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USE OF HABITAT AND PERCHES, CAUSES OF MORTALITY AND TIME UNTIL DISPERSAL IN POST-FLEDGING AMERICAN KESTRELS

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Abstract.—The use of habitat and perches, causes of mortality and time until dispersal of American Kestrels (*Falco sparverius*) after they fledged from nest boxes on the backs of highway signs were studied along Interstate 35 in central Iowa. Between 1988 and 1990, radio-transmitters were attached to 61 nestlings in 47 nests just before nest departure. During the first week after fledging and before hunting began, kestrels spent substantial amounts of time perched on the ground along the interstate right-of-way and in row-crop fields. All but one of the 16 kestrels found dead died during the first week after they fledged, before their flying skills had developed. Mammalian predation accounted for six of the deaths and was the main cause of mortality. Only two deaths resulted from collisions with vehicles on the interstate. After the first week, fledgling kestrels began hunting along secondary roads and increased the use of this habitat throughout the 4 wk birds were observed. Mean time until the initiation of dispersal was 22.7 d after fledging. Only one of 17 birds recaptured in a nest box as a breeding bird was banded as a nestling.

USO DE HABITAT Y PERCHAS, CAUSAS DE MORTALIDAD Y LAPSO HASTA QUE SE DISPERSAN INDIVIDUOS POST-VOLANTONES DE *FALCO SPARVERIUS*

Sinopsis.—El uso de habitats y perchas, las causas de mortalidad y el lapso de tiempo que toman antes de dispersarse volantones del falconcito *Falco sparverius* (desde cajas colocadas detrás de rótulos de carreteras) fue estudiado a lo largo de la Interestatal 35 en la parte central de Iowa. Entre el 1988 y 1990, se le colocaron radiotransmisores a 61 pichones (de 47 nidos) antes de que éstos dejaran el nido. Durante la primera semana, luego de dejar el nido y antes de comenzar a cazar de forma independiente, los falconcitos pasaron gran parte del tiempo posados en el suelo a lo largo de los "ceda el paso" de la interestatal y en las filas de sembradíos. Todos, excepto uno de los 16 falconcitos, murieron durante la primera semana luego de dejar el nido, cuando aún las destrezas de vuelo no habían sido totalmente desarrolladas. La depredación por parte de mamíferos (seis muertes) fue la principal causa de mortalidad. Sólo dos muertes fueron causadas por colisiones con vehículos. Luego de la primera semana, los falconcitos comenzaron a cazar a lo largo de carreteras secundarias e incrementaron el uso del habitat a través de las cuatro semanas de observación. El período promedio de tiempo para que estos se dispersaran resultó ser de 22.7 d. luego de abandonar el nido. Sólo uno, de las 17 aves recapturadas en una caja de anidamiento, fue anillado como pichón.

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The American Kestrel (*Falco sparverius*) requires open country for hunting (Cade 1982). The species is remarkably adaptable, which is evident from its distribution over a wide range of habitats such as agricultural lands, urban and suburban environments, and highway and railroad rights-of-way (Bird and Palmer 1988, Brown and Amadon 1968, Cade 1982). Bird and Palmer (1988) suggested that deforestation and development have caused a continent-wide increase in the size of the American Kestrel population.

Before settlement, Iowa's land was mainly prairie, with about 19% woodlands (Thomson and Hertel 1981) and about 11% wetlands (Dahl 1990). Today, the landscape of Iowa is an agricultural mosaic of row-crop fields and pastures, interspersed with cities and towns and an extensive network of roadways. Only isolated fragments of remnant prairie remain, and woodlands and wetlands constitute 4% and 1% of the land area, respectively (Dahl 1990, Thomson and Hertel 1981).

In 1988, we began a study of kestrels nesting in nest boxes attached to the backs of highway signs along Interstate 35 (I-35) in central Iowa (Varland et al. 1991, Varland and Loughin 1992). In this paper, we describe the use of habitat and perches, causes of mortality and time until dispersal of kestrels fledging from these nests.

