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DEVELOPMENT OF FORAGING BEHAVIOR IN THE AMERICAN KESTREL

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ABSTRACT.—We observed the development of foraging behavior after nest departure in 12 sibling groups of American Kestrels (*Falco sparverius*). Perch resting decreased whereas perch hunting, eating self-captured prey, and flying increased over the 5-wk period that young were observed. Kestrels used perch hunting more than other types of hunting and fed exclusively on invertebrates, primarily grasshoppers. Perch hunting success (captures/pounces) increased significantly 3 wk after fledging. After this period there was no significant change. Significant increases in capture rate (captures/hour) occurred 4 and 5 wk after fledging due to increased pounce rates. We observed social hunting among siblings, families, and also among unrelated kestrels. Social hunting occurred during both perch hunting and ground hunting. Social foraging in these kestrels was imitative rather than cooperative.

Desarrollo de los hábitos de cacería en los Halcones Cernícalos

EXTRACTO.—Hemos observado el desarrollo de los hábitos de búsqueda de alimento en Halcones Cernícalos (*Falco sparverius*) con 12 grupos de hermanos. Después de un período de 5 semanas de observación, notamos que estos jóvenes halcones disminuyeron la frecuencia del posarse para descansar, mientras que aumentaron la frecuencia en el posarse para cazar, el comer su presa capturada, y el volar. La cacería desde una percha ocurrió más que otros tipos de cacería. Se alimentaron exclusivamente de invertebrados, principalmente de saltamontes o longostas. El éxito de la cacería desde una posición perchada (captura/embestida) creció significativamente después de 3 semanas de haber dejado el nido. Después de esto no hubo cambio significativo. Un notable incremento en la proporción de capturas (captura/hora) ocurrió entre 4 y 5 semanas después de dejar el nido, y se debió al incremento en la proporción de embestidas. Se observó cacerías en grupos entre hermanos, familias, y también entre individuos sin parentesco. Las cacerías en grupo se realizaron o bien desde el suelo o desde una percha. La provisión de comida en grupo en estos cernícalos fue más bien imitativa que cooperativa.

[Traducción de Eudoxio Paredes-Ruiz]

The post-fledging period, here defined as the period of parental dependency for food in young birds after leaving the nest (see van Tyne and Berger 1966), has received relatively little attention in avian research. This is partly because of the difficulties in observing the behavior of young once they leave the nest (e.g., Brown and Amadon 1968, Newton 1979, Alonso et al. 1987).

The post-fledging period and the subsequent period of recent independence from parents are important life history stages, when young develop foraging skills essential to survival (Weathers and Sullivan 1989). High mortality rates of recently independent juveniles and others during their first year of life reflects the critical nature of this time (e.g., Lack 1954, Henny 1972, Sullivan 1989).

In 1988 we began a study of American Kestrels nesting in nest boxes attached to the backs of highway signs along Interstate Highway 35 (I-35) in Central Iowa. In this paper we describe the development of foraging behavior in young kestrels during the post-fledging phase and during the period of recent independence from parents.

STUDY AREA AND METHODS

Several years prior to the initiation of this study, kestrel nest boxes were attached to the backs of highway signs along I-35 at approximately 2-km intervals, from northern Polk County to northern Worth County in northcentral Iowa. The study area was a corridor approximately 2 km wide on either side of I-35 from 18 km south to 99 km north of Ames. Land bordering I-35 was farmed intensively with row crops.

We banded 97 fledglings observed in 1988 and 1989

with U.S. Fish and Wildlife Service leg bands, and individually marked them with colored vinyl leg jesses before they fledged. We captured 76 percent (35/46) 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 fledged young for behavioral studies we used the signals from back-mounted radio transmitters (Holohil Systems, Ltd., Woodlawn, Ontario, Canada). We attached transmitters to birds several days before fledging. In 1988 we attached radio transmitters to 12 nestlings in 10 nest boxes. Survival of radio-marked kestrels was high (11 of 12 survived the post-fledging period) and siblings generally maintained close contact for 4 to 5 wk after fledging. This confirmed the technique's usefulness and feasibility for monitoring family group activity. We made observations in 1988 to gain insight into American Kestrel post-fledging behavior and to develop an efficient data recording system. These data are not part of the present analysis.

