 males and 13 females exposed to same-sex intruders and an equal number exposed to opposite-sex intruders), and males tended to give more responses of higher intensity (Fig. 6a). Once a response was initiated, defending males
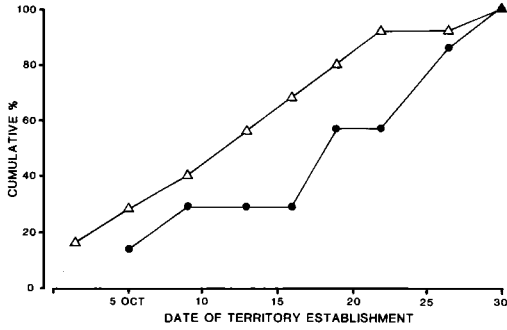
Fig. 4. Temporal pattern of territory establishment by American Kestrels of known age and sex wintering in south-central Florida, 1985. Closed circles represent adult males ($n = 7$); open triangles represent adult females and immatures of both sexes ($n = 25$).

were more likely to strike intruding males than intruding females. Defending females avoided contact with intruders of either sex (Table 2). The time from release of the intruder until the initiation of a response by the territory holder (an approach, if it occurred) was similar for males and females (median values of 13 and 11 s, respectively; 2-tailed Wilcoxon's rank sum test, $Z = 0.000$, $P > 0.99$). The time from initiation of a response until the intruder was driven from the territory was similar (70 s for male territory holders, 74 s for females; $Z = 0.114$, $P = 0.91$), as was the total duration of each intrusion episode (90 s for male defenders, 92 s for females; $Z = 0.329$, $P = 0.74$).

The response rate of males was greater than that of females (92% vs. 62%) when territory holders were tested with opposite-sex intruders ($n = 26$ trials), and males tended to give more responses of higher intensity (Fig. 6b). The time from release of an intruder until an approach by the territory holder was similar for males and females (median values of 13.5 and 8.5 s, respectively; 2-tailed Wilcoxon's rank sum test, $Z = 0.271$, $P = 0.78$). The time from response initiation until the intruder was driven from the territory was similar (72.5 s for male defenders, 59.5 s for females; $Z = 0.039$, $P = 0.97$), as was the total duration of each intrusion episode (106.5 s for male defenders, 129.0 s for females; $Z = 0.039$, $P = 0.97$).

The response rates of defending kestrels toward tethered and free-flying intruder kestrels were similar (Table 3). The responses of kestrels toward untethered intruders were less likely to
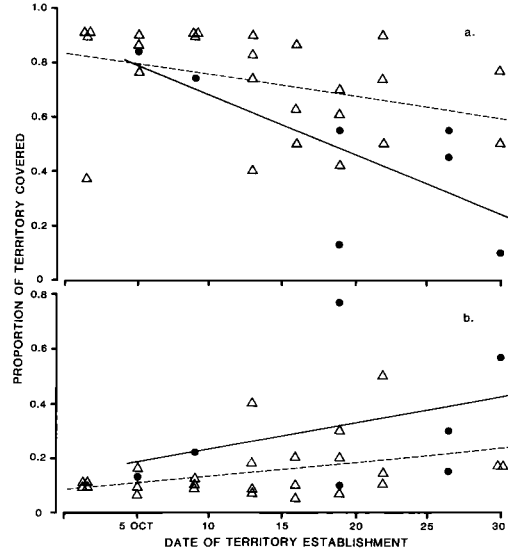

Fig. 5. Foraging quality and date of territory establishment by American Kestrels of known age and sex in south-central Florida, 1985. (a) Proportion of territory covered by suitable hunting substrate (grasses or weedy forbs <25 cm in height). (b) Proportion of territory covered by woody canopy. Closed circles and solid lines represent adult males; open triangles and broken lines represent adult females and immatures of both sexes. Regression lines were fitted by the least-squares method (McClave and Dietrich 1979).

culminate in physical contact than those toward tethered intruders (Table 4).

DISCUSSION

The late arrival of most adult males onto the study area skewed the sex ratio of early arrivals toward females. Banding-data analysis suggests that differential timing is a general characteristic of kestrel migration in eastern North America. The proportion of each age-sex group in the sample may have differed from the proportions in nature. Even so, these data provide strong evidence of temporal differences in the fall migration because it is unlikely that the potential biases in age determination or capture techniques were dependent on date of banding (within the 3-month period). In addition, the large sample size ($n = 18,367$ records of known-age kestrels) provides a high degree of confidence.

