Behavior and ecology of post-fledging American Kestrels

Daniel E. Varland
Iowa State University

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Behavior and ecology of post-fledging American kestrels

Varland, Daniel Edward, Ph.D.

Iowa State University, 1991
Behavior and ecology of post-fledging American Kestrels

by

Daniel E. Varland

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY
Major: Animal Ecology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Département

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa
1991
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GENERAL INTRODUCTION

The post-fledging period in birds, the time between nest departure and independence from parents (van Tyne and Berger 1966), has received relatively little attention in avian research. This is partly because of the difficulty in monitoring young after 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 skills essential to survival (Weathers and Sullivan 1989). High mortality rates of recently independent juveniles and other birds during their first year of life reflect the critical nature of this time (e.g., Lack 1954, Henny 1972, Sullivan 1989, Village 1990).

I studied the behavior and ecology of post-fledging American Kestrels during spring and summer 1988-1990 in central Iowa. I used radio-transmitters to monitor kestrel activity. I attached transmitters to 64 birds in 50 nests. All young in the study fledged from nest boxes; 47 were attached to the backs of highway signs along the Interstate-35 (I-35) right-of-way, two were on farmsteads, and one was at the College of Veterinary Medicine at Iowa State University in Ames.

In Section I of the dissertation I describe the development of foraging behavior in young kestrels during the first five
weeks after fledging. For this phase of the research, I made preliminary observations in 1988 to gain insight into kestrel post-fledging behavior and to develop an efficient data recording system. The analyses presented in Section I are based on data collected in 1989.

In 1989 I determined that, during hunting bouts, fledgling kestrels spent 12-46% of their time hunting socially. Kestrels used a type of social foraging described by Wilson (1975) as imitative social foraging, during which "the animal simply goes where the group goes and eats what it eats". Others have observed imitative social foraging by American Kestrels, and have provided anecdotal accounts of this behavior (Cade 1955, Wheeler 1979, Wilmers 1982, Kellner 1990).

My observations of imitative social foraging during the first two years of the study led me in 1990 to frame two concept-based hypotheses: 1) imitative social foraging increases the foraging efficiency of individuals in large broods, and 2) individuals that develop their foraging skills in large broods will disperse sooner than individuals that develop these skills in small broods. To test these hypotheses, I experimentally adjusted the size of kestrel broods to either two or five young just before they fledged. I then monitored the development of foraging behavior and dispersal time in individuals from each brood size. Section
II describes the results of this investigation.

In Section III, I describe perch and habitat use, causes of mortality, and time to dispersal of fledgling kestrels along the interstate highway. I restricted these analyses to 61 kestrels fledging from the 47 nest boxes along I-35.

Explanation of dissertation format

My dissertation is written in the Alternate Format. The three sections were prepared separately for submission to professional journals. Erwin E. Klaas, professor of Animal Ecology at Iowa State University, and Thomas M. Loughin, a Doctoral Candidate and Research Assistant in the Department of Statistics at ISU, are co-authors of Sections I and III of the dissertation. Section I has been published in The Journal of Raptor Research and appears in Volume 25, pages 9-17. I am the sole author of Section II. The "General Summary" of the dissertation is on pages 81-83. Citations in the "General Introduction" are found in the "Additional Literature Cited" section on page 84.
SECTION I. DEVELOPMENT OF FORAGING BEHAVIOR IN THE AMERICAN KESTREL
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 and 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.
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 other birds during their first year of life reflect 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 before this study was begun, kestrel nest boxes were attached to the backs of highway signs along I-35 at about 2-km intervals, from northern Polk County to northern Worth County in North central Iowa. The study area was a
corridor about 2 km wide on either side of I-35 from 18 km south to 99 km north of Ames. Land bordering the interstate was farmed intensively with row crops.

We banded 104 fledglings observed in 1988 and 1989 with U.S. Fish and Wildlife Service leg bands and individually marked them with colored vinyl leg jesses (Bednarz 1987) before they fledged. We captured 70% (32/46) 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 pack-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 9 nest boxes. Survival of radio-marked kestrels was high (11 of 12 survived the post-fledging period) and siblings generally maintained close contact with each other for 4-5 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
interstate 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, S.D. = 1.4), from 11 June through 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 whether 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 at a distance of 70-100 m with a 20x or 20-60x 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 about 6 km² 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 from among those visible (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-s 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 nonhunting 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
Figure 1. American Kestrels hunting socially after fledging.
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 of young with their 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 other 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 pounces with known outcomes that were successful. Outcomes were unknown in 5% (18/345) of the observed pounces. 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 Institute 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 wk 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 of tests being made on a set of non-independent behaviors.

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

RESULTS

Kestrels spent progressively less time in inactive behavior and more time in active foraging as they grew older (Table 1). A significant decrease occurred in perch resting behavior (P < 0.001) with wk 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 wk 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).
Table 1. Time (mean % ±SE) spent engaged in 10 behavior categories by post-fledging American Kestrels in Iowa.

<table>
<thead>
<tr>
<th>BEHAVIOR</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>1-5</th>
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</thead>
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<tr>
<td></td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>P-VALUES</td>
</tr>
<tr>
<td>(N)b</td>
<td>(12)</td>
<td>(10)</td>
<td>(10)</td>
<td>(7)</td>
<td>(4)</td>
<td></td>
</tr>
<tr>
<td>Perch resting</td>
<td>75.3 ±4.0</td>
<td>53.8 ±5.2</td>
<td>41.4 ±3.3</td>
<td>19.5 ±7.2</td>
<td>23.8 ±2.1</td>
<td>&lt; 0.0010</td>
</tr>
<tr>
<td>Perch hunting</td>
<td>0.2 ±0.2</td>
<td>6.0 ±2.0</td>
<td>18.3 ±2.7</td>
<td>43.4 ±8.8</td>
<td>48.6 ±2.8</td>
<td>&lt; 0.0010</td>
</tr>
<tr>
<td>Ground hunting</td>
<td>0.0</td>
<td>0.9 ±0.7</td>
<td>3.6 ±1.6</td>
<td>10.0 ±5.4</td>
<td>1.8 ±1.1</td>
<td>0.0580</td>
</tr>
<tr>
<td>Flying</td>
<td>0.4 ±0.1</td>
<td>2.1 ±0.4</td>
<td>3.9 ±0.9</td>
<td>5.8 ±3.3</td>
<td>7.5 ±2.6</td>
<td>0.0018</td>
</tr>
<tr>
<td>Eating self-captured prey</td>
<td>0.0</td>
<td>&lt; 0.1 ±&lt; 0.1</td>
<td>1.5 ±0.8</td>
<td>6.6 ±2.6</td>
<td>7.9 ±0.8</td>
<td>&lt; 0.0010</td>
</tr>
<tr>
<td>Maintenance</td>
<td>14.5 ±2.0</td>
<td>19.1 ±4.2</td>
<td>17.4 ±3.4</td>
<td>9.3 ±3.8</td>
<td>8.7 ±0.8</td>
<td>0.3215</td>
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<td>Lying on belly</td>
<td>4.1 ±3.2</td>
<td>7.3 ±4.1</td>
<td>2.9 ±1.6</td>
<td>0.0</td>
<td>0.0</td>
<td>0.1750</td>
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<td>Begging</td>
<td>1.7 ±1.1</td>
<td>2.5 ±0.6</td>
<td>2.6 ±0.9</td>
<td>0.0</td>
<td>0.0</td>
<td>0.1394</td>
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<tr>
<td>Out of sight</td>
<td>2.3 ±0.9</td>
<td>5.4 ±1.2</td>
<td>7.9 ±2.4</td>
<td>5.3 ±1.6</td>
<td>1.6 ±0.6</td>
<td>0.1794</td>
</tr>
<tr>
<td>Other</td>
<td>1.4 ±0.4</td>
<td>2.8 ±1.4</td>
<td>0.4 ±0.2</td>
<td>0.1 ±0.1</td>
<td>0.1 ±0.1</td>
<td>0.0547</td>
</tr>
</tbody>
</table>