We tested the transmitters used in 1989 along the highway right-of-way at a height of 1 m. Signal range averaged 2.3 km (N = 13, SD = 0.60, range = 1.1–3.5 km). In 1989, we radio-tagged one randomly selected nestling from each of 13 nests. Young observed in 1989 (50 individuals from 13 nests) fledged between 27 and 31 d after hatching (mean = 29.2, SD = 1.4), from 13 June to 3 July.

One radio-tagged nestling died 7 d after fledging before we could collect behavioral data. We lost signals from 3 of the remaining 12 transmitters within 5 d after the tagged birds fledged. For two of these sibling groups, we were unable to determine whether the transmitters failed or if the individuals left the area. For the third, transmitter failure became evident when we observed the radio-marked kestrel with another sibling group in the study 37 d after fledging. Despite the early loss of signals from these three transmitters, we were able to collect data on behavior of individuals in these broods.

We observed fledglings between 0600 and 1300 H at a distance of 70–100 m with a 20× or 20–60× spotting scope. We did not use a blind because birds under observation frequently changed locations. We monitored fledgling groups on a rotational basis at 1–3 d intervals until we lost contact with the brood. When we could not find a brood, we searched by vehicle an area of approximately 6 km^2 around their last known location.

We adopted Wyllie's (1985) definition of dispersal, which is movement of a fledged 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 (N = 9).

At the beginning of each observation session, we randomly selected one fledgling, which was not necessarily the one with the transmitter, as the focal bird (Altmann 1974). Two people observed behavior; typically one individual collected data on a sibling group while the other observed another group elsewhere on the study area. In 39 cases two people collected data simultaneously on two birds in the same sibling group, or one person made consecutive observations on different birds in the same sibling group. For analysis, we combined these simultaneous or consecutive observations into one observation session.

Sessions lasted 5 to 60 min or until the focal bird disappeared from view. We did not use data if the bird left in <5 min. We analyzed data for 93 observation sessions (mean length = 57.5 min, SD = 32.0).

A metronome timing device (Wiens et al. 1970), set at 20 sec intervals, cued spot observations of behavior and social activity. At each sound of the tone, we recorded behavior and social activities of the focal kestrel. We recorded four main classes of activity: general behavior, social behavior, hunting behavior, and allopreening and beaking. We recognized nine subclasses of general behavior and five of social behavior.

General Behavior. "Perch resting" describes a kestrel perched and not engaged in any other observed behavior. Rudolf (1982) and Toland (1987) distinguished "perch hunting" from other perching activity by alert posture, erect body or body leaning slightly forward, frequent staring at ground (Fig. 1), and head bobs. Because young kestrels that have never hunted may exhibit some of these behaviors without attempting prey captures, behavior was not recorded as perch hunting until at least one pounce was observed. Flights to and from the ground and flights between perches during perch hunting bouts were included in perch hunting behavior. We defined "ground hunting" as a bird on the ground searching for prey for >20 sec. Searches of shorter duration involving flight from a perch were considered perch hunting. "Flight" was any non-hunting flight. We use the term "eating" only for kestrels eating self-captured prey. "Maintenance activity" included preening, plumage rousals (shaking), and stretching. "Lying on belly" describes a posture young kestrels often assumed on fenceposts, utility poles, and large tree branches. "Begging" was solicitation of food from parents. "Out of sight" refers to a focal kestrel concealed by vegetation or other objects. A session was discontinued when a bird was out of sight >5 min. "Other" was used to categorize behaviors observed relatively infrequently, and included walking, hover hunting, aggressive interactions among siblings, parent-to-young prey transfers, and eating prey caught by parents. During observation sessions, one or both adults frequently vocalized aggressively at us. We therefore suspect that the interactions with parents occurred less frequently than they would have in the absence of observers.

Social Behavior. Lett and Bird (1987) defined social behavior for American Kestrel fledglings as any behavior which occurred within 2 m of one or more siblings. We adopted this operational definition with two modifications. We extended the distance to 3 m and included non-sibling kestrels in social interactions (adults late in the post-fledging period which no longer feed their young and kestrels from outside the parent/sibling family unit). "Association" was any activity of the focal kestrel except social hunting, which occurred ≤3 m from one or more kestrels. "Social hunting" was hunting activity by the focal kestrel which occurred ≤3 m from one or more kestrels that also were hunting (Fig. 1). "Nonsocial" refers to activity of the focal kestrel occurring >3 m from one or more kestrels. When we could not see whether other kestrels were ≤3 m from the focal kestrel because of dense vegetation we recorded its social status as "Undetermined."

