AMERICAN KESTREL SEX RATIOS AND HABITAT SEPARATION

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UNBALANCED sex ratios of wintering American Kestrels (*Falco sparverius*) have been reported by many authors (Broun 1949, Roest 1957, Willoughby and Cade 1964, Heintzelman and Nagy 1968, Koplin 1973, Mills 1975). Differential mortality and migration have been suggested as explanations for these unbalanced ratios, but no evidence to support them has been presented. Two cases of Kestrel fledgling sex ratios unbalanced in favor of females have been reported (Roest 1957, Smith et al. 1972), but ratios very nearly one to one have been reported in three others (Nagy 1963, Heintzelman and Nagy 1968, Porter and Wiemeyer 1972). Koplin (1973) discovered that the sexes of wintering kestrels in northern California showed a marked difference in habitat utilization. Here I present evidence that differential habitat utilization by the sexes of wintering kestrels is widespread and discuss the nature and possible origin of this behavior.

METHODS

I recorded sex ratios and habitats of kestrels along roadsides from November 1972 to October 1974 as follows: in winter in south Texas, southern California, and Nayarit, Mexico; throughout a year in Arizona; and in late summer in Colorado and New Mexico. Kestrels were sexed with the aid of 10-power binoculars and a 15–60-power telescope. Only kestrels identified to sex are included in the results but, Nayarit excepted, the incidence of unsexed kestrels was very low. Densities were calculated as total kestrels seen per kilometer driven. Major habitats were classified on the basis of the dominant vegetation of the entire area. Thus the habitat of a kestrel in a small grove of trees within a large expanse of open agricultural land was recorded as the latter. In most cases the vegetation immediately beneath the kestrel was also recorded. Some kestrels were trapped and color-marked in Arizona.

RESULTS

I collected data in south Texas from just north of San Antonio to Brownsville in November and December 1972. Major habitats included open agricultural land, thick mesquite scrub, and short deciduous forest of the "hill country" of the Edwards Plateau. Although the ratio of the 128 male to 147 female kestrels observed does not differ significantly from one to one ($\chi^2 = 1.31$, $P > 0.20$), a comparison of the 16 male and 78 female kestrels seen in agricultural lands with the 112 males and 69 females seen in forest and scrub habitats shows a highly significant difference in distribution between the sexes ($\chi^2 = 50.2$, $P < 0.001$). A comparison of the distributions of the sexes within the forest and scrub habitats with respect to the vegetation immediately beneath the bird showed 6 males and 6 females in areas of no or very sparse vegetation, 66 males and 57 females in scattered grass to scattered shrubs, and 40 males and 6 females in shrubs and trees. The difference between the sexes is significant ($\chi^2 = 16.4$, $P < 0.001$).

No significant difference ($\chi^2 = 1.46$, $P > 0.4$) between the sexes existed in agricultural land with respect to vegetation immediately beneath kestrels, where the distributions were 6 males and 42 females in areas of no or very sparse vegetation, 8 males and 34 females in scattered grass to scattered shrubs, and 2 males and 2 females in shrubs and trees. For statistical analysis the last two vegetation categories were combined. Densities, expressed as birds per 100 km, were 18 in agricultural areas, 15 in mesquite scrub, and 11 in forests. Of course, densities in specific areas varied as did densities in the same regions at different times.

I collected data intermittently in southern Arizona from October 1973 to October 1974. Major habitats visited included grasslands, pecan groves, and a variety of deserts, but 54% of the 423 sightings were made in irrigated agricultural land.

The distributions of the sexes in winter (October through February) were as follows: 42 males and 93 females in irrigated agricultural land, 2 males and 17 females in grasslands, 45 males and 38 females in deserts, 32 males and 6 females in orchards or forests, and 20 males and 5 females within cities. A significant difference ($\chi^2 = 57.5$, $P < 0.001$) in habitat utilization is shown, although the ratio of 141 males to 159 females does not differ significantly from one to one ($\chi^2 = 1.08$, $P > 0.2$).

All types of deserts are lumped into one category because no significant difference ($\chi^2 = 2.9$, $P > 0.2$) in distribution between the sexes within desert habitats was noted. These distributions were 21 males and 13 females in very sparsely vegetated deserts, 11 males and 16 females in deserts of intermediate vegetation, and 13 males and 9 females in thick saguaro or palo verde forest. Densities were recorded on most trips, but relatively short routes were covered several times so densities may reflect local conditions only. Representative densities in major habitats, expressed as birds per 100 km were: 16 in agricultural lands, 11 in deserts, and 9 in grasslands. A comparatively high 49 was obtained in pecan groves, but a distance of only 21 km was driven five times.