Differential timing of autumn migration is widespread in the Falconiformes. In general, immatures precede adults (e.g. Northern Har-
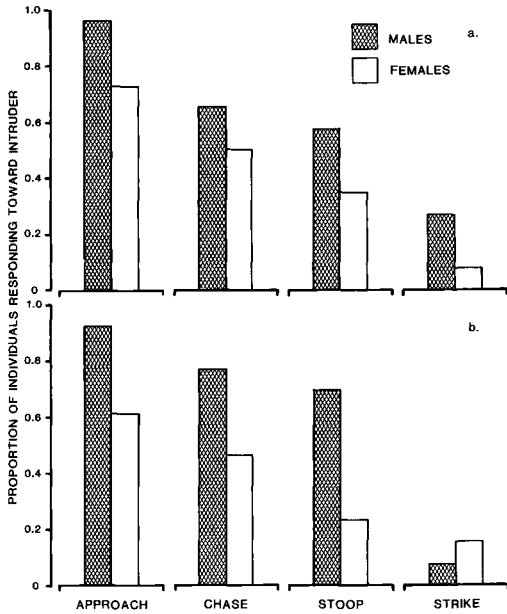
Fig. 6. Responses of territorial American Kestrels toward free-flying conspecific intruders. See text for definitions of approach, chase, stoop, and strike. (a) Pooled results: 13 male and 13 female territory holders each were exposed to a same-sex intruder, and an equal number were exposed to opposite-sex intruders, for a total of 52 trials. Approach, $P = 0.025$; chase, $P = 0.20$; stoop, $P = 0.082$; strike, $P = 0.070$; Fisher's exact tests. (b) Opposite-sex intrusions ($n = 26$) from the pooled results above. Approach, $P = 0.080$; chase, $P = 0.11$; stoop, $P = 0.024$; strike, $P = 0.50$; Fisher's exact tests.

TABLE 2. Differences in the intensity of responses by territorial American Kestrels toward free-flying intruding kestrels during winter in south-central Florida, 1985.

| Defender[a] | Intruder | Response | | Fisher's exact test |
		Struck intruder	Did not strike intruder	P
Male	Male	6	7	0.046
	Female	1	11	
Female	Male	2	6	0.16
	Female	0	11	

[a] Significant block effect; Mantel-Haenszel test, MH = 2.644, $P = 0.004$ (Mantel and Haenszel 1959).

riers, *Circus cyaneus,* Bildstein et al. 1984; Sharp-shinned Hawks, *Accipiter striatus,* Mueller and Berger 1967, Rosenfield and Evans 1980; and Cooper's Hawks, *A. cooperii,* Mueller et al. 1981). Females precede males in Sharp-shinned Hawks (Mueller pers. comm.) and Merlins (*Falco columbarius;* Clark 1985), and, specifically, adult males are last to migrate in harriers (Bildstein et al. 1984), Sharp-shinned Hawks (Rosenfield and Evans 1980), and Peregrine Falcons (*F. peregrinus;* W. Mattox pers. comm.).

The pattern of territory establishment along the census route clearly indicated that the locations of highest foraging quality were occupied first. Although most adult males arrived later than females and immatures, the first adult males to arrive established territories of essentially identical foraging quality, measured by amounts of suitable hunting substrate and lack of woody canopy, as territories concurrently established by females and immatures. Arrival date was apparently the principal determinant of the availability of habitats of various foraging quality; for the adult males and for the females and immatures, the later the date of territory establishment, the lower the foraging quality of the territories.

I examined the possibility that female dominance on the wintering grounds may have played a role in territory acquisition. Of 10 agonistic encounters between opposite-sex kestrels observed during autumn, males were as successful as females in driving off competing conspecifics and maintaining their territories. A female is not guaranteed to win a territorial dispute with a male. The female-dominance hypothesis predicts that females usually can displace established males, either adults or immatures. In fact, there was no evidence that an intruder of either sex was successful in displacing an opposite-sex territory holder. No conclusions may be made about the territorial status of the unmarked kestrels involved in the remaining 33 agonistic encounters, all involving same-sex competitors.

Territory defense was studied in greater detail by means of the intruder-release experiments. The overall response rate of males toward same-sex and opposite-sex intruders, indicated by the lowest-intensity response (approach), was 23% higher than that of females. Males were more likely to give the three higher-intensity responses as well. Apparently, males defended winter territories more tenaciously

TABLE 3. Tendencies of American Kestrels holding solitary winter territories to respond by flying toward tethered or free-flying intruder kestrels.