STUDY AREA AND METHODS

Fieldwork was conducted in central Iowa between May and September 1988–1990. Nest boxes were located at about 2-km intervals. Land bordering I-35 was intensively farmed with row crops.

We banded 99% (206/207) of the young in 93 nest boxes with U.S. Fish and Wildlife Service leg bands and, just before they fledged, we marked each bird with colored vinyl leg jesses (Platt 1980). Jesses were made with Norcross virgin vinyl (Norcross Industries, West Palm Beach, Florida) strips that were 6.3 cm long and 1.4 cm wide and riveted together with a trailing tab about 2.5 cm long. We captured 59% (113/190) of the adult kestrels in the nest box or with *bal-chatri* noose traps (Berger and Mueller 1959). We banded and individually marked adults with colored vinyl leg jesses.

To locate birds for observation, we attached back-mounted radio-transmitters to 61 kestrels in 47 nest boxes 1–3 d before fledging. We followed birds in a vehicle with top-mounted dual yagi antennae. Brood sizes ranged from one to six young, and the number of radio-marked individuals in a brood ranged from one to all siblings. We radio-marked 12 individuals in nine nests in 1988, 14 individuals in 14 nests in 1989, and 35 individuals in 24 nests in 1990. In 1990, the size of broods was experimentally adjusted to two siblings in 15 nests and five siblings in nine nests to study the influence of brood size on foraging efficiency (Varland and Loughin 1992).

We observed the radio-marked individual(s) in a fledgling group between 0600 and 1300 hours on a rotational basis at 1–3 d intervals until contact was lost. Loss of contact occurred when we were unable to receive a radio signal either because the transmitter failed or because the kestrels left the area. As we did not locate every radio-marked kestrel daily, the exact day of dispersal or death was sometimes unknown; we estimated the time of death or dispersal as the midpoint between the last two visits.

We recorded data on the use of perches and habitat after a radio-marked bird was sighted. These data describe "use" of habitat and not "selection" of habitat in the sense of use by availability (Alldredge and Ratti 1986, Johnson 1980).

Data were collected in 1989 and 1990 just before or during 5–60 min behavioral observation sessions (Varland et al. 1991, Varland and Loughin 1992). Before beginning an observation session, we recorded the perch type and habitat within a circle of 2-m radius centered on each radio-marked individual in the brood. We recorded the habitat where hunting kestrels pounced within a circle of 2-m radius centered on each pounce site during behavior sessions. For each behavior session, one individual was randomly selected to serve as the focal bird for observation (Varland et al. 1991, Varland and Loughin 1992). In 1989, focal birds were either radio-marked or color-marked with jesses. In 1990, only radio-marked kestrels served as focal birds.

We classified structures that kestrels used as perches: fence or fencepost, tree, ground, interstate sign, billboard, utility pole or wire, or other (e.g., hay bales, buildings). In 1989 only, we recorded the perch from which hunting kestrels initiated pounces.

We recognized 11 different habitat types: right-of-way (the grassy area of the interstate highway), secondary road (the grassy area and road surface of any road that was not an interstate highway), cornfield or soybean field (actively farmed cropland), farmstead (contained farm buildings and usually trees and shrubs), old field (ungrazed field with scattered trees), pasture (grazed field with or without trees), grassy fencerow (fence line with a 0.5–1.0 m strip of grass), wooded fencerow (fence line with woody trees or shrubs), grassland (land in the federal Conservation Reserve or Set Aside Program), and other (alfalfa fields and woodlands).