Foraging Behavior. We recorded pounces, captures, and prey type. Foraging success was the percentage of

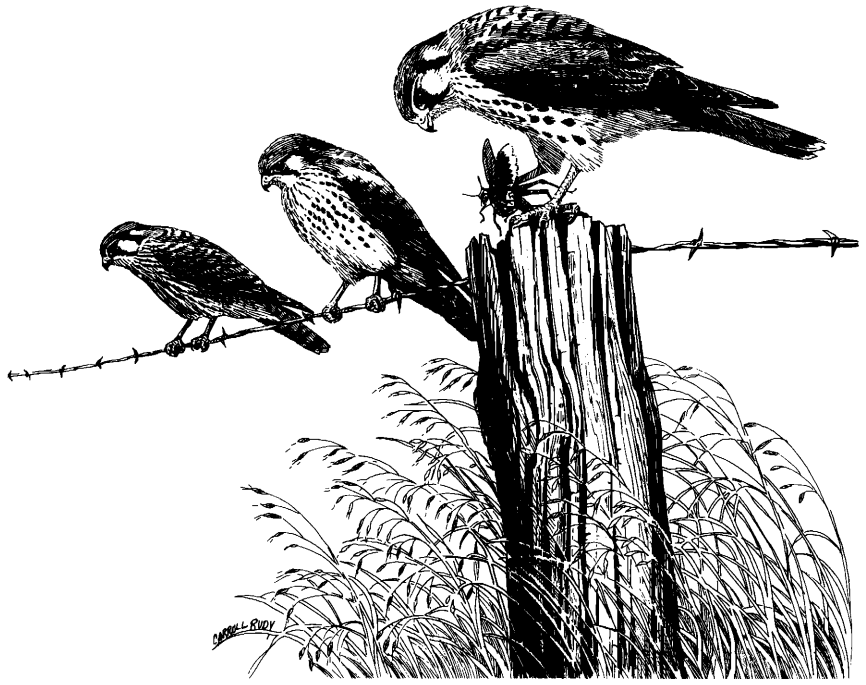

Figure 1. American Kestrels hunting socially after fledging.

pounces with known outcomes that were successful. Outcomes were unknown in 5% of the observed pounces (18/345). We converted pounces and captures to hourly rates based on session length.

Allopreening and Beaking. We recorded the frequencies and the individuals involved in allopreening and beaking, forms of direct social contact. Allopreening is the preening of a conspecific individual's plumage. Our observations of beaking paralleled those of Sherrod (1983: 182), who adopted the term beaking to describe behavior in young Peregrine Falcons (*Falco peregrinus*) in which "one falcon nibbles at the beak and lore area of its sibling."

Statistical Analysis. We grouped behavioral data according to 7-d intervals starting with fledging. The experimental unit (n) was the sibling group, and observations of the number of groups observed ranged from 12 during the first wk after fledging to 4 during the fifth. We computed statistics for behavior, social, and hunting activity for each sibling group in each 7-d, post-fledging interval for which data were available.

We used the general linear model procedure (PROC GLM, SAS 1985) to obtain an analysis of variance (ANOVA) and tested for linear trends in specific behaviors during 5 wk post-fledging. Because not all sibling groups were represented in all weeks and data were missing from some cells, we used Type III sum of squares to calculate P values. We selected 0.05 as the level of significance for linear trends in behavior. Because behaviors were not independent, we adjusted the significance level of P values using Bonferroni's inequalities (Snedecor and Cochran 1989:116). Thus, the level of significance for these tests is 0.05 divided by the total number tests being made on a set of non-independent behaviors.

To compare differences in means for foraging activity between weeks after fledging, we used least significant difference (LSD) t-tests (SAS 1985). We selected 0.05 as the level of significance for t-tests.

RESULTS

Kestrels spent progressively less time inactive and more time foraging as they grew older (Table 1). A significant decrease occurred in perch resting behavior ($P < 0.001$) with weeks post-fledging, whereas significant increases occurred in perch hunting ($P < 0.001$), eating self-captured prey ($P < 0.001$), and flying ($P < 0.002$). We did not observe young eating prey captured by their parents after the third week post-fledging. Mean time of dispersal for radio-marked kestrels ($N = 9$) was 23.6 d after fledging.