*P values are based on ANOVA F-tests for linear trends across 5 wk post-fledging (df = 1, 27). All tests for lack of linearity were nonsignificant (P > 0.05).

bNumber of sibling groups observed.
Significant increases occurred with time in perch hunting pounces ($P < 0.001$), captures ($P < 0.001$), and success ($P < 0.05$) (Fig. 2). Ground hunting success also increased significantly ($P < 0.01$).

We identified nearly all the 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 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
Figure 2. Mean foraging pounce rates (a), percent success (b), and capture rates (c) for post-fledged American Kestrels at weekly intervals. P values are based on ANOVA F-tests across 5 wk post-fledged (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.
(a) Perch Hunting

Pounces/hr (P < 0.001) +/− 1 SE

(b) Perch Hunting

% Success (P < 0.05) +/− 1 SE

(c) Perch Hunting

Captures/hr (P < 0.001) +/− 1 SE

Hunting on Ground

Pounces/hr (n.s.) +/− 1 SE

% Success (P < 0.01) +/− 1 SE

Captures/hr (n.s.) +/− 1 SE
Table 2. Time (mean % ±SE) spent engaged in social and nonsocial activity by post-fledging American Kestrels in Iowa.

<table>
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<th>WEEKS POST-FLEDGING</th>
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<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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<tr>
<td>BEHAVIOR BY SOCIAL ACTIVITY</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
</tr>
<tr>
<td>Perch resting (N)b</td>
<td>(12)</td>
<td>(10)</td>
<td>(10)</td>
<td>(6)</td>
<td>(4)</td>
</tr>
<tr>
<td>Association</td>
<td>57.7 ± 10.8</td>
<td>48.9 ± 8.2</td>
<td>38.3 ± 6.0</td>
<td>25.8 ± 16.3</td>
<td>13.5 ± 8.2</td>
</tr>
<tr>
<td>Nonsocial</td>
<td>28.2 ± 7.5</td>
<td>48.9 ± 8.1</td>
<td>56.1 ± 5.8</td>
<td>74.2 ± 16.3</td>
<td>86.5 ± 8.2</td>
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<tr>
<td>Undetermined*</td>
<td>14.1 ± 8.6</td>
<td>2.2 ± 1.0</td>
<td>5.6 ± 3.3</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Perch hunting (N)</td>
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<td>(6)</td>
<td>(10)</td>
<td>(6)</td>
<td>(4)</td>
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<tr>
<td>Association</td>
<td>0.0</td>
<td>17.3 ± 11.7</td>
<td>19.4 ± 6.8</td>
<td>6.6 ± 6.0</td>
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<td>Social hunting</td>
<td>0.0</td>
<td>11.6 ± 5.3</td>
<td>21.3 ± 7.1</td>
<td>30.4 ± 16.2</td>
<td>14.5 ± 8.4</td>
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<tr>
<td>Nonsocial</td>
<td>100.0</td>
<td>69.8 ± 12.5</td>
<td>53.0 ± 6.1</td>
<td>63.0 ± 18.3</td>
<td>82.2 ± 8.5</td>
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<td>Undetermined</td>
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<td>6.3 ± 4.9</td>
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<td>0.0</td>
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<tr>
<td>Ground hunting (N)</td>
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<td>(5)</td>
<td>(7)</td>
<td>(5)</td>
<td>(3)</td>
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<tr>
<td>Association</td>
<td>0.0</td>
<td>15.0 ± 15.0</td>
<td>21.7 ± 10.3</td>
<td>1.2 ± 1.2</td>
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<td>Social hunting</td>
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<td>20.4 ± 13.6</td>
<td>33.6 ± 13.9</td>
<td>45.9 ± 22.7</td>
<td>0.0</td>
</tr>
<tr>
<td>Nonsocial</td>
<td>0.0</td>
<td>44.6 ± 17.5</td>
<td>44.6 ± 8.4</td>
<td>52.9 ± 22.1</td>
<td>100.0</td>
</tr>
</tbody>
</table>
Table 2 (cont.)

<table>
<thead>
<tr>
<th>BEHAVIOR BY SOCIAL ACTIVITY</th>
<th>MEAN ±SE</th>
<th>MEAN ±SE</th>
<th>MEAN ±SE</th>
<th>MEAN ±SE</th>
<th>MEAN ±SE</th>
<th>1-5 P-VALUES*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undetermined</td>
<td>0.0</td>
<td>20.0±20.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

*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 nonlinearity were not significant.

*number of sibling groups observed.

*social status of the focal bird was undetermined.
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 it to leave the area. Social hunting among nonsibling 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.

**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 allopreaming in breeding birds is important in maintaining pair bonds. Our observations of allopreaming 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 that allopreaming 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 allopreaming 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 of allopreaming 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 (Heintzleman 1964, Bent 1938).
In this study, young kestrels progressed from relative inactivity to active foraging within 3 to 4 wk 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 Common 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 similar success rates for males (76%) and females (73%).

In this study, mean perch hunting success increased significantly from 3.3% the second week after fledging to 49.7% 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 the Yellow-eyed Juncos (Junco phaeontus; 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, b) compared the foraging behavior of sibling pairs of Ospreys and single young and found that sibling pairs and singles both reached the same level of success but that sibling pairs developed their skills sooner. Sibling pairs also used similar foraging techniques and had similar diets. Edwards suggested the differences between single young and pairs 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 rate (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 non-socially, 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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LITERATURE CITED


Section II. Foraging Efficiency in Small and Large Broods of Post-fledging American Kestrels
ABSTRACT.—Presumably young American Kestrels (*Falco sparverius*) learn foraging skills during the first 4-6 wk after fledging. Imitative social foraging during this period may provide an adaptive advantage to individuals later in the juvenile period if there is strong selection for learned efficiency in foraging. I report the results of a test of an hypothesis that imitative foraging in large broods increases foraging efficiency of post-fledged American Kestrels. I test a second hypothesis that individuals that develop their foraging skills in large broods will disperse sooner than individuals that develop these skills in small broods. To test these hypotheses, I experimentally adjusted the size of kestrel broods prior to fledging to either two or five young for behavioral observation. No differences in foraging efficiency or in dispersal time were detected during the 4 wk that birds were observed. However, sample sizes were small because of high mortality or signal failure among radio-marked birds. Nearly all deaths occurred during the first wk after fledging, and predation was the main cause of mortality. Starvation was not an important cause of mortality, but may be significant later in the first year of life. Because of movement of young away from their natal areas, I was unable to observe any kestrel longer than 39 d after fledging.
Wilson (1975:51) described two types of social foraging, imitative and cooperative. During imitative foraging individuals observe others and may initiate, copy, increase, or learn foraging behavior. According to Wilson, "the animal simply goes where the group goes, and eats what it eats". Cooperative foragers usually use a signal (or signals) to coordinate pursuit, whereas during imitative foraging, communication is thought to be without signals and group members do not divide labor (Hector 1986). Several investigators have reported feeding benefits associated with imitative foraging (e.g., Krebs 1973; Rubenstein et al. 1977; Sullivan 1984; and Edwards 1989a, b). Edwards (1989a, b) compared the foraging behavior of sibling pairs of Ospreys (Pandion haliaetus) and singletons, and found that pairs developed foraging skills sooner, used similar foraging techniques, and had similar diets.

