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THE POST-FLEDGING DEPENDENCE PERIOD OF THE LESSER KESTREL (*Falco naumanni*) IN SOUTHWESTERN SPAIN

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ABSTRACT.—We studied the post-fledging dependence period of individually marked lesser kestrels (*Falco naumanni*) in southwestern Spain. Chicks fledged at a mean age of 37 d and remained at the breeding colony, depending on their parents for food, on average 5 d more. Parents declined food provisioning to offspring during the post-fledging dependence period. We did not observe play with objects, social play, training or learning of hunting skills among the fledglings. Family groups dissolved once the fledglings dispersed from the colony. The adults tend to remain at the breeding colony while juveniles have been observed up to 164 km NE-NW from their natal colony before starting fall migration.

KEY WORDS: *dispersal*; Falco naumanni; *fledging*; *lesser kestrel*; *post-fledging.*

El periodo de emancipación del Cernícalo Primilla (*Falco naumanni*) en el suroeste de España

RESUMEN.—Estudiamos el período de emancipación de Cernícalos Primilla (*Falco naumanni*) marcados individualmente en el suroeste de España. Los pollos realizaron sus primeros vuelos a una edad media de 37 días y permanecieron en la colonia de cría, dependiendo de las presas aportadas por sus padres, una media de 5 días más. Los padres fueron disminuyendo la cantidad de presas aportadas a su descendencia durante el periodo de emancipación. No observamos que los jóvenes cernícalos jugaran con objetos, realizaran persecuciones u otros juegos sociales ni aprendieran o practicaran la captura de presas antes de emanciparse. Los grupos familiares se disolvieron una vez que los jóvenes abandonaron la colonia de cría. Los adultos tienden a permanecer en la colonia de cría mientras que algunos jóvenes han sido observados hasta a 164 km de su colonia natal en dirección NE-NO antes de iniciar la migración postnupcial.

[Traducción Autores]

The period from fledging to independence is known as the post-fledging dependence period and very little is known about this period for most species of raptors. No published information on the length of this period exists for the lesser kestrel (*Falco naumanni*). Brown and Amadon (1968) said that chicks fledge 26–28 d after hatching and are fed at the nest and in the vicinity of the colony for some time after that, apparently based on a few observations made by Blondel (1964) on two nests in the south of France. According to Pomarol (1990), chicks hatched in captivity and released by hacking, although able to fly at 30 d of age, delayed their first flight till 35–40 d old, and remained 0–25 d at the hacking site before dispersing.

In this study we report the first detailed data on fledging age, duration of the post-fledging dependence period, and behavior during this period of individually marked lesser kestrels in the wild.

STUDY AREA AND METHODS

The post-fledging dependence period of lesser kestrels was studied during 1989 at a breeding colony in the castle of Mairena del Alcor (37°22'N, 5°45'W), Seville, southwestern Spain. The study area is an agricultural plain in the Guadalquivir River basin with small fields of cereals (wheat and barley), sunflowers, olive and fruit trees. The colony consisted of 42 pairs of lesser kestrels breeding in holes in the walls of the castle.

Five neighboring nests (brood-sizes: 4, 4, 3, 2 and 2 chicks), referred hereafter as focal nests, were selected for observations during late nestling and post-fledging dependence period, but only three of these nests produced fledglings. All focal nests could be observed simultaneously from a point 70 m from the colony. All the adults attending the focal nests, except one male and one female, had been banded with laminated plastic bands with an alphanumeric code. The adult male and female attending one of the focal nests were also equipped with a radiotransmitter

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Table 1. Lesser kestrels banded as nestlings and recovered or resighted in a locality different from their natal locality before fall migration.

BANDING LOCALITY	BANDING DATE	RECOVERY LOCALITY	RECOVERY DATE	DISTANCE TRAVELED (km)	DIRECTION TRAVELED	AGE AT RECAPTURE[a]
Arahal	23 June 1988	Fuencaliente	14 July 1988	164	NNE	31 d
Arahal	23 June 1989	Lora del Río	22 July 1989	44	N	49 d
Morón	29 June 1989	Arahal	17 July 1989	18	NNW	34 d
Arahal	10 July 1989	Hinojos	25 August 1989	75	W	78 d
Mairena	5 July 1991	Hacienda Ntra. Sra. de la Luz	18 August 1991	3	E	40 d
Arahal	3 July 1991	Mairena	10 September 1991	22	NW	89 d

[a] Days after hatching.

(5 g, 3% of body mass) attached to two central tail feathers (Kenward 1978).