Dispersal.—When contact with a radio-marked kestrel was lost, we searched an area of about 64 km^2 around its last known location. We followed Wyllie's (1985) definition of dispersal, which is movement of a bird farther than 1 km from its nest without return. We determined time of dispersal only for kestrels with transmitters known to be functioning 1 wk after fledging. Birds whose signal was lost <1 wk after fledging ($n = 8$) were not classified as dispersed because young kestrels at this age were relatively inactive and incapable of long sustained flight. Thus, signal loss from these transmitters because a bird moved from the search area was unlikely. Transmitter failure was confirmed for three of the eight transmitters with early signal loss when the kestrels wearing these units were observed with other radio-marked kestrels. Data on dispersal were collected during 1988–1990.

Causes of mortality.—Data on the causes of mortality of kestrels were collected during 1988–1990. We classified mortality as mammalian or avian predation, collisions with moving vehicles or trees, starvation, dehydration, and unknown. Mammalian predation was distinguished from avian predation by the presence of teeth marks on radio-transmitters, sheared instead of plucked feathers, and mammal tracks or scat near the kill (Bull et al. 1989, Fitzner 1980). Necropsies to determine the cause of death of two birds were conducted at the College of Veterinary Medicine at Iowa State University.

Statistical analysis.—We grouped use of habitat and perches by week, starting with fledging and ending 4 wk after fledging. For six radio-marked kestrels, data on use of perches and habitat were collected during the fifth week after fledging. As few observations were made during the fifth week, we combined these data with the data on use of perches and habitat by kestrels during the fourth week post-fledging.

The observational unit (n) was the sibling group. We computed means for observations of use of habitat and perches for each week post-fledging by first averaging the data from observations of all radio-marked members of a sibling group and then averaging the means obtained for each sibling group.

We used the general linear model procedure (PROC GLM, SAS Institute 1985) for an analysis of variance (ANOVA) and tested for linear trends in habitat use over time. As data were missing from some cells (not all sibling groups were represented in all weeks), we used Type III sum of squares to calculate P values. We selected 0.05 as the level of significance for linear time trends in habitat use. As habitats were not independent, we adjusted the significance level of P values using Bonferroni's inequalities (Snedecor and Cochran 1989). Thus, the level of significance for these tests is 0.05 divided by the total number of tests being made on a set of non-independent habitats.

RESULTS AND DISCUSSION

Habitat use.—During the first week after fledging, kestrels spent <1% of their time foraging or flying; the remainder was spent in inactive behavior, primarily perch resting (Varland et al. 1991, Varland and Loughin 1992). At this time, we observed kestrels mostly along the interstate right-of-way and in cornfields and soybean fields (Table 1). In cropland, kestrels frequently perched at field perimeters in trees and on fences and fenceposts (Table 2). Trees and fences and fenceposts on the interstate right-of-way were also common perches for fledglings. Fences and fenceposts were at the perimeter of the right-of-way, whereas trees generally were midway between the fence line and the road.

Kestrels often perched on the ground along the interstate right-of-way and in cropland (Table 2). Nearly all observations of kestrels perched on the ground (39/44) were from the first week after fledging, and 82% (36/44) were from the first 4 d after nest departure.

Young kestrels fed almost exclusively on insects, and most of those identified were grasshoppers (Order Orthoptera; Varland et al. 1991, Varland and Loughin 1992). When kestrels began hunting the second week after fledging, they spent substantial time hunting in soybean fields (Table 3). Pounces in soybean fields at this time (data for 1989 only; n = 4) were most often from the fields' edge; 37.5% (SE = 23.9) occurred while perch hunting from utility wires or poles, 20.8% (SE = 12.5) while

TABLE 1. Observations (Obs) of post-fledging American Kestrels in 11 habitats in Iowa.