Hector (1986) reported that imitative foraging (as defined by Wilson) is more common among raptors than cooperative foraging, and he cited several examples of species that forage in this manner. Kellner (1990) observed imitative foraging in one sibling group of five kestrels and among three of these siblings and five other juveniles. Other anecdotal accounts of imitative foraging include observations of up to 20 juveniles hunting in a single field (Cade 1955), 18 juveniles "perched along one short stretch of road" (Wheeler
1979), and aggregations of as many as 14 juvenile and adults on reclaimed surface mines (Wilmers 1982).

In 1988 I began a study of the post-fledging behavior of American Kestrels (Varland et al. 1991). I quantified the occurrence of imitative foraging among siblings and among siblings and other kestrels. In this paper, I report the results of tests of two hypotheses: 1) imitative social foraging increases the foraging efficiency of individuals in large broods, and 2) individuals that develop their foraging skills in large broods will disperse sooner than individuals that develop these skills in small broods. I experimentally adjusted the size of kestrel broods prior to fledging to either two or five young for behavioral observation. I then monitored the development of foraging behavior and dispersal time in individuals from each brood size after they fledged.

STUDY AREA AND METHODS

I studied a population of wild kestrels nesting in 27 nest boxes in central Iowa in 1990. A total of 24 nest boxes was attached to highway signs along I-35. Two nest boxes were located on farmsteads, and one was located at the College of Veterinary Medicine at Iowa State University, Ames, Iowa.

I banded all 86 young with U.S. Fish and Wildlife Service leg bands and individually marked them with colored vinyl leg jesses prior to fledging (Bednarz 1987). I captured 46%
(25/54) of the adults in these nest boxes and banded and color marked them.

The size of broods was adjusted 1-3 d before the oldest bird in the brood fledged. Where possible, the natural make-up of young in the brood was retained. Natural broods of five young were left intact, and broods with ≤4 young were reduced to broods of two. Young removed from nests with ≤4 young were placed in other nests in the study to increase the size of broods or were released by hacking (see Barclay 1987: 243) at the Iowa Department of Natural Resources Wildlife Research Station near Boone. One young was added to a brood of one and one was added to a brood of four to create broods of two and five, respectively. The age of introduced young was matched closely with the age of young already in these nests. These adjustments resulted in 15 broods of 2 siblings each and 12 broods of 5 siblings each (Table 1).

Back-mounted radio-transmitters were attached to one randomly selected individual in each of the 12 broods of 2; both individuals were radio-tagged in three broods. Among broods of five, one individual was radio-marked in each of nine broods and five, four, and two individuals were radio-marked in each of the other three broods.

The 38 radio-marked kestrels fledged 26 May through 8 August. The median fledging date was 29 June.

Only kestrels fitted with radio-transmitters were
Table 1. Number of broods of two or five American Kestrels (N) with radio-tagged individuals prior to nest departure and number of broods observed at weekly intervals after fledging.

<table>
<thead>
<tr>
<th>Group size</th>
<th>Number of broods with radio-tagged individuals</th>
<th>WEEKS POST-FLEDGING</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Two siblings</td>
<td>15</td>
<td>8</td>
</tr>
<tr>
<td>Five siblings</td>
<td>12</td>
<td>8</td>
</tr>
</tbody>
</table>
selected for observation as focal birds (Altmann 1974). When >1 individual in a brood was radio-marked, one fledgling was randomly selected for observation from among those visible.

Nine radio-marked kestrels in eight small sibling groups died within 1 wk after fledging. During the first 2 wk after fledging, five radio-tagged kestrels from five large sibling groups also died. Signals failed in five transmitters, two in small sibling groups and three in large, within 3 d after the radio-tagged birds fledged.

Fledglings were observed between 0600 and 1300 at a distance of 70-100 m with a 20x or 20-60x spotting scope. Family groups were monitored on a rotational basis; generally once during the first wk post-fledging and then at 1-3 d intervals until contact with all radio-marked kestrels in a brood was lost. When I could not find a radio-marked kestrel, I searched by vehicle an area of about 6 km² around the kestrel's last known location.

I adopted Wyllie's (1985) definition of dispersal, which is movement of a fledged bird farther than 1 km from its nest without return. I 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 = 5) were not classified as dispersed because young kestrels at this age are relatively inactive (Varland et al.)
1991). Transmitter failure was confirmed in two of these five birds when they were observed with other radio-marked siblings. Thus, it was unlikely that signal loss in the other three birds was the result of movement from the search area.

Observation sessions lasted 5 to 60 min or until the focal bird disappeared from view. I did not use data if visual contact with the bird was lost in <5 min. I attempted to initiate a second observation session with the same focal bird or with another radio-marked kestrel from the brood if the bird disappeared in 5-30 min. This resulted in a total of 15 paired sessions. For the analysis, I combined each pair of consecutive sessions into one session. I analyzed data for 85 observation sessions (mean length = 43.6 min, S.D. = 19.6).

A metronome timing device (Wiens et al. 1970) set at 20-s intervals cued spot observations of behavior and social activity. At each sound of the tone, I recorded behavior and social activities of the focal kestrel. Except for the social activity subclass "social hunting", I used the classes and subclasses of activity described in Varland et al. (1991): general behavior (nine subclasses), social behavior (five subclasses), foraging behavior, and allopreening and beaking.

General Behavior. "Perch resting" describes a kestrel perched and not engaged in any other behavior. "Perch hunting" was distinguished from other perching activity by alert posture, erect body or body leaning slightly forward,
frequent staring at ground, and head bobs (Toland 1987, Village 1990). "Ground hunting" was defined as a bird searching on the ground for prey for >20 seconds. Searches of shorter duration involving flight from a perch were recorded as perch hunting. "Flight" was any nonhunting flight. I used 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" referred to a focal kestrel concealed by vegetation or other objects. A session was discontinued when a bird was out of sight >5 minutes. "Other" was used to categorize behaviors observed relatively infrequently: walking, hover hunting, aggressive interactions among siblings, parent-to-young prey transfers, and eating prey caught by parents. It was not uncommon for one or both adults to vocalize aggressively at observers during observation sessions (see also Varland et al. 1991). Thus, interactions between broods and parents probably occurred less frequently than they would in the absence of observers.