Defender	Intruder	Tethered intruders[a]		Free-flying intruders		Fisher's exact test
		Trials	Response rate (%)	Trials	Response rate (%)	P
Male	Male	14	79	13	100	0.12
	Female	12	67	13	92	0.14
Female	Male	19	79	13	62	0.25
	Female	16	81	13	85	0.60

[a] Data from Cade (1955).

than did females. This supports the hypothesis that males typically defend smaller surpluses of prey resources above the average minimum level necessary to survive the winter. Kestrels in the study area feed exclusively on arthropods during winter (Smallwood 1987), and, because winter is the dry season in south Florida, the arthropod prey base is essentially a nonrenewable resource for wintering kestrels. Therefore, males would appear to be more vulnerable than females to the effects of an intrusion by a food competitor.

Male territory holders were more likely to respond toward intruding females than vice versa. No significant difference was detected between the durations of intrusion episodes by male intruders and those by females. Although intruding males spent a similar amount of time in the more open territories of females, they were less likely to be attacked.

In opposite-sex intrusions, males defended territories more aggressively than did females but generally stopped short of striking females. Twenty-five percent of female attacks on males produced contact, but contact occurred in only 8% of male attacks on females. The lower incidence of maximal response intensity by males, relative to females, probably represents a tactic for males to avoid physical engagement with a larger intruder. Females also avoided contact with other females, however; of 11 cases in which a female defender responded to a female intruder, physical contact never occurred.

Cade (1955) found that males were less likely to contact female intruders than vice versa, but that result was due primarily to the responses of paired birds; responses of solitary male and female territory holders did not differ significantly. In that study the intruders were restrained by tethers. Compared with the solitary kestrels observed by Cade, I found that kestrels

of both sexes were less likely to make contact with an untethered intruder of either sex, and that birds of both sexes especially avoided physically engaging females. For territorial kestrels physical contact is probably unnecessary for repelling an intruder (for numerous examples of effective, noncontact territorial defense in birds, see Nice 1941).

On more than 650 winter territories observed in the study area between 1983 and 1985 (Smallwood 1987, unpubl. data), there was no evidence that an intruding kestrel of either sex ever displaced an established territory holder. Apparently, a territorial kestrel, regardless of gender, holds a substantial defensive advantage over conspecific intruders, a circumstance that has been documented for many taxa (e.g. spiders, Riechert 1978; crabs, Hyatt and Salmon 1978; fish, Phillips 1971, Zayan 1975; mice, Metzgar 1967). Asymmetries in territorial contests in birds have been attributed to unequal expected payoffs, with the resident having more to gain (White Wagtails, Motacilla alba, Davies and Houston 1981; Great Tits, Parus major, Krebs 1982).

In addition to a possible effect on payoff expectation, prior knowledge of prey distributions represents an advantage for a kestrel defending its winter territory. Territory holders frequently were observed capturing prey during intrusion episodes. If an intruder initiated a pounce, an approach by the defender caused sufficient interference to prevent a successful prey capture. The probability of an intruder capturing prey in a tenaciously defended area is essentially zero, and the only viable option for the intruder is to leave the occupied area. In autumn 1985 only 6.7% of the sightings were of kestrels engaged in territorial disputes. Evidently, disputes are generally brief in nature, lasting only long enough for an intruder to de-

TABLE 4.   Responses by American Kestrels holding solitary winter territories that resulted in physical contact with tethered or free-flying intruder kestrels.

Defender	Intruder	Tethered intruders[a]		Free-flying intruders		Fisher's exact test
		No. responses	Contacts (%)	No. responses	Contacts (%)	P
Male	Male	11	73	13	46	0.18
	Female	8	50	12	8	0.058
Female	Male	15	73	8	25	0.037
	Female	13	69	11	0	0.0005

[a] Data from Cade (1955).

termine the extent of an occupied area. If female dominance on the wintering grounds plays a role in habitat segregation, it is probably restricted to cases in which a male and female arrive at the same location at essentially the same time, presumably an infrequent occurrence. Only then, when neither bird has a defensive advantage because of familiarity with the particular site, might the female's larger size be a significant factor.

The adult males that arrived after the females and immatures probably did not establish territories in the same habitats they would have settled had they arrived earlier. The earliest adult males to arrive were just as likely as females and immatures to establish territories in high-quality habitats (Fig. 5). Apparently, habitat segregation was not due to different preferences.

One might hypothesize that some late-arriving adult males would establish territories in habitats of inferior foraging quality compared with the territories being established concurrently by immatures and adult females. Early in the season an arriving kestrel of either age or sex has a high probability of encountering a vacancy in a prime habitat. A late-arriving adult female, if returning to a high-quality habitat that it occupied the previous winter, would probably find that site occupied and therefore unavailable. Immatures have no previous experience with the wintering grounds. Late-arriving females and immatures must spend time searching for vacancies, and must evaluate the quality of vacancies when deciding to stay or continue searching; this decision process is analogous to the marginal-value theorem ("giving up times," Charnov 1976).