Habitat	Weeks post-fledging 1 (Obs = 97) Mean % (SE) (n^a = 30)	2 (Obs = 60) Mean % (SE) (n = 21)	3 (Obs = 59) Mean % (SE) (n = 19)	4 (Obs = 49) Mean % (SE) (n = 14)	P^b
Right-of-way	23.5 (6.3)	4.4 (2.7)	1.3 (1.3)	3.6 (3.6)	0.068
Cornfields	23.9 (6.0)	11.9 (6.1)	9.2 (4.7)	1.8 (1.8)	0.958
Soybean fields	15.0 (4.5)	19.8 (7.4)	8.9 (3.5)	6.2 (3.1)	0.449
Farmsteads	8.4 (4.0)	21.8 (8.0)	25.1 (8.4)	36.5 (11.2)	0.173
Old fields	6.5 (3.7)	7.1 (5.2)	0.0	0.0	0.053
Pastures	5.0 (3.7)	6.0 (4.8)	9.6 (6.1)	13.7 (8.1)	0.795
Grassy fencerows	4.3 (2.2)	5.6 (3.9)	6.1 (5.3)	0.0	0.942
Grasslands[c]	4.2 (2.4)	9.5 (5.3)	6.6 (2.8)	4.1 (3.6)	0.554
Secondary roads	3.7 (3.3)	9.1 (4.6)	27.4 (7.3)	33.0 (9.9)	0.003
Wooded fencerows	3.3 (3.3)	4.8 (3.7)	2.6 (2.6)	0.0	0.934
Other	2.2 (2.2)	0.0	3.1 (2.6)	1.2 (1.2)	0.486

[a] Number of sibling groups observed.
[b] P-values are based on ANOVA F-tests for linear trends across 4-wk post-fledging (df = 1, 48).
[c] Land in Conservation Reserve or Set Aside Programs.

perch hunting from trees, 9.4% (SE = 9.4) while perch hunting from fences or fenceposts, 7.3% (SE = 7.9) while perch hunting from the ground, and 25.0% (SE = 25.0) while hover hunting (three unsuccessful pounces on insect prey by one kestrel).

As foraging and flying skills developed, kestrels shifted their use of habitat from the interstate right-of-way and crop fields to secondary roads and farmsteads (Table 1). Use of secondary roads increased linearly with

TABLE 2. Observations (Obs) of American Kestrel perch locations along the I-35 right-of-way, in cornfields and in soybean fields the first week after fledging in Iowa.

Perch	Habitat: Right-of-way (Obs = 23) Mean % (SE) (n^a = 14)	Cornfields (Obs = 28) Mean % (SE) (n = 16)	Soybean fields (Obs = 32) Mean % (SE) (n = 12)
Trees	33.3 (14.4)	22.9 (10.4)	2.1 (2.1)
Fences or fenceposts	39.3 (11.9)	31.2 (12.0)	45.6 (12.7)
Ground	23.8 (10.0)	43.8 (12.8)	40.0 (12.6)
Interstate signs	3.6 (3.6)	0.0	0.0
Billboards	0.0	0.0	8.3 (11.2)
Utility wires or poles	0.0	0.0	1.9 (1.9)
Other	0.0	2.1 (2.1)	2.1 (2.1)

[a] Number of sibling groups observed.

TABLE 3. Observations (Obs) of hunting pounces by post-fledging American Kestrels in 10 habitat types in Iowa.

Habitat	Weeks post-fledging[a] 2 (Obs = 62) Mean % (SE) (n^b = 10)	3 (Obs = 187) Mean % (SE) (n = 18)	4 (Obs = 332) Mean % (SE) (n = 14)	P^c
Right-of-way	2.5 (2.5)	0.0	0.0	—
Cornfields	10.0 (10.0)	8.3 (6.1)	0.5 (0.5)	0.869
Soybean fields	42.5 (15.8)	16.0 (6.4)	9.5 (7.1)	0.048
Farmsteads	0.3 (0.3)	0.3 (0.3)	0.0	—
Pastures	0.0	3.7 (2.9)	13.4 (7.1)	—
Grassy fencerows	0.0	4.2 (4.2)	0.0	—
Grasslands[d]	17.9 (12.0)	22.3 (8.6)	10.8 (5.3)	0.568
Secondary roads	27.1 (13.2)	32.4 (8.8)	61.6 (9.3)	0.249
Unknown	0.0	5.6 (5.6)	0.0	—
Other	0.0	7.2 (5.6)	4.3 (3.6)	—

[a] Observed one pounce by a kestrel the first week after fledging.