Social Behavior. "Association" was any activity (except social hunting) of the focal kestrel that occurred ≤3 m from one or more siblings (kestrels other than siblings were sometimes included, see Varland et al. 1991). "Nonsocial"
refers to activity of the focal kestrel occurring >3 m from one or more kestrels. When I could not see whether other kestrels were ≤3 m from the focal kestrel because of dense vegetation, I recorded the kestrel's social status as "undetermined". "Social hunting" was hunting activity by the focal kestrel which occurred ≤10 m from one or more kestrels that also were hunting. This social hunting distance was increased from ≤3 m (Varland et al. 1991), because I observed that social interactions among foraging kestrels could occur at distances of up to 10 m.

**Foraging Behavior.** I recorded number of pounces, number of captures, and prey type. Foraging success was the percentage of pounces with known outcomes that were successful. Outcomes were unknown in 15% (46/310) of the observed pounces. In these cases, either the capture phase of prey pursuit occurred out of sight or the pursuit occurred too far away and I was unable to determine the outcome. Pounces and captures were converted to hourly rates based on session length.

**Allopreening and Beaking.** I recorded the frequencies and the individuals involved in allopreening and beaking (Varland et al. 1991), forms of direct social contact.

**Statistical Analysis.** I grouped behavioral data according to 7-d intervals starting with fledging. The experimental unit (N) was the sibling group, and the number of
groups observed during each of the 4 wk that birds were under study ranged from eight to seven for sibling groups of five and from eight to three for sibling groups of two (Table 1). I computed statistics for behavior, social, and foraging activity for each sibling group in each 7-d post-fledging interval for which data were available.

I used the general linear model procedure (PROC GLM, SAS Institute 1985) for an analysis of variance (ANOVA). The split-plot approach to repeated measures was used (Winer 1971) to test for differences in behavior, social, and foraging activities between large and small sibling groups of kestrels. Thus, for specific activities during the 4 wk after fledging, I conducted tests for average brood size effect (BROOD SIZE), for linear trends over time (TIME), and for differences in the rates of development (TIME x BROOD SIZE interaction). Because data were missing from some cells (not all sibling groups were represented in all weeks), I used Type III sum of squares to calculate P-values. I selected 0.05 as the level of significance for linear time trends in behavior. Because tests of several behaviors were considered in each phase of analysis, the significance level of P-values was adjusted 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 of tests being made on a set of non-independent behaviors.
RESULTS

Tests for differences in behavior by brood size (average brood size effect) across the 4 wk post-fledging period were nonsignificant (Table 2). Significant decreases across wk occurred in perch resting and maintenance behaviors, and significant increases occurred in perch hunting and eating self-captured prey (Table 2). The rates of decrease in perch resting and maintenance and the rates of increase in perch hunting and eating self-captured prey did not differ significantly between large and small sibling groups (Table 2).

No differences were detected in mean pounce rates, percent success, and capture rates (Fig. 1). Significant increases occurred with time in mean pounce rates, percent success, and capture rates (Fig. 1), but no differences were observed between small and large groups in the rates of increase of these foraging activities (Fig. 1).

Young American Kestrels fed primarily on insects, which comprised 95% (71/75) and 97% (107/110) of the prey items caught by small and large sibling groups respectively. Sixteen percent (28/178) of these insects were grasshoppers (order Orthoptera). I was unable to identify the other insects caught.

No differences in social activity were found between brood sizes (Table 3) or in linear trends in social activity
Table 2. Percent time (mean % ±SE) spent engaged in ten behaviors by broods of two and five American Kestrels at weekly intervals after fledging in Iowa.

<table>
<thead>
<tr>
<th>BEHAVIOR</th>
<th>BROOD SIZE</th>
<th>mean ±SE 1</th>
<th>mean ±SE 2</th>
<th>mean ±SE 3</th>
<th>mean ±SE 4</th>
<th>BROOD SIZE a</th>
<th>TIME b</th>
<th>TIME x BROOD SIZE c</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N)</td>
<td>2 (8)</td>
<td>(5)</td>
<td>(5)</td>
<td>(3)</td>
<td></td>
<td>0.4731</td>
<td>&lt;0.0010</td>
<td>0.1565</td>
</tr>
<tr>
<td>Perch resting</td>
<td>2</td>
<td>77.4 ± 6.1</td>
<td>63.5 ± 7.7</td>
<td>34.2 ± 9.7</td>
<td>21.0 ± 10.0</td>
<td>0.4731</td>
<td>&lt;0.0010</td>
<td>0.1565</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>78.2 ± 4.6</td>
<td>69.4 ± 3.5</td>
<td>46.3 ± 4.2</td>
<td>39.0 ± 9.2</td>
<td>0.4731</td>
<td>&lt;0.0010</td>
<td>0.1565</td>
</tr>
<tr>
<td>Perch hunting</td>
<td>2</td>
<td>0.0</td>
<td>5.6 ± 5.6</td>
<td>42.4 ± 15.9</td>
<td>56.4 ± 11.0</td>
<td>0.2633</td>
<td>&lt;0.0010</td>
<td>0.2309</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.0</td>
<td>4.2 ± 3.0</td>
<td>24.5 ± 6.0</td>
<td>39.1 ± 11.0</td>
<td>0.2633</td>
<td>&lt;0.0010</td>
<td>0.2309</td>
</tr>
<tr>
<td>Ground hunting</td>
<td>2</td>
<td>0.0</td>
<td>0.6 ± 1006</td>
<td>1.0</td>
<td>0.5 ± 0.4</td>
<td>0.4547</td>
<td>0.2309</td>
<td>0.7542</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.0</td>
<td>1.2 ± 1.1</td>
<td>1.3 ± 0.8</td>
<td>1.5 ± 0.8</td>
<td>0.4547</td>
<td>0.2309</td>
<td>0.7542</td>
</tr>
<tr>
<td>Flying</td>
<td>2</td>
<td>0.3 ± 0.2</td>
<td>7.0 ± 5.6</td>
<td>7.3 ± 4.2</td>
<td>2.5 ± 1.5</td>
<td>0.3753</td>
<td>0.1683</td>
<td>0.8572</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.2 ± 0.2</td>
<td>2.8 ± 0.7</td>
<td>4.3 ± 2.0</td>
<td>3.5 ± 1.2</td>
<td>0.3753</td>
<td>0.1683</td>
<td>0.8572</td>
</tr>
<tr>
<td>Eating self-captured prey</td>
<td>2</td>
<td>0.0</td>
<td>0.4 ± 0.3</td>
<td>2.4 ± 0.7</td>
<td>7.4 ± 4.1</td>
<td>0.0605</td>
<td>&lt;0.0010</td>
<td>0.1519</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.0</td>
<td>0.1 ± 0.1</td>
<td>0.3 ± 0.1</td>
<td>3.5 ± 1.4</td>
<td>0.0605</td>
<td>&lt;0.0010</td>
<td>0.1519</td>
</tr>
<tr>
<td>Maintenance</td>
<td>2</td>
<td>17.1 ± 4.2</td>
<td>8.8 ± 3.3</td>
<td>8.2 ± 3.0</td>
<td>4.0 ± 2.4</td>
<td>0.1596</td>
<td>0.0034</td>
<td>0.7748</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>14.4 ± 3.8</td>
<td>9.0 ± 2.2</td>
<td>11.7 ± 2.1</td>
<td>7.5 ± 1.8</td>
<td>0.1596</td>
<td>0.0034</td>
<td>0.7748</td>
</tr>
<tr>
<td>Lying on belly</td>
<td>2</td>
<td>2.8 ± 2.2</td>
<td>7.6 ± 6.8</td>
<td>0.0</td>
<td>0.0</td>
<td>0.2246</td>
<td>0.9376</td>
<td>0.8044</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.2 ± 0.1</td>
<td>&lt;0.1 &lt;0.1</td>
<td>0.0</td>
<td>0.0</td>
<td>0.2246</td>
<td>0.9376</td>
<td>0.8044</td>
</tr>
<tr>
<td>Begging</td>
<td>2</td>
<td>1.7 ± 1.1</td>
<td>0.7 ± 0.7</td>
<td>1.1 ± 0.7</td>
<td>0.0</td>
<td>0.2837</td>
<td>0.3259</td>
<td>0.3787</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>3.5 ± 1.3</td>
<td>3.8 ± 1.7</td>
<td>3.2 ± 1.9</td>
<td>1.1 ± 0.7</td>
<td>0.2837</td>
<td>0.3259</td>
<td>0.3787</td>
</tr>
<tr>
<td>Out of sight</td>
<td>2</td>
<td>0.2 ± 0.2</td>
<td>3.0 ± 1.8</td>
<td>3.1 ± 1.5</td>
<td>7.6 ± 4.9</td>
<td>0.0688</td>
<td>0.3938</td>
<td>0.3259</td>
</tr>
<tr>
<td></td>
<td>5</td>
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<td><strong>Behavior</strong></td>
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<tr>
<td>Brood Size</td>
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<td>Mean ± SE</td>
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<tr>
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<td>2</td>
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<td>0.8885</td>
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<td>0.9 ± 0.9</td>
<td>1.2 ± 1.0</td>
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*P-values are based on ANOVA F-tests for average brood size effect across 4 wk post-fledging (df = 1, 28). All tests for nonlinearity were not significant.