All nestlings in the colony ($N = 59$) were banded with laminated plastic bands and 10 (including one from a focal nest) were also equipped with a radiotransmitter (5 g) attached with a back-pack harness (Beske 1978). Observations of the post-fledging period at the colony started the 7 July before the first chick of a focal nest fledged and ended the 25 July when all the fledglings from focal nests had abandoned the colony. We performed 4-hr observation periods every 1–2 d, at different times of the day from sunrise to sunset, totalling 36 hr of observations at the colony. One observer (J.B.) remained at the colony while two observers in a vehicle simultaneously tracked the adults equipped with radiotransmitters or tried to locate the fledglings that were dispersing.

At least every 2 d we checked at sunset to find if individuals equipped with radiotransmitters were roosting at the colony. When fledglings started to disperse, we included other roosts habitually used by adults in a 4 km radius of the colony in our sunset checks. We performed checks until all fledglings with radiotransmitters had disappeared from the neighborhood of the colony (31 July).

Hatching date was known for some chicks and for the remaining individuals it was estimated from the length of the 8th primary feather at the time of banding (Donazar et al. 1991). Because hatching asynchrony is small (J.J. Negro unpubl. data) a mean hatching date—obtained from the estimates for each sibling—was assigned to each brood. Fledging date was the first date a chick was observed flying or on a perch it could not have reached walking from the nest. We considered that focal fledglings no longer being fed by their parents at the colony were independent, and that fledglings with radiotransmitters no longer roosting at the colony at sunset had dispersed.

Since 1988, chicks at the colony of Mairena and at two other colonies in a 40-km radius (Morón and Arahal), have been marked with plastic bands. From 1988 to 1992, during the period from fledging to fall migration (July and August), the colonies were visited regularly for other studies. The identity and location of chicks present at the colony was recorded and their age was estimated from the length of the 8th primary feather at banding. Observations were classified in two categories: (1) chicks at the entrance of their nest or on a perch they could have reached walking from it, and (2) chicks seen flying or on a perch they could only have reached by flying. To check if chicks observed in 1989 in Mairena fledged at an older age than is typical for this area, we compared the distribution of observations of chicks of different ages considered to be flying from Mairena in 1989 ($N = 38$) with that from Mairena, Morón and Arahal in 1988, 1990, 1991 and 1992 ($N = 100$) with a Kolmogorov-Smirnov two-sample one-tailed test (Siegel and Castellan 1988).

RESULTS

Fledging Age and Duration of the Post-fledging Dependence Period. Chicks from the focal nests fledged at a mean age of 37.1 d (range 36–40 d, SD = 1.6, $N = 7$). Fledglings from the focal nests became independent a mean of 5.1 d after fledging (range 2–8 d, SD = 1.9, $N = 7$), at a mean age of 42.4 d (range 39–40 d, SD = 1.7, $N = 7$). Fledglings with radiotransmitters dispersed at a mean age of 42 d (range 36–46 d, SD = 3.1, $N = 7$). The only focal fledgling with radiotransmitter became independent and dispersed on the same day at an age of 42 d.

Kestrels in 1989 were not seen flying at the colony at significantly older ages than in the years 1988, 1990, 1991, and 1992 pooled (Kolmogorov-Smirnov test $D_{38, 100} = 0.097$, $\chi^2 = 1.036$, df = 2, $P > 0.5$). No chick younger than 32 d was recorded at a colony as able to fly (Fig. 1), although a chick was recovered 31 d after hatching 164 km from its natal colony (Table 1). There are few observations of chicks older than 42 d still present at their natal colony (Fig. 1).