[b] Number of sibling groups observed.

[c] P-values are based on ANOVA F-tests for linear trends across 3-wk post-fledging (df = 1, 18).

[d] Land in Conservation Reserve or Set Aside Program.

time (Table 1, $P = 0.003$) because kestrels frequently foraged there (Table 3). Most of these roads were gravel surfaced and had little vehicular traffic. Kestrels perch-hunted along secondary roads from utility poles or wires, fences or fenceposts, and the ground. Pounces for which we identified the specific location of the strike (n = 21 sibling groups; observations for 1989 and 1990), 49.2% (SE = 7.4) were on the road surface, 25.2% (SE = 7.0) on the grassy roadside, and 25.6% (SE = 7.4) at the interface between the road surface and the roadside grass.

Secondary roads were good foraging sites for kestrels because they had low traffic volume and a variety of perches, and they provided an unobstructed surface from which insects could be easily caught. Utility poles and wires were particularly useful perches for foraging because they provided kestrels with an unrestricted view and an opportunity for positioning at specific locations along the perch continuum of the utility line (Shrubb 1982).

The interstate right-of-way was not a frequent foraging site for fledgling kestrels (Table 3). One contributing factor probably was a general lack of utility poles and lines for perching in this habitat. If vocal communication occurs between kestrels during social hunting (Varland et al. 1991, Varland and Loughin 1992) or other behavioral interactions, vehicular noise would prevent or limit information transfer. The constant traffic along the interstate probably prevented kestrels from foraging on or near the road surface, an important foraging location on secondary roads.

Kestrels used farmsteads throughout the post-fledging period (Table 1), primarily as night roosts and as resting sites between daily hunting forays. Farmsteads were not frequent foraging habitat (Table 3).

Mortality.—All but one of the 16 kestrels found dead died the first week after fledging. At this time, and especially during the first 3–4 d after fledging, kestrels were not proficient fliers. This lack of proficiency probably contributed to mortality from mammalian predation and collisions. Six of 14 birds for which the cause of death was known were killed by mammalian predators. Three were killed by avian predators, two by colliding with vehicles on I-35, one by starvation, and one by dehydration. The cause of death for two birds was unknown. Red foxes (*Vulpes vulpes*) were identified as the predators of two kestrels. We were unable to identify the mammals or birds that killed the others. We found one kestrel dead at the base of a solitary tree along a drainage ditch 225 m west of the interstate. Necropsy at the Iowa State University College of Veterinary Medicine indicated that the bird had a fractured skull and a subdural hematoma, injuries received as a result of a sharp blow to the head (A. Fix, pers. comm.). We concluded that the bird died after colliding with the tree.

Traffic on I-35 was a lower than expected source of fledgling mortality, given that the nest boxes were on highway signs just 20–25 m from the road. Village (1990) reported that during 30 yr road deaths among kestrels (*Falco tinnunculus*) in Europe increased in frequency and became the most commonly reported cause of mortality. He suggested that the increase was a result of the greater numbers of vehicles on the roadways and the increased speed of modern traffic.

In our study, transmitter failure was confirmed for three of eight transmitters with signal loss when the kestrels wearing these units were observed with other radio-marked kestrels. It is possible that signal loss in the five other radio-transmitters occurred when these kestrels were hit by vehicles. If so, the total mortality of kestrels from collisions with vehicles may have been as high as seven. We have some evidence, however, that the transmitters were capable of functioning after receiving a severe blow. We attached a radio-transmitter to one kestrel that subsequently died after colliding with a vehicle. We recovered the transmitter in working condition and attached it to another kestrel. The functioning transmitter was recovered again after this bird also collided with a vehicle.

Mortality among radio-marked kestrels was substantially greater in 1990 than in the preceding 2 yr. In 1990, 40% (14/35) of all radio-marked birds died, whereas in 1988 and 1989, only 8% (2/26) died.