Perch hunting constituted a greater percentage of foraging time than ground hunting in all 5 wk post-fledging (Table 1). Significant increases occurred with time in perch hunting pounces ($P < 0.001$), captures ($P < 0.001$), and success ($P < 0.05$; Fig.

Table 1. Time (mean % ± SE) spent engaged in 10 behavior categories by post-fledging American Kestrels in Iowa.

Behavior	Weeks Post-Fledging 1 Mean ± SE	2 Mean ± SE	3 Mean ± SE	4 Mean ± SE	5 Mean ± SE	1–5 *P*-Values[a]
Perch resting	75.3 ± 4.0	53.8 ± 5.2	41.4 ± 3.3	19.5 ± 7.2	23.8 ± 2.1	<0.0010
Perch hunting	0.2 ± 0.2	6.0 ± 2.0	18.3 ± 2.7	43.4 ± 8.8	48.6 ± 2.8	<0.0010
Ground hunting	0.0	0.9 ± 0.7	3.6 ± 1.6	10.0 ± 5.4	1.8 ± 1.1	0.0580
Flying	0.4 ± 0.1	2.1 ± 0.4	3.9 ± 0.9	5.8 ± 3.3	7.5 ± 2.6	0.0018
Eating self-captured prey	0.0	<0.1 ± 0.1	1.5 ± 0.8	6.6 ± 2.6	7.9 ± 0.8	<0.0010
Maintenance	14.5 ± 2.0	19.1 ± 4.2	17.4 ± 3.4	9.3 ± 3.8	8.7 ± 0.8	0.3215
Lying on belly	4.1 ± 3.2	7.3 ± 4.1	2.9 ± 1.6	0.0	0.0	0.1750
Begging	1.7 ± 1.1	2.5 ± 0.6	2.6 ± 0.9	0.0	0.0	0.1394
Out of sight	2.3 ± 0.9	5.4 ± 1.2	7.9 ± 2.4	5.3 ± 1.6	1.6 ± 0.6	0.1794
Other	1.4 ± 0.4	2.8 ± 1.4	0.4 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.0547

[a] *P*-values are based on ANOVA *F*-tests for linear trends across 5 wk post-fledging (df = 1, 27). All tests for lack of fit were not significant ($P > 0.05$).

2). Ground hunting success also increased significantly ($P < 0.01$).

We identified nearly all prey items caught by young kestrels as grasshoppers (order Orthoptera). We saw one kestrel feeding on a dragonfly (order Odonata), and some items were too small to identify.

During four sessions we observed seven brief bouts of hover hunting in birds 12–37 d post-fledging. None of these attempts were successful. We observed five flycatching attempts (see Suring and Alt 1981) among birds 23–25 d post-fledging during three sessions, four were successful.

When perch resting, fledged kestrels became progressively less social with time. The significant decrease in association ($P < 0.001$) and the significant increase in nonsocial behavior ($P < 0.001$; Table 2) reflect this trend.

Allopreening and beaking exchanges occurred

Table 2. Time (mean % ± SE) spent engaged in social and nonsocial activity by post-fledging American Kestrels in Iowa.