Spring data from March to May in Arizona agricultural lands showed no difference in sex ratio from one to one (39 males, 47 females; $\chi^2 = 0.75$, $P > 0.3$), whereas in winter the sex ratio in these same lands had been very different from one to one (42 males, 93 females; $\chi^2 = 7.1$, $P < 0.01$). Many kestrels in spring appeared to be paired and limited individual marking (26 individuals) indicated that many were transitory, whereas earlier marked birds had appeared more sedentary.

Summer data were collected in July and August mainly in the grasslands of southeastern Arizona. Small samples exclude Chi-square testing, but the distributions of 1 male and 7 females in agricultural land, 2 males and 17 females in grassland, and 7 males and 3 females in thick mesquite and heavily wooded riparian areas indicate the same trends as in winter. Of interest is that all three females in the wooded areas were seen with males. The sex ratio for these summer data favored females and differed significantly from one to one ($\chi^2 = 7.8$, $P < 0.01$).

Large concentrations of kestrels were encountered on two occasions in Arizona. On 4 November, I counted at least 11 kestrels, 10 females and 1 male, in a recently plowed field of about 90 acres. Many were hovering and capturing insects from the ground while others were sitting on the ground. Several chases between kestrels were noted. On 5 October 1974 I counted 15 male and 7 female kestrels in less than 1 mile (1.6 km) along the west side of the Chiricahua Mountains. Many were perched in groups of two or three, often of the same sex, in a grassy field with scattered shrubs. No aggressive interactions were seen.

The distributions of kestrels recorded in Colorado, northwestern New Mexico, and northeastern Arizona in mid-August were as follows: no males and 7 females in agricultural areas, 3 males and 3 females in alpine grasslands, 21 males and 33 females in grasslands with scattered junipers, 7 males and 7 females in sagebrush with scattered juniper, and 4 males and 1 female in wooded areas. Although no significant difference in sex ratio from one to one ($\chi^2 = 3.76$, $P > 0.05$) is shown and small samples in some vegetation categories exclude use of the Chi-square test, the data suggest the same trends observed elsewhere. In addition, only males were seen immediately over densely vegetated places within the major habitat types and one stretch of grassland in New Mexico produced 13 females to only 3 males. No densities were calculated.

Although sample size is small and data can be no more than suggestive, the following information merits mention because of its striking nature.

Of 23 kestrels seen in the vicinity of El Centro, California on 3 January 1974, 19 were females. All four males were seen on telephone wires in the city whereas only females were seen in the agricultural fields outside the city.

In coastal Nayarit, Mexico near Mazatlan on 22 March 1974, only seven of hundreds of kestrels seen in open agricultural fields were identified to sex because of rough road conditions. All seven were females. Of 14 kestrels seen on 22 and 23 March from Mexico Route 40 in thorn scrub, oaks, and pines, only 2 were females and 12 were males.

DISCUSSION

The above data, along with that of Koplin (1973) in California and Mills (1975) in Ohio, indicate that winter habitat separation by the sexes of the American Kestrel is widespread, with females more often found in open, sparsely vegetated habitats and males more often found in habitats of denser vegetation. Data from Texas indicate that within these more heavily vegetated habitats males are more likely to be seen in clearings. Habitat separation in summer may also be widespread, but perhaps not to the extent as in winter. Summer data from southern Arizona showed marked differences in distributions of the sexes but data from Colorado and New Mexico were not conclusive. More data are needed before definite conclusions can be reached.

Perhaps the unbalanced sex ratios reported in the literature are simply reflections of the habitat sampled, but other factors may also affect the distributions of the Kestrel sexes. A differential degree of migration or timing of migration is still possible, but the former may be difficult to establish on the basis of sex ratio alone as differences between areas may reflect habitat separations. Some data suggest that males may winter at the northern limit of the winter range regardless of habitat. Johnson and Enderson (1972) reported that 17 of 21 kestrels identified to sex in open agricultural land in Colorado in winter were males, and Roest (1957) reported that wandering kestrels in eastern Oregon in winter were all males. A selection for the earlier arrival of males on the breeding grounds to find a suitable nest site may be responsible for these northern males. Roest (1957) and Smith et al. (1972) have indicated an earlier spring arrival of males in regions where kestrels do not winter, although Enderson (1960) detected no difference.