We do not know why mortality was substantially higher in 1990 than in the previous 2 yr. It is possible that the adjustment of the size of kestrel broods in 1990 increased fledgling mortality. Greater rainfall in 1990 may also have increased mortality. Mean monthly rainfall from March through August was 5.2 cm in 1988, 6.5 cm in 1989, and 15.6 cm in 1990 (National Oceanic and Atmospheric Administration 1988, 1989, 1990). Heavy rainfall during spring 1990 delayed crop planting. As a result, the young kestrels may have been less able to conceal themselves from ground predators. The remains of five of the six kestrels that died from mammalian predation were found in crop fields.

Dispersal.—Mean time until dispersal for radio-marked birds was 22.7 d after fledging (n = 29; SE = 1.07; range = 9–39 d). No differences were detected in time until dispersal among years (ANOVA, $P = 0.8609$) or between small and large broods in 1990 (ANOVA, $P = 0.8104$).

We found no evidence that fledgling kestrels were forced from their natal areas by aggressive parents, a behavior that has been observed between parent Spanish Imperial Eagles (*Aguila heliaca*) and their young (Alonso et al. 1987). Kestrels left their natal areas as foraging behavior developed (Varland et al. 1991, Varland and Loughin 1992) and as they became independent from their parents for food. Mean age of young observed in parent-to-young prey transfers was 9.3 d post-fledging (n = 17; SD = 5.7). We never observed a parent feeding young >22 d after fledging.

We lost contact with 24 birds in 20 family groups on the day of dispersal from their natal areas. On one or more occasions, we were able to locate one radio-marked kestrel in each of 11 broods after dispersal movement started. We were unable to determine whether other kestrels were present with four of these birds, but saw the other seven birds perch resting or social hunting (Varland et al. 1991, Varland and Loughin 1992) with 1–8 other kestrels. These kestrels included siblings, siblings and kestrels from other family units, and, in one instance, a sibling and a female parent.

The mean age at the loss of contact with kestrels followed after dispersal from the natal area was 28.3 d post-fledging (SD = 6.0). As the birds moved from the area, we were unable to monitor any kestrel longer than 39 d after nest departure. The greatest straight-line distance any radio-marked kestrel was found from the nest box from which it fledged was 7.5 km.

To date, we have band recoveries away from the natal area for three kestrels banded as nestlings in 1988–1990. One kestrel was banded on 3 Jun. 1988 and found dead on 26 Feb. 1989 near Slater, Iowa, 50 km from its natal area. The second bird was banded on 17 Jun. 1989 and was found dead on 21 Oct. 1989 near Jewett, Texas, 1300 km from its natal area. We banded the third kestrel on 3 Aug. 1990, and it was found dead near Sulfur, Oklahoma, on 1 Feb. 1991, 950 km from its natal area.

During the study, only one of 113 adults captured on the study area was banded as a nestling. In contrast, during the same period we recaptured 16 adult kestrels nesting on the study area in either the same nest box used in a previous year or in another nest box.

Natal dispersal was defined as movement of young from birth site to first breeding site (Greenwood 1980, Johnston 1961), and this definition has been widely adopted (Warkentin and James 1990). Applying the definition to this study, the mean time until the initiation of natal dispersal was 22.7 d post-fledging. American Kestrels breed as yearlings (Bird and

Palmer 1988). We were unable to track any kestrel longer than 39 d after fledging; however, we could not determine where radio-marked kestrels that fledged from nest boxes along I-35 bred their first year.

Data from band recoveries indicate that at least some birds that fledged on the study area are migratory, a phenomenon that makes study of the process of dispersal difficult (Morton et al. 1991). That only one of 17 birds recaptured in a nest box as a breeding bird was banded as a nestling indicates that natal philopatry on the study area probably is not strong. More research is needed to determine the movements of kestrels after the initiation of dispersal.

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