**P-values are based on ANOVA F-tests for time trends across 4 wk post-fledging (Perch resting df = 1, 31; perch hunting df = 1, 11). All tests for nonlinearity were not significant.

° P-values are based on ANOVA F-tests for differences in time trends across 4 wk post-fledging (df = 1, 28). All tests for nonlinearity were not significant.

*Total number of broods of two and five siblings observed.
Figure 1. Mean (± SE) pounces/hr (a), percent success (b), and captures/hr (c) for sibling groups of two and five American Kestrels (left) and for groups combined (right) at weekly intervals after fledging. P-values are based on ANOVA F-tests for average brood size effect (df = 1, 28), time trends across wk (df = 1, 28), and for differences in time trends (df = 3, 28) during 4 wk after fledging. All tests for nonlinearity were not significant.
(a) Two and five sibling groups

<table>
<thead>
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<table>
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<tr>
<th>Pounces/hr (+/- 1 S.E.)</th>
<th>Brood Size (P = 0.3515)</th>
<th>Time x Brood Size (P = 0.3462)</th>
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<td>2 Siblings</td>
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(b) % Success (+/- 1 S.E.)

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<th>% Success (+/- 1 S.E.)</th>
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<th>Time x Brood Size (P = 0.1229)</th>
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<td>2 Siblings</td>
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(c) Captures/hr (+/- 1 S.E.)

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<th>Time x Brood Size (P = 0.3011)</th>
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<td>2 Siblings</td>
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Table 3. Percent time (mean % ±SE) spent engaged in social and nonsocial activity by broods of two and five American Kestrels at weekly intervals after fledging in Iowa.

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<thead>
<tr>
<th>WEEKS POST-FLEDGING</th>
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<th>3</th>
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<td>P-VALUES</td>
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<tr>
<td>BEHAVIOR BY SOCIAL ACTIVITY</td>
<td>BROOD SIZE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
<td>MEAN ±SE</td>
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<tr>
<td>Perch resting (N)*</td>
<td>2</td>
<td>(8)</td>
<td>(5)</td>
<td>(5)</td>
<td>(3)</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>(8)</td>
<td>(8)</td>
<td>(7)</td>
<td>(7)</td>
</tr>
<tr>
<td>Association</td>
<td>2</td>
<td>19.9 ± 13.6</td>
<td>11.8 ± 11.8</td>
<td>22.3 ± 13.8</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>23.5 ± 9.5</td>
<td>38.1 ± 12.0</td>
<td>32.2 ± 8.1</td>
<td>23.9 ± 9.7</td>
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<tr>
<td>Nonsocial</td>
<td>2</td>
<td>80.1 ± 13.6</td>
<td>88.2 ± 11.8</td>
<td>77.7 ± 13.8</td>
<td>100.0 ± 0.0</td>
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<tr>
<td></td>
<td>5</td>
<td>71.3 ± 11.6</td>
<td>61.1 ± 12.2</td>
<td>67.4 ± 8.2</td>
<td>76.1 ± 9.7</td>
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<tr>
<td>Undetermined*</td>
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<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>5.2 ± 4.1</td>
<td>0.7 ± 0.7</td>
<td>0.4 ± 0.4</td>
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<tr>
<td>Perch hunting (N)†</td>
<td>2</td>
<td>(0)</td>
<td>(1)</td>
<td>(5)</td>
<td>(3)</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>(0)</td>
<td>(2)</td>
<td>(7)</td>
<td>(7)</td>
</tr>
<tr>
<td>Association</td>
<td>2</td>
<td>0.0</td>
<td>0.0</td>
<td>12.8 ± 12.1</td>
<td>13.6 ± 13.6</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.0</td>
<td>10.1 ± 10.1</td>
<td>10.6 ± 11.3</td>
<td>9.0 ± 7.0</td>
</tr>
<tr>
<td>Social hunting</td>
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<td>8.7 ± 0.0</td>
<td>14.8 ± 8.4</td>
<td>6.2 ± 6.2</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.0</td>
<td>36.7 ± 13.3</td>
<td>42.0 ± 13.4</td>
<td>22.7 ± 7.9</td>
</tr>
<tr>
<td>Nonsocial</td>
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<td>91.3 ± 0.0</td>
<td>72.4 ± 19.2</td>
<td>80.2 ± 19.8</td>
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<tr>
<td></td>
<td>5</td>
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<td>51.2 ± 1.2</td>
<td>47.1 ± 14.5</td>
<td>68.3 ± 13.4</td>
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<tr>
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<td>5</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3 ± 0.3</td>
<td>0.0</td>
</tr>
</tbody>
</table>

* P-values are based on ANOVA F-tests for average brood size effect across 4 wk post-fledging (df = 1, 28). All tests for nonlinearity were not significant.
† P-values are based on ANOVA F-tests for average brood size effect across 4 wk post-fledging (Perch resting, df = 1, 31; perch hunting, df = 1, 11). All tests for nonlinearity except perch resting/nonsocial behavior (TIME, P = 0.0002) were not significant.
‡ P-values are based on ANOVA F-tests for time trends across 4 wk post-fledging (df = 1, 28). All tests for nonlinearity were not significant.
§ Total number of broods of two and five siblings observed.
# Social status of focal bird could not be determined.
over time (Table 3). Allopreening or beaking exchanges were observed among 7% (2/30) and 14% (8/55) of the observation sessions on small and large sibling groups respectively. Allopreening or beaking was observed at least once in 25% (2/8) of the small sibling groups and in 75% (6/8) of the large groups.