Behavior by Social Activity	Weeks Post-Fledging 1	2	3	4	5	1–5 *P*-Values[a]
Perch resting (N)[b]	(12)	(10)	(10)	(6)	(4)	
Association	57.7 ± 10.8	48.9 ± 8.2	38.3 ± 6.0	25.8 ± 16.3	13.5 ± 8.2	<0.0010
Social hunting	—	—	—	—	—	—
Nonsocial	28.2 ± 7.5	48.9 ± 8.1	56.1 ± 5.8	74.2 ± 16.3	86.5 ± 8.2	<0.0010
Undetermined	14.1 ± 8.6	2.2 ± 1.0	5.6 ± 3.3	0.0	0.0	0.2722
Perch hunting (N)	(1)	(6)	(10)	(6)	(4)	
Association	0.0	17.3 ± 11.7	19.4 ± 6.8	6.6 ± 6.0	3.3 ± 1.7	0.1658
Social hunting	0.0	11.6 ± 5.3	21.3 ± 7.1	30.4 ± 16.2	14.5 ± 8.4	0.0772
Nonsocial	100.0	69.8 ± 12.5	53.0 ± 6.1	63.0 ± 18.3	82.2 ± 8.5	0.4673
Undetermined	0.0	1.3 ± 0.8	6.3 ± 4.9	0.0	0.0	0.7646
Ground hunting (N)	(0)	(5)	(7)	(5)	(3)	
Association	0.0	15.0 ± 15.0	21.7 ± 10.3	1.2 ± 1.2	0.0	0.0955
Social hunting	0.0	20.4 ± 13.6	33.6 ± 13.9	45.9 ± 22.7	0.0	0.9385
Nonsocial	0.0	44.6 ± 17.5	44.6 ± 8.4	52.9 ± 22.1	100.0	0.4887
Undetermined	0.0	20.0 ± 20.0	0.0	0.0	0.0	—

[a] *P*-values are based on ANOVA *F*-tests for linear trends across 5 wk post-fledging. Perch resting df = 1, 26; perch hunting df = 1, 12; hunting on ground df = 1, 7. All tests for lack of fit were not significant ($P > 0.05$).

[b] Number of sibling groups observed.