In addition to the above, the extent of habitat separation between the sexes is surely affected by other factors. Some likely ones are: (1) Transition and patchy habitats may provide requirements for both sexes. Therefore habitat separation should be most obvious where major habitat divisions are marked, as was the case in Texas and northern California (Koplin 1973). (2) Paired winter kestrels as reported by Cade (1955) and Mills (1975) could reduce the extent of separation, but the extent of winter habitat separation suggested by this paper indicates that many kestrels do not pair for life as has been suggested (Bent 1938). (3)

The onset of courtship and nesting behavior would necessarily cause a breakdown of habitat separation as evidenced by spring data from Arizona and Ohio (Mills 1975). (4) Migrating kestrels may concentrate where prey, such as grasshoppers, are temporarily abundant. This may have contributed to the reduction in separation noted in August in Colorado, New Mexico and northeastern Arizona. Indeed, if habitat separation functions to reduce intersexual competition for food as discussed below, it should be most evident when food is most limiting.

Koplin (1973) interpreted winter habitat separation by kestrels as character displacement that reduces competition for food between the sexes consistent with the ideas of Selander (1966). Such displacement is especially likely if winter food is limiting. Some information consistent with the hypothesis that winter food limits kestrel populations follows: (1) As the winter range of North American kestrels is less than two-thirds that of the summer range (Bent 1938, Robbins et al. 1966), winter density must be higher than in summer. (2) In the northern part of the winter range, at least, winter food is limited largely to vertebrates, whereas in summer both vertebrates and invertebrates are eaten (Bent 1938, Craighead and Craighead 1956, Heintzelman 1964, Collapy 1973). Even in southern Arizona and Texas I have noted a marked decrease in insect abundance in the colder winter months. (3) Territoriality appears to be well established in winter (Cade 1955, Mills 1975) but several authors have commented on weak territorial defense in summer or high, almost "colonial," nesting densities (Stochard 1905, Cade 1955, Roest 1957, Nagy 1963, Smith et al. 1972). Although I noted no definite territorial behavior in winter in Arizona, I did see far fewer kestrels of the same sex perched near each other in winter than in spring or early fall. The large concentrations reported in this study suggest that kestrels are not territorial during migration. I believe sufficient evidence exists to indicate that winter territoriality in kestrels functions mainly to protect a food supply. Thus territoriality should be most strongly established when prey are scarce.

Reconstructing the origins of behaviors is often difficult as secondary adaptations may obscure them. Still it is interesting to speculate on the selective pressures that have resulted in habitat separation by kestrels. Here I develop an argument consistent with current theories of size dimorphism in raptors (see Reynolds 1972 for review) to which differential habitat utilization is undoubtly related.

Evidence discussed suggests habitat separation by kestrel sexes as a mechanism to reduce winter competition. The other major possibility is that it is a carryover of selection to reduce competition during breeding. During the breeding season the sexes may hunt in different habitats or select different prey, causing selection of different habitats in winter where optimum prey are found. At the annual meeting of the Cooper Ornithological Society in 1973, Thomas Balgooyen reported a form of breeding habitat separation for kestrels in which the male occupies most of the territory and acts as food provider for the female and young. The male's role as common food provider was also noted by others (Sherman 1913, Roest 1957, Willoughby and Cade 1964). But this is quite different from the nature of the winter separation, and food competition could occur only at some time when both sexes hunt to feed the young, as was indicated for Goshawks (*Accipiter gentilis*) (Schnell 1958). Such an increase in female hunting activity was reported for kestrels by Smith et al. (1972). In addition, Cade (1960) indicated that no difference in the kinds or sizes of prey taken by the sexes of kestrel exists, but records of birds as prey of kestrels where the sex of the kestrel has been identified (Table 1) show a marked predominance of males. The dates of these records suggest that the difference is not limited to one time of the year. But even if males do prey more on birds, this seems more likely a result of habitat separation and not a cause.

Differential habitat use in winter, though it does not seem to be a carryover of breeding selection, must still have a foundation in the breeding season because the separation is on a sex basis. Sexual size dimorphism, although less than in many raptors (Cade 1960), could provide the initial difference to cause habitat separation. Whether this size difference is due to energetic reasons as proposed by Reynolds (1972) and Mosher and Matray (1974), or some aspect of female dominance as proposed by Cade (1960) and Amadon (1959), it seems reasonable that winter habitat separation is a result of female dominance because of her larger size. Several authors (Sherman 1913, Roest 1957, May *in* Bent 1938) commented on the more aggressive behavior of both young and adult female kestrels. Cade (1955) reported a difference in winter territorial defense with females apparently more aggressive.