Fledgling Behavior. Fledglings remained close

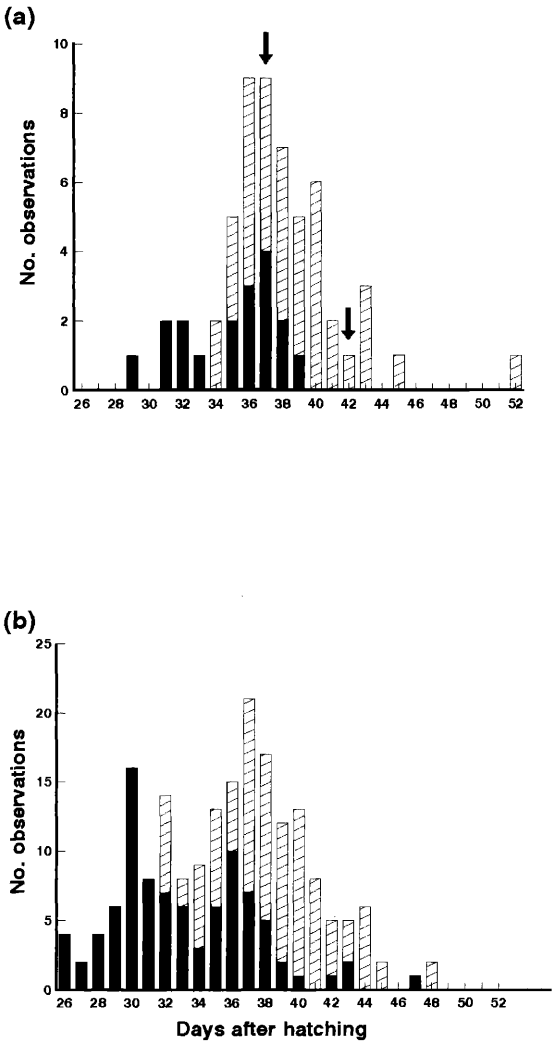

Figure 1. Frequency distribution of observations at breeding colonies of juveniles of known age around the time of fledging classified as still in their nest (solid bar) or able to fly (striped bar). (a) Data from Mairena 1989. The arrows show the average fledging age and average dispersal age of focal fledglings. (b) Data from Mairena, Morón and Arahal 1988, 1990, 1991 and 1992.

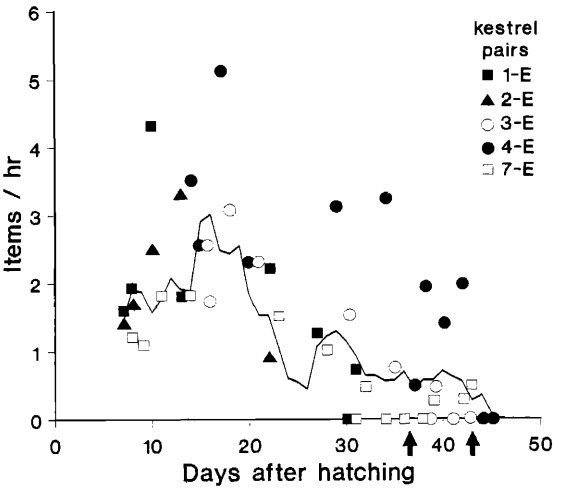

Figure 2. Feeding frequency during the nestling and post-fledging periods at the five lesser kestrel focal nests, estimated from 4-hr observation periods. The line is a moving average smoothing of the data with a 5-d span. The arrows show the average fledging age and the average dispersal age of the fledglings. At nests 1-E and 2-E all chicks died before fledging.

to their nests during the post-fledging dependence period, and most of the perching sites used were within 100 m of the nest. They made short flights between perches, wandered around the colony, and frequently entered other kestrels' nests. Fledglings never showed any signs of aggression toward other lesser kestrels—adults or chicks—that came close to them or that eventually entered the fledgling's nest. Fledglings were observed on 30 occasions begging to kestrels that were not their parents (22 occasions begging to adults and 8 to fledglings). We did not observe fledglings catching prey, playing with objects, or chasing other kestrels or other birds (121 hr × fledgling).

Adult Behavior. Both parents continued to feed their offspring during the post-fledging dependence period. Adults fed their fledglings at the colony with big- and medium-sized invertebrates (mainly Orthoptera) that they brought in their bills. Parents initially flew with prey to their nest but when their offspring were not there, they searched around the colony. Observed prey transfers took place at the nest (50% of all prey transfers, $N = 25$) or at perches within 100 m of it. No aerial prey transfers were observed. Daily feeding frequency during fledging and post-fledging periods (3.3 items/juvenile, SD = 1.3, $N = 3$ pairs) was lower than during the nestling period (10.3 items/juvenile, SD = 3.2, $N = 5$ pairs), and tended to decrease through the post-fledging dependence period (Fig. 2).

The breeding pair equipped with radiotransmitters decreased not only the number of prey they

brought but the number of visits they made to the colony throughout the post-fledging dependence period, and stopped feeding their offspring before the fledglings left the colony. These two adults were radiotracked for 12 hr, on three different days, during the post-fledging dependence period and for 15 hr on days two and four after their offspring dispersed. Neither the male nor the female was observed with any of its offspring away from the colony. These adults continued roosting near the colony the 31 July after all the fledglings with radiotransmitters had dispersed.