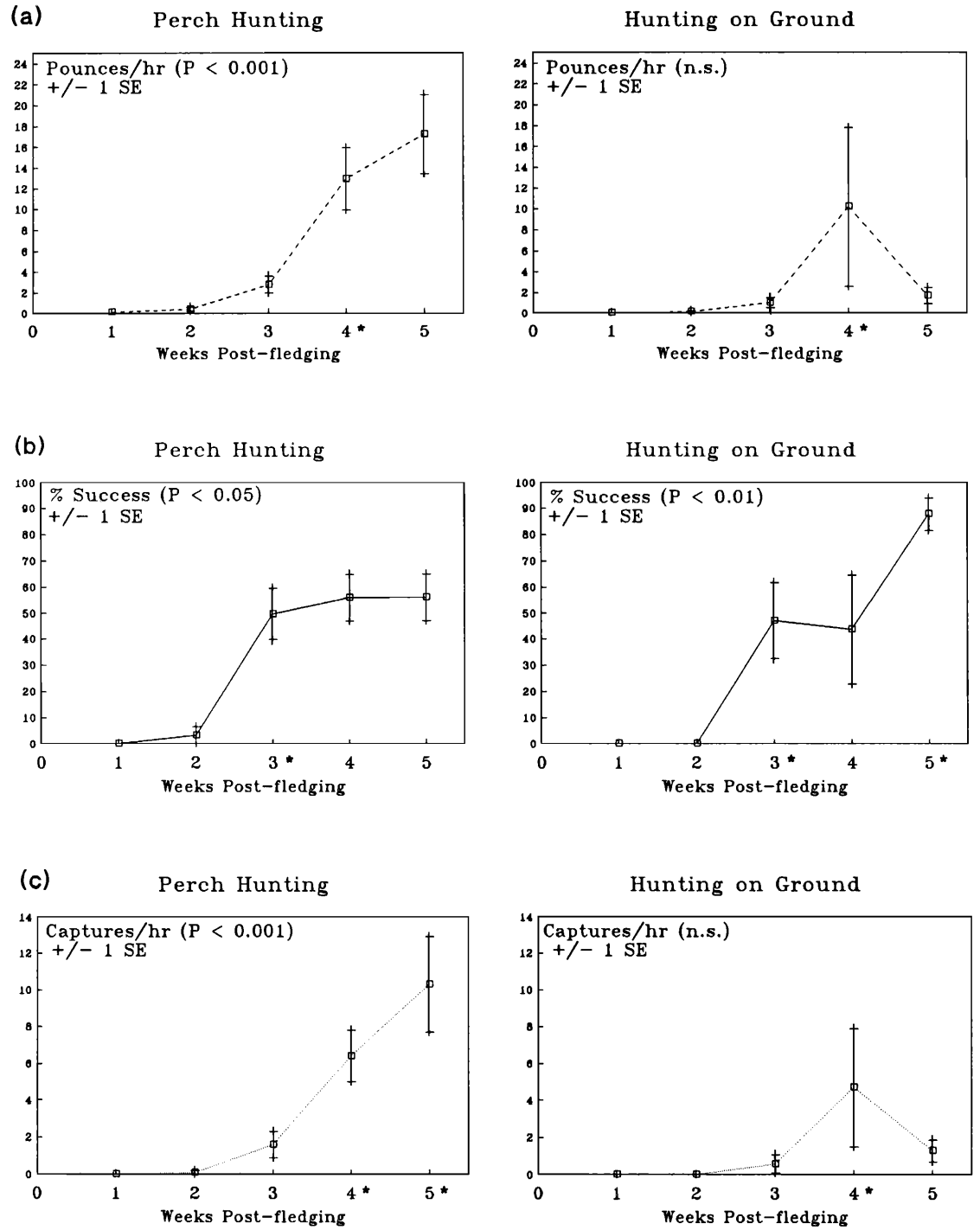

Figure 2. Mean foraging pounce (a), percent success (b), and capture rates (c) for post-fledging American Kestrels at weekly intervals. *P* values are based on ANOVA *F*-tests across 5 wk post-fledging (perch and ground hunting pounce and capture rate df = 1, 27; perch and ground hunting success df = 1, 10). Weekly means with * differ significantly ($P < 0.05$, least significant difference *t*-test) from the preceding week.

during 15% (14/93) of the sessions. We observed the behaviors in 9 of 12 family groups among young ranging from 3–23 d post-fledging.

Kestrels were social while perch and ground hunting and spent a substantial amount of time in these activities (Table 2). We observed social hunting during 41% (20/49) of the sessions in which hunting occurred. We saw social hunting in 10 of 12 sibling groups and quantified it in 8. In three of these eight groups, social hunting involved siblings and nonsiblings. We saw extra-familial social hunting in 20% (4/20) of the sessions with social hunting. In one of these groups we observed social hunting involving siblings, a parent, and a non-sibling female of unknown age. The female parent did not feed the young but called and flew aggressively at a Red-tailed Hawk (*Buteo jamaicensis*) perched within 20 m of the group, causing the hawk to leave the area. Social hunting among non-sibling groups occurred just before or after dispersal from the natal area. We observed social hunting on one or two occasions and then lost contact due to signal loss from the radio-tagged kestrel. We are uncertain whether these groups remained together.

DISCUSSION

Association. Association among fledgling kestrels occurred mostly during the first 2 wk after fledging, when young are most dependent on parents. Moreno (1984) found that fledgling Northern Wheatears (*Oenanthe oenanthe*) fed by one parent perched closer to each other than fledglings fed by both parents, and that a tendency for fledglings to associate (perch <1 m apart) diminished as they became increasingly more independent. Distance between sibling Spanish Imperial Eagles (*Aquila heliaca*; Alonso et al. 1987) and Black Kites (*Milvus migrans*; Bustamante and Hiraldo 1990) increased with age, and there was a positive correlation between increased sibling distance and flying proficiency.

Wittenberger (1981) suggested that the allopreening in breeding birds is important in maintaining pair bonds. Our observations of allopreening and beaking provide evidence that American Kestrels are social after fledging. Thus, fledgling kestrels do not perch close together merely to improve their chances of being fed or because they lack flying skills. We suggest allopreening and beaking may maintain social bonds between siblings during the post-fledging period. Both behaviors occur in the social repertoire of fledgling Peregrine Falcons (Sherrod 1983), and Komen and Meyer (1989) observed allopreening in fledgling Common Kestrels (*Falco tinnunculus*). Other researchers have reported close associations among fledged American Kestrels (Sherman 1913, Cade 1955, Roest 1957, Smith et al. 1972, Balgooyen 1976, Wheeler 1979, Lett and Bird 1987), but we have not found any reference in the literature to allopreening or beaking.

Development of Foraging Behavior. Bird and Palmer (1988) described various foraging methods used by American Kestrels. Toland (1987) grouped American Kestrel foraging methods into three categories: perch hunting (which he observed 70–97% of the time); hover hunting (2–20%); and horizontal flight (<5%). The American Kestrel is a generalist predator of invertebrates and small vertebrates, and its diet varies with season and geographic area (Heintzelman 1964, Bent 1938).