Density data from this study and from Koplin (1973) circumstantially support the female dominance theory. With the exception of the Arizona pecan groves, the highest densities were consistently found in the more open country where females predominated, suggesting that females were occupying the best habitats. Even in more densely vegetated places where males predominated, these males were more often seen in clearings. Much of this difference in densities may simply be due to a greater conspicuousness of kestrels in open lands. This and variables such as weather, time of day, specific local conditions, and the distribution of utility lines where kestrels often perch may make much of the density data unreliable.

TABLE 1

RECORDS OF BIRDS AS PREY OF THE AMERICAN KESTREL[1]

Sex of kestrel	Prey species	Month	Authority
Male[2]	Cliff Swallow[3] (*Petrochelidon pyrrhonota*)	April	Bonnot 1921
Male	Tree Sparrow[4] (*Spizella arborea*)	Nov.	Wharton 1930
Female	Song Sparrow[4] (*Melospiza melodia*)	March	Broun 1932
Male	Hermit Warbler (*Dendroica occidentalis*)	May	Grinnell 1933
Female	Eastern Bluebird[3] (*Sialia sialis*)	June	Drinkwater 1953
Male	American Robin (*Turdus migratorius*)	July	Lamore 1956
Male	American Robin	—[5]	Marshall 1957: 72
Male	Mourning Dove (*Zenaida macroura*)	March	Lesser 1966
Male	Ruby-throated Hummingbird (*Archilochus colubris*)	Sep.	Mayr 1966
Male	Bank Swallow[6] (*Riparia riparia*)	June	Freer 1973
Male	Least Sandpiper[7] (*Calidris minutilla*)	—[7]	Page and Whitacre 1975
Male	"small shorebird"[7]	—[7]	Page and Whitacre 1975
Male	Water Pipit (*Anthus spinoletta*)	—[7]	Page and Whitacre 1975
Male	*Savannah Sparrow* (*Passerculus sandwichensis*)	—[7]	Page and Whitacre 1975
Male	Townsend's Warbler (*Dendroica townsendi*)	—[7]	Page and Whitacre 1975
Male	White-crowned Sparrow (*Zonotrichia leucophrys*)	—[7]	Page and Whitacre 1975
Male	Western Bluebird (*Sialia mexicana*)	June	M. Robbins pers. comm
Male	Verdin (*Auriparus flaviceps*)	March	S. Alden pers. comm.
Male	House Sparrow (*Passer domesticus*)	March	S. Alden pers. comm.
Male	Brewer's Sparrow (*Spizella breweri*)	April	R. Glinsky pers. comm.
Male	"small bird"	Jan.	R. Glinsky pers. comm.
Male	Mourning Dove	Dec.	Pers. obs.
Male	Inca Dove (*Scardafella inca*)	Dec.	Pers. obs.
Male	Starling (?) (*Sturnus vulgaris*)	Jan.	Pers. obs.
Female	House Sparrow	Dec.	Pers. obs.
Male	House Sparrow	Sep.	Pers. obs.
Male	House Sparrow	Nov.	Pers. obs.

[1] Includes only records that indicate the sex of the kestrel.

[2] No sex mentioned, but referred to as "he."

[3] Taken from nest.

[4] Taken from bird trap.

[5] No date given, but spring is indicated because the robin was a juvenile and was taken from the male by a female.

[6] Many occurrences, always male kestrel involved when specified.

[7] Twelve definite records for Least Sandpiper and two for "small sandpipers." At least three different male kestrels were involved in these records of Page and Whitacre. Records were observed in January, February, and December.

If female dominance were forcing males into less suitable habitats, selection would favor males that were more adaptable and possibly males would eventually select these habitats. A greater flexibility in behavior of males appears to exist as evidenced by males appearing more often in cities and at the northern limit of the winter range. As Roest (1957) said, "the male Sparrow Hawk may have the greater ability to adjust to changed conditions." This same ability to adjust may also contribute to the breeding fitness in his role of common food provider.

Once a habitat separation between the sexes has been established many secondary adaptations are likely to result. One possibility is that some of the size dimorphism may be a result of selection on the wintering grounds. Storer (1966) indicated a relationship between migration and size dimorphism in North American accipiters and suggested that selection in winter may contribute to dimorphism.

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SUMMARY

Data are presented that indicate differential habitat utilization by American Kestrel sexes in winter is widespread. Factors affecting the extent of habitat separation are discussed, and it is suggested that this behavior, with range and food reductions and changes in territoriality, indicate winter limitation of kestrel populations. A possible origin for habitat separation is discussed.

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