On the other hand, a late-arriving male 2 yr old or older may have the option of returning to the territory held the previous winter. If the

territory is in a marginal habitat, it is likely to still be vacant because of the correlation between habitat quality and arrival date, and because habitats occupied by late-arriving kestrels (of either sex) did not appear to be limited. Much of this habitat, such as citrus groves and residential developments, remained unoccupied by kestrels during winter. Even though a few vacancies in superior habitats may exist late in the season, there would be intense competition for those sites. The best strategy for such a male would be to return to the winter territory of the previous year.

Arrival date was apparently the principal determinant of what habitat was available for winter territories, and the reasons most adult males arrived so late in the season are complex. During summer a breeding male provides a substantial amount of supplemental food for his mate before egg laying and then does most of the provisioning for the incubating or brooding female and the young nestlings (Sherman 1913, Roest 1957, Willoughby and Cade 1964, Balgooyen 1976). As a result of the different sex roles, body mass in males probably declines at the same time females reach their maximum body mass (see Village 1983 for *Falco tinnunculus*). Adult females begin the complete annual prebasic molt during incubation (Balgooyen 1976). As the food demands of the growing young increase and they are brooded less, females resume hunting (Willoughby and Cade 1964, Balgooyen 1976).

At the end of the breeding season the juveniles undergo an incomplete molt, involving some or all of the body feathers (Parkes 1955). By this time the adult females have nearly completed their flight feather molt. Adult males, however, have only recently regained enough body mass to begin the complete adult prebasic molt (Willoughby 1966, Balgooyen 1976). A

similar delayed molt in adult males has been attributed to male provisioning of incubating females and small young in Ospreys (*Pandion haliaetus*) and Eurasian Sparrowhawks (*Accipiter nisus*; Heinroth and Heinroth 1958).

Migration begins at the end of the molt. Indeed, the last pair of flight feathers to be replaced (secondaries or rectrices) were still in sheath on some of the adult kestrels (2 of 4 males, 4 of 7 females) captured in the study area within 8 days of their arrival. Molting of primaries, the loss of which may impose the greatest increase in the aerodynamic costs of flight (Welty 1975: 447), was complete in all but one adult examined on arrival. The delayed departure of adult males is probably the result of their delayed molt.

Adult females were more likely than males to retain secondaries. Interrupted molt of flight feathers in adult females may improve their ability to compete for winter territories, as these birds may begin the fall migration at the earliest possible date. In postbreeding adult males with a later prebasic molt, interruption of the flight feather molt would not overcome the competitive advantage held by adult females employing the same strategy, or by immatures, which do not molt flight feathers. Interrupted molt during migration has been documented in European Quail (*Coturnix coturnix*), Dunlins (*Calidris alpina*; Holmes 1966), Ringed Turtle-Doves (*Streptopelia risoria*), Common Scops-Owls (*Otus scops*), Honey Buzzards (*Pernis apivorus*), Northern Hobbies (*Falco subbuteo*), and Peregrine Falcons (Stresemann 1967).

Molt may be expensive energetically, especially the replacement of flight feathers. In fact, the molt appears to be constrained to occur during favorable periods in the annual energy budgets of Ring-necked Pheasants (*Phasianus colchicus*; Kabat et al. 1950), Dunlins (Holmes 1966), Rufous-collared Sparrows (*Zonotrichia capensis*; King 1972), White-crowned Sparrows (*Z. leucophrys*; Wingfield and Farner 1979), and House Sparrows (*Passer domesticus*; Mathew and Naik 1986). Migration also imposes a substantial energy cost. Nonmigrating kestrels are sit-and-wait predators; in winter in south Florida they spend only 5.5% of the daylight hours in flight (pers. obs.). Migration during a complete molt would result in reduced foraging efficiency, due to crossing regions of unfamiliar prey distributions, during a period of substantially increased energy demand (see King and Murphy

1985 for alternative explanations for reduced locomotory activity during the annual molt).

Differential sex roles of kestrels on the breeding grounds result in a delayed molt in adult males, which in turn delays the migratory departure of adult males and skews the sex ratio of early arrivals on the wintering grounds toward females. Because the areas with the highest proportions of suitable hunting substrate and the lowest proportions of woody canopy cover are occupied first, females, on average, establish most of the territories in the habitats of superior foraging quality. Once a healthy kestrel of either sex is established on a territory, it is unlikely to be displaced. Indeed, males, which defend territories more likely to contain fewer prey resources and therefore potentially suffer more from an intrusion by a food competitor, defend winter territories more tenaciously than females.

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