In this study, young kestrels progressed from relative inactivity to active foraging within 3 to 4 weeks of leaving the nest (Fig. 2, Table 1). The two hunting methods observed most frequently, perch hunting and ground hunting, were probably least dependent on flying ability. Early reliance on hunting techniques requiring relatively simple flight patterns has been reported for post-fledging Common Kestrels (Shrubb 1982), Peregrine Falcons (Sherrod 1983), Red-tailed Hawks (Johnson 1986), Northern Wheatears (Moreno 1984), and Spotted Flycatchers (*Muscicapa striata*; Davies 1976).

Fledged American Kestrels fed on easily-caught invertebrate prey. Dunstan (1970), Johnson (1986) and Shrubb (1982) reported invertebrates as the earliest prey of Great Horned Owls (*Bubo virginianus*), Red-tailed Hawks, and kestrels. Toland (1987) found an 82% success rate among American Kestrels (both sexes, all ages) hunting invertebrates, with lower rates for rodents (66%) and birds (33%). Collopy (1973) reported that kestrels wintering in California had 64% hunting success for invertebrates and 25% for vertebrates. Smallwood (1987) found kestrels wintering in Florida fed only on arthropods, with comparable success rates for males (76%) and females (73%).

In this study, mean perch hunting success increased significantly from 3.3% in the second week after fledging to 49.7% in the third, but did not change significantly thereafter (Fig. 2). These success rates for invertebrates are substantially lower than rates cited above and indicate that kestrels further develop their foraging skills after dispersal. We

observed significant increases in mean capture rates by perch hunting kestrels at 4 and 5 wk post-fledging due to increased pounce rates (Fig. 2). The observed increases in perch hunting success and pounce rates may be at least partially due to increases in grasshopper density during the post-fledging period. Grasshoppers were abundant in central Iowa in July and August 1989 (Rice 1989).

Reports of increasing numbers of kills by maturing Peregrine Falcons released from hack sites (Sherrod 1983) and increasing hunting success with age in fledged Red-tailed Hawks (Johnson 1986) were supported by few quantitative data. Increased hunting success over time was quantified for fledgling Ospreys (*Pandion haliaetus*; Edwards 1989a) and passerines, including Northern Wheatears (Moreno 1984), Spotted Flycatchers (Davies 1976), and Yellow-eyed Juncos (*Junco phaeonotus*; Sullivan 1988).

Social Hunting. Wilson (1975:51) described two types of social foraging, imitative and cooperative. The net effect of such social hunting probably is greater foraging efficiency.

During imitative foraging, individuals observe others in the group and may initiate, copy, increase, or learn foraging behavior. All of these may occur during social hunting but are difficult to differentiate. Communication among imitative foragers probably is indirect, and group members do not coordinate their efforts during the hunt. Several investigators reported feeding benefits associated with imitative foraging (e.g., Krebs 1973, Rubenstein et al. 1977, Sullivan 1984). Edwards (1989a, 1989b) compared the foraging behavior of sibling pairs of Ospreys and single young and found that pairs and singles both reached the same level of success but that siblings developed their skills sooner. Sibling pairs also used similar foraging techniques and had similar diets. Edwards suggested these differences were a result of observational learning between siblings.

Hector (1986) listed six characteristics distinguishing cooperative foraging from imitative foraging, including division of labor and use of signals to coordinate movements. He reported that mated pairs of Aplomado Falcons (*Falco femoralis*) cooperatively hunting for birds had greater success (45%) than when alone (21%). Group size in cooperatively foraging Harris' Hawks (*Parabuteo unicinctus*) was positively correlated with capture (Bednarz 1988).

After the breeding season American Kestrels may hunt in social groups of 10–20 juveniles and adults (Cade 1955, Wheeler 1979, Wilmers 1982). We also observed post-breeding adults and juveniles hunting in groups, but social hunting was observed most frequently among siblings prior to or just after dispersal. Young kestrels hunted socially from 12–46% of the time (Table 2). We saw nothing to indicate that individuals in groups were coordinating their efforts or using signals to coordinate movements. Thus, social foraging in these kestrels was imitative rather than cooperative.

We considered the possibility that differences might exist between the hunting efficiency of kestrels hunting socially and those hunting nonsocially, but the study design was not adequate to test this idea. Further research is needed to document whether social hunting influences foraging efficiency in the American Kestrel.

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