Social hunting occurred during 36% (5/14) of the sessions in which hunting was observed in small broods and 59% (16/27) of the sessions in large broods. Social hunting was observed at least once in 50% (4/8) of the small broods and 75% (6/8) of the large broods. Mean group size during social hunting was 2.0 for small broods and 2.8 for large broods. Siblings only were observed social hunting in 71.4 % (15/21) of all sessions in which social hunting was observed, 14.3 % (3/21) involved siblings and parents, and 14.3 % (3/21) involved siblings and unrelated kestrels outside the parent-sibling family unit.

Mean time of dispersal was 23.2 d for small broods (N = 6, SE = 1.9) and 26.7 d for large broods (N = 7, SE = 2.0). This difference was not significant (ANOVA, P = 0.2989).

DISCUSSION

All tests for average brood size effects for kestrel behavior, foraging, and social activities were nonsignificant. When trends in behavioral change over time were detected, no significant differences occurred in the rates of change
between small and large broods. Thus, broods of two and five kestrels did not differ in behavior, social, or foraging activity during the 4 wk that broods were observed.

Mean time of dispersal did not differ by brood size. I expected that individuals in large broods would achieve self-sufficiency sooner and thereby disperse sooner because they would have more opportunities to interact with other kestrels as their foraging skills developed.

Although I was unable to demonstrate any brood size effects, the power of my statistical tests was reduced because of unexpected reductions in sample sizes. Mortality or loss of the radio signal was high among radio-tagged kestrels the first wk after fledging, and resulted in 47 and 33% decreases in sample size for groups of two and five siblings respectively (Table 1). Predation was the largest source of mortality for small and large broods, and accounted for 9 of 14 deaths.

Predation pressure has been suggested by many as an important force in the evolution of social groups (e.g., Alexander 1974, Wittenberger 1981, Krebs and Davies 1987). Gregariousness increases the probability of survival because more animals are searching for predators (e.g., Altmann 1974, Treisman 1975). Predation may occur relatively infrequently within groups and yet be an important selective force (Stacey 1986). The data are insufficient to compare the rates of
predation between the two brood sizes. However, whether sociality increases predator detection and hence survival for individuals in a kestrel brood merits further study.

Starvation was not an important cause of mortality (1 of 14 deaths), but may have been significant later in the first year of life. Because of movement of young away from their natal areas, I was unable to observe any kestrel longer than 39 d after fledging. Starvation was the most important cause of mortality after independence from parents among juvenile Yellow-eyed Juncos (Junco phaeotus; Sullivan 1989) and Tawny Owls (Strix aluco; Hirons et al. 1979).

Presumably young kestrels learn foraging skills during the first 4-6 wk after fledging. Imitative social foraging during this period may provide an adaptive advantage to individuals later in the juvenile period, if there is strong selection for learned efficiency in foraging. Mean hunting success from perches in this study and in earlier research (Varland et al. 1991) did not exceed 55%. This is a substantially lower success rate than previously reported for older kestrels hunting invertebrates (Collopy 1973, Smallwood 1987, Toland 1987).

The high mortality observed among fledgling kestrels in 1990 was unexpected. Only 2 of 26 birds radio-marked in 1988 and 1989 died (Section III). Further research is needed, perhaps using the experimental approach presented here but
with larger sample sizes, to document whether social foraging influences foraging efficiency in American Kestrels.

ACKNOWLEDGMENTS

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LITERATURE CITED


SECTION III. HABITAT AND PERCH USE, CAUSES OF MORTALITY, AND TIME TO DISPERAL IN POST-FLEDGING AMERICAN KESTRELS ALONG AN INTERSTATE HIGHWAY
Abstract.—We studied habitat and perch use, causes of mortality, and time to dispersal of American Kestrels (*Falco sparverius*) after fledging from nest boxes attached to the backs of highway signs along Interstate-35 in Central Iowa. We attached radio-transmitters to 61 nestlings in 47 nests just prior to nest departure between 1988 and 1990. During the first wk 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 1 of the 16 kestrels found dead died during the first wk after fledging, before 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 along the interstate. After the first wk, fledgling kestrels began hunting along secondary roads, and the use of this habitat increased throughout the 4 wk birds were observed. Mean time until the initiation of dispersal was 22.7 d after fledging. We found little evidence of natal philopatry. Only 1 of 17 birds recaptured in a nest box as a breeding bird was banded as a nestling.
INTRODUCTION

The American Kestrel requires open country for hunting (Cade 1982). The species is remarkably adaptable, and this is evident in its distribution over a wide range of habitats such as agricultural lands, urban and suburban environments, and highway and railroad rights-of-way (Brown & Amadon 1968, Cade 1982, Bird and Palmer 1988). Bird and Palmer 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 the rest 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 woodland comprises 4% of the land area (Thomson and Hertel 1980).

After observing kestrels forage along an interstate highway right-of-way, in 1983 R.D. Andrews (Iowa Department of Natural Resources) implemented a kestrel nest box program whereby nest boxes were attached to the backs of highway signs (Fig. 1; Dybas 1991). There are >200 nest boxes placed along Iowa's interstate rights-of-way (Dybas 1991), and eight states have copied the Iowa program (Timp 1986).

In 1988 we began a study of kestrels nesting in these nest
Figure 1. American Kestrel nest box attached to the back of an interstate highway sign.
boxes along Interstate-35 (I-35) in Central Iowa (Varland et al. 1991; Section II). In this paper we describe habitat and perch use, causes of mortality, and time to 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 individually marked each with colored vinyl leg jesses just before they fledged. We captured 60% (112/186) 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 using a vehicle with top-mounted dual yagi antennae. The number of individuals radio-marked in a brood ranged from one to all siblings. We radio-marked 12 individuals in 9 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 2 siblings in 15 nests and 5 siblings in 9 nests to study the
influence of brood size on foraging efficiency (Section II).

We observed the radio-marked individual(s) in a fledgling group between 0600 and 1300 hr 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 from transmitter failure or because the kestrels left the area. Since we did not locate every radio-marked kestrel daily, the exact day of dispersal or death was sometimes unknown. For these birds, we estimated the time of death or dispersal as the mid-point between the last two visits.

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

Data were collected in 1989 and 1990 just before or during 5-60 min behavioral observation sessions (Varland et al. 1991; Section II). 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 pounces occurred 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; Section II). In 1989 focal birds were either radio-marked or color-marked with jesses.
In 1990 only radio-marked kestrels served as focal birds. Kestrels used the following structures 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 pounces of perch hunting kestrels were initiated.

We recognized 11 different habitat types. The interstate "right-of-way" was the grassy area associated with the roadway. All roads that were not interstate highway were "secondary roads" and included the grassy roadside and the road surface. "Cornfields" or "soybean fields" were actively farmed croplands. A "farmstead" contained farm buildings and usually trees and shrubs. "Old field" was an ungrazed field with scattered trees, and "pasture" was a grazed field with or without trees. A fence line with a 0.5-1.0 m strip of grass was a "grassy fencerow" and a fence line with woody trees or shrubs was a "wooded fencerow". "Grasslands" were lands in federal Conservation Reserve or Set Aside Programs. The "other" category included alfalfa fields and woodlands.

**Dispersal**.—When contact with a radio-marked kestrel was lost, we searched an area of about 6 km² 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, it was unlikely that signal failure from these transmitters resulted from a bird’s movement from the search area. Transmitter failure was confirmed in three of the eight cases with early signal loss when the kestrels wearing these units were observed with other radio-marked kestrels. Data on dispersal were collected 1988-1990.

Causes of mortality.--Data on the causes of mortality were collected 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 in radio-transmitters, sheared instead of plucked feathers, and mammal tracks or scat near the kill (Fitzner 1980, Bull et al. 1989). Necropsies were conducted at the College of Veterinary Medicine at Iowa State University to determine the cause of death of two birds.

Statistical analysis.--We grouped habitat and perch use data by wk, starting with fledging and ending 4 wk after fledging. For six radio-marked kestrels, data on perch and
habitat use were collected during the 5th wk after fledging. Because relatively few observations were made during the 5th wk, we combined these data with the data on perch and habitat use by kestrels during the 4th wk post-fledging.

The observational unit (N) was the sibling group. We computed means for observations of habitat and perch use for each wk 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 during 4 wk post-fledging. Because data were missing from some cells (not all sibling groups were represented in all wk), we used Type III sum of squares to calculate P values.

RESULTS AND DISCUSSION

Habitat Use—During the first wk 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; Section II). 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 along field perimeters in trees and on fences and fenceposts (Table 2). Trees, fences and fenceposts were also common perches for fledglings using the interstate right

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<td>Mean % (SE)</td>
<td>Mean % (SE)</td>
<td>Mean % (SE)</td>
</tr>
<tr>
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<td>(N = 30)</td>
<td>(N = 21)</td>
<td>(N = 19)</td>
<td>(N = 14)</td>
</tr>
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<td>6.6 (2.8)</td>
<td>4.1 (3.6)</td>
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<td>0.0</td>
<td>3.1 (2.6)</td>
<td>1.2 (1.2)</td>
</tr>
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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.
TABLE 2. Observations (Obs) of American Kestrel perch locations along the I-35 right-of-way, in cornfields and in soybean fields the first wk after fledging in Iowa in 1989 and 1990.

<table>
<thead>
<tr>
<th>Perch</th>
<th>Habitat</th>
<th>Right-of-way (Obs = 23)</th>
<th>Cornfields (Obs = 28)</th>
<th>Soybean fields (Obs = 32)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean % (SE)</td>
<td>N = 14</td>
<td>Mean % (SE)</td>
<td>Mean % (SE)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(N = 16)</td>
<td>(N = 12)</td>
</tr>
<tr>
<td>Trees</td>
<td>39.3 (11.9)</td>
<td>22.9 (10.4)</td>
<td>40.0 (12.6)</td>
<td></td>
</tr>
<tr>
<td>Fences or fenceposts</td>
<td>33.3 (14.4)</td>
<td>31.2 (12.0)</td>
<td>2.1 (2.1)</td>
<td></td>
</tr>
<tr>
<td>Ground</td>
<td>23.8 (10.0)</td>
<td>43.8 (12.8)</td>
<td>45.6 (12.7)</td>
<td></td>
</tr>
<tr>
<td>Interstate signs</td>
<td>3.6 (3.6)</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>Billboards</td>
<td>0.0</td>
<td>0.0</td>
<td>8.3</td>
<td></td>
</tr>
<tr>
<td>Utility wires or poles</td>
<td>0.0</td>
<td>0.0</td>
<td>1.9 (1.9)</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>0.0</td>
<td>2.1 (2.1)</td>
<td>2.1 (2.1)</td>
<td></td>
</tr>
</tbody>
</table>

* Number of sibling groups observed.
of-way. Fences and fenceposts occurred at the perimeter of the right-of-way whereas trees were generally mid-way 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) occurred during the first wk after fledging, and 82% (36/44) of the total occurred during 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; Section II). Post-fledging kestrels spent substantial amounts of time hunting in soybean fields when hunting began the second wk after fledging (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 perch hunting from trees, 9.4% (SE = 9.4) while perch hunting from fences or fenceposts (9.4%; SE = 9.4), 7.3% (SE = 7.9) while perch hunting from the ground, and 25.0% (SE = 25.0) while hover hunting (3 unsuccessful pounces on insect prey by one kestrel).

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

<table>
<thead>
<tr>
<th>Habitat</th>
<th>2 (Obs = 62)</th>
<th>3 (Obs = 187)</th>
<th>4 (Obs = 332)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean % (SE)</td>
<td>Mean % (SE)</td>
<td>Mean % (SE)</td>
</tr>
<tr>
<td></td>
<td>(N = 10)</td>
<td>(N = 18)</td>
<td>(N = 14)</td>
</tr>
<tr>
<td>Right-of-way</td>
<td>2.5 (2.5)</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Cornfields</td>
<td>10.0 (10.0)</td>
<td>8.3 (6.1)</td>
<td>0.5 (0.5)</td>
</tr>
<tr>
<td>Soybean fields</td>
<td>42.5 (15.8)</td>
<td>16.0 (6.4)</td>
<td>9.5 (7.1)</td>
</tr>
<tr>
<td>Farmsteads</td>
<td>0.3 (0.3)</td>
<td>0.3 (0.3)</td>
<td>0.0</td>
</tr>
<tr>
<td>Pastures</td>
<td>0.0</td>
<td>3.7 (2.9)</td>
<td>13.4 (7.1)</td>
</tr>
<tr>
<td>Grassy fencerows</td>
<td>0.0</td>
<td>4.2 (4.2)</td>
<td>0.0</td>
</tr>
<tr>
<td>Grasslands</td>
<td>17.9 (12.0)</td>
<td>22.3 (8.6)</td>
<td>10.8 (5.3)</td>
</tr>
<tr>
<td>Secondary roads</td>
<td>27.1 (13.2)</td>
<td>32.4 (8.8)</td>
<td>61.6 (9.3)</td>
</tr>
<tr>
<td>Unknown</td>
<td>0.0</td>
<td>5.6 (5.6)</td>
<td>0.0</td>
</tr>
<tr>
<td>Other</td>
<td>0.0</td>
<td>7.2 (5.6)</td>
<td>4.3 (3.6)</td>
</tr>
</tbody>
</table>

* Observed one pounce by a kestrel the first wk after fledging.
** Number of sibling groups observed.
° Land in Conservation Reserve or Set-aside Program.
secondary roads increased linearly with time (Table 1, \( P = 0.0031 \)) because kestrels frequently foraged there (Table 3). Most of these roads were gravel surfaced and had relatively little vehicle traffic. Kestrels perch hunted along secondary roads from utility poles or wires, fences or fenceposts, and the ground (Table 4). For pounces where we identified the specific location of the strike (\( N = 21 \) sibling groups; observations for 1989 and 1990), 49.2\% (SE = 7.4) occurred 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 were relatively free of traffic, contained a variety of perches, and provided an unobstructed surface from which insect prey could be easily caught. Utility poles and wires are particularly useful perches for foraging kestrels because they provide the birds with an unrestricted view and an opportunity for positioning at specific locations along the perch continuum created by the utility line (Shrubb 1982).

The interstate right-of-way was not an important foraging site for fledgling kestrels (Table 3). One contributing factor was probably 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; Section II) or other behavioral interactions, vehicle noise
Table 4. Observations (Obs) of perch locations of post-fledging American Kestrels hunting along secondary roads in Iowa in 1989.

<table>
<thead>
<tr>
<th>Perch</th>
<th>Weeks post-fledging</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>(Obs = 2)</td>
</tr>
<tr>
<td></td>
<td>Mean % (SE) (N* = 2)</td>
</tr>
<tr>
<td>Utility wires or poles</td>
<td>50.0 (50.0)</td>
</tr>
<tr>
<td>Ground</td>
<td>50.0 (50.0)</td>
</tr>
<tr>
<td>Fences or fenceposts</td>
<td>0.0</td>
</tr>
</tbody>
</table>

*Number of sibling groups observed.*
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 along secondary roads.

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

Mortality.—All but 1 of the 16 kestrels found dead died the first wk after fledging. At this time, and especially during the first 3-4 d after nest departure, kestrels were not proficient fliers. This lack of proficiency probably contributed to mortality caused by mammalian predation and collisions. Six of the 14 birds for which the cause of death was known were killed by mammalian predators. Three were killed by avian predation, two by colliding with vehicles on I-35, one by starvation, and one by dehydration. For two birds, the cause of death was unknown. Red fox (Vulpes vulpes) tracks were found at the sites of two of the deaths. We were unable to identify the mammals or birds causing the other kills. We found one dead kestrel 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 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. commun.). We concluded the bird died after colliding with the tree.

It is surprising that traffic on I-35 was not a more important source of fledgling mortality, given that the nest boxes are attached to highway signs just 20-25 m from the road. Village (1990) reported that, over a 30 year period, road deaths among Common Kestrels (Falco tinnunculus) in Europe increased in frequency and became the most commonly reported cause of mortality. He suggested the increase was a result of the greater volume and speed of modern traffic.

In our study, transmitter failure was confirmed in three of eight cases of signal loss when the kestrels wearing these units were observed with other radio-marked kestrels. It is possible that signal loss in the other five radio-transmitters occurred when these kestrels were hit by vehicles. If this happened, the total number of vehicle-caused kestrel mortalities could be as high as seven. However, we have some evidence 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 it was the previous 2 yr, but differences in the amount of rainfall during these yr may have played a role. Mean monthly rainfall from March through August in 1988 was 5.2 cm, in 1989 6.5 cm, and in 1990 15.6 cm (National Oceanic and Atmospheric Administration 1988, 1989, 1990). Heavy rainfall during spring 1990 delayed crop planting, and as a result kestrels may have been more accessible to ground predators. The remains of five of the six kestrels that died from mammalian predation were found in cropfields.

Dispersal.—Mean time of 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 of 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 out of their natal areas by aggressive parents, a behavior which has been observed between parent Spanish Imperial Eagles (Aquila heliaca) and their young (Alonso et al. 1987). Kestrels left their natal areas as foraging behavior developed (Varland et al. 1991; Section II) 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 if other kestrels were present with four of these birds but the other seven birds were observed perched resting or social hunting (Varland et al. 1991; Section II) with 1-8 other kestrels. These dispersing groups included siblings, as well as kestrels from outside the family unit, and, in one case, a sibling and a female parent.

The mean age at the loss of contact with those kestrels that were followed after dispersal from the natal area was 28.3 d post-fledging ($SD = 6.0$). Because of movement of birds 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 June 1988 and found dead on 26 February 1989 near Slater, Iowa; 50 km from its natal area. The second bird was banded on 17 June 1989 and was found dead
on 21 October 1989 near Jewett, Texas; 1300 km from its natal area. We banded the third kestrel on 3 August 1990, and it was found dead near Sulfur, Oklahoma on 1 February 1991; 950 km from its natal area.

During the study we captured one adult nesting on the study area that was banded as a nestling. In contrast, during the same time period we re-captured 16 adult kestrels nesting on the study area in either the same nest box that they used in a previous year or in another nest box.

Natal dispersal has been defined as movement of young from birth site to first breeding site (Johnston 1961, Greenwood 1980), 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. However, since we were unable to track any kestrel longer than 39 d after fledging, we could not determine where radio-marked kestrels fledging from nest boxes along I-35 bred their first year.

Data from band recoveries indicate that at least some birds fledging on the study area are migratory, a phenomenon that makes the process of dispersal difficult to study (Morton et al. 1991). Only 1 of 17 birds recaptured in a nest box as a breeding bird was originally banded as a nestling. The low recapture rate indicates that natal philopatry on the study area is probably not strong. More research is needed to
determine the movements of kestrels after the initiation of dispersal.

ACKNOWLEDGMENTS

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LITERATURE CITED


GENERAL SUMMARY

In 1988-1990, I documented the behavior, habitat and perch use, causes of mortality, and time to dispersal of post-fledging American Kestrels in Central Iowa. I attached radio-transmitters to 64 birds in 50 nests to monitor kestrel activity. All young in the study fledged from nest boxes, 47 were attached to the backs of highway signs along the Interstate-35 right-of-way, two were on farmsteads, and one was at the College of Veterinary Medicine at Iowa State university in Ames.

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. Kestrels fledging from nests along the interstate were observed at this time primarily in cropland and along the interstate right-of-way, where they frequently perched on the ground.

All but 1 of the 16 kestrels found dead died during the first week after fledging, before flying skills had developed. Mammalian predation accounted for six deaths and was the main cause of death. Three kestrels were killed by avian predators. Only two deaths resulted from collisions with vehicles along the interstate. One fledgling kestrel died after colliding with a tree, one died from starvation, one from dehydration, and for two kestrels the cause of death could not be determined.
As kestrels grew older, perch resting decreased whereas perch hunting increased. Kestrels used perch hunting more than other types of hunting and fed almost exclusively on invertebrates. Most of the invertebrate prey identified were grasshoppers (order Orthoptera). Mean hunting success did not exceed 55% during the 4-5 weeks that fledglings were observed. Kestrels fledging from nest boxes along the interstate hunted extensively along secondary roads, and the use of this habitat increased throughout the time birds were observed.

Kestrels hunted socially with siblings, families, and also with unrelated kestrels. Social hunting, which occurred during both perch hunting and ground hunting, was imitative rather than cooperative.

I hypothesized that in post-fledging American Kestrels:
1) imitative social foraging increases foraging efficiency, and
2) individuals that develop their foraging skills in large broods will disperse sooner than individuals that develop these skills in small broods. To test these hypotheses, I compared foraging efficiency and dispersal time in experimentally adjusted broods of two and five American Kestrels after fledging. No differences in foraging efficiency or in dispersal time were detected, but sample sizes were small because of high mortality or signal failure among radio-marked birds. Further research is needed to
determine whether social foraging influences foraging efficiency in American Kestrels.

Mean time from fledging until the initiation of dispersal was 22.7 d. I found little evidence of natal philopatry. Only 1 of 17 birds recaptured in nest boxes as adults was originally banded as a nestling. More research is needed to determine the movements of kestrels after the initiation of dispersal.
ADDITIONAL LITERATURE CITED