Breeding adults behaved aggressively toward lesser kestrels that were not their offspring that perched close to or came into their nest. We observed 22 aggressive interactions by kestrels and always the aggressor was an adult. In the 18 instances that the identity of the aggressor was known, it was an adult attending a nest within 2 m. At least 55% of the aggressive acts were directed toward unrelated fledglings and 32% toward adults. In three instances an adult kestrel evicted a fledgling from a different nest that had entered the adult's nest. However, in one instance an adult, after initially trying to avoid it, fed a fledgling from a different nest that had entered the adult's nest.

Fledgling Mortality. Eighteen of 25 chicks (51%) from the focal nests or other neighboring nests, plus the nine other chicks marked with radiotransmitters, died at around the time of fledging. The chicks were found dead at ages between 17–35 d (mean age at death 27.8 d, SD = 4.3, $N = 14$) and all seemed to have died from starvation (Negro et al. 1993b).

Fledgling Dispersal. Lesser kestrel migration at Gibraltar Straits peaks around the 15 September (Bernis 1980). All lesser kestrels banded as nestlings during 1988–91 and observed or recovered in July and August of the same year away from their natal colony had moved 3–164 km in directions north, east, and west (Table 1).

DISCUSSION

The mean fledging age of 37 d that we observed was 32% higher than the 26–28 d estimate quoted by other authors (Brown and Amadon 1968, Newton 1979, Cramp and Simmons 1980), but agrees with the observations of Pomarol (1990) on birds released by hacking. Lesser kestrels' reproductive success was poor in 1989, as was shown by the high mortality from starvation around the time of fledging (50% mortality). The growth of the surviving chicks may also have been retarded thus delaying the fledging age, as seems to happen in other raptors feeding on prey with unpredictable abundance (Viñuela and Bustamante 1992). However, the ages at which chicks were observed out of the nest in other years and colonies (Fig. 1a) still suggests that lesser kestrels in southwestern Spain fledged on average at an older age than the estimate given in general sources (Brown and Amadon 1968, Newton 1979, Cramp and Simmons 1980). The 26–28 d period estimate was a rough estimate made by Blondel (1964) who observed only two nests.

The post-fledging dependence period observed was very short compared to that of other raptors. Low food availability in the area might have had an effect on this, although, in general, when food availability is low raptors tend to have longer post-fledging dependence periods (J. Bustamante unpubl. data). We think that juveniles became independent once they left the colony because the two adults radiotracked never interacted with their offspring away from the colony, and did not leave the neighborhood of the colony when their offspring did. None of the fledglings with radiotransmitters could be found after dispersal at the roosts habitually used by breeding adults in a 4-km radius of the colony (Negro et al. 1993a), and were not found in a 10-km radius of the colony while we were tracking the adults with radiotransmitters. Adults did not hunt far from the colony. The largest distance from the colony traveled by radiotracked adults during the nestling period was 14.5 km for females and 8 km for males (Negro et al. 1993a).

Lesser kestrel migration peaks in September, 45 d after all the fledglings of our colony had dispersed. Observations and recoveries of fledglings in July and August indicated that juveniles moved far from their natal colony shortly after fledging and before starting a true migration south (Table 1). Adults remain at their breeding colonies until fall migration or even throughout the winter (Negro et al. 1991, and unpubl. data). Two of the juveniles observed were at distances of 18 and 164 km from their natal colony 34 d and 31 d after hatching, respectively, (Table 1) supporting the hypothesis that lesser kestrel family breakup tends to take place shortly after fledging. In contrast to the black kite (*Milvus migrans*) in southern Spain in which migratory urgency determines the timing of family breakup (Bustamante and Hiraldo 1990), lesser kestrel family groups break up long before migration starts.

Lesser kestrel fledglings do not appear to participate in manipulative play with objects, or learning or practicing of hunting skills during the post-fledging dependence period in contrast to the common occurrence in most species of falcons (*Falco* spp.; e.g., Schuyl et al. 1936, Tinbergen 1940, Lawrence 1949, Cade 1953, Parker 1975, Sherrod 1983, Oliphant and Tessaro 1985, Komen and Myer 1990, Bollen 1991, Debus et al. 1991, Lawrence and Gay 1991, Varland et al. 1991). Manipulative play with objects during the post-fledging dependence period occurs more frequently in species feeding on agile prey. There is hardly any information on other raptors that feed exclusively on insects to know if it is something uncommon in insect feeders.

Adults behaved aggressively toward fledglings entering or coming near their nest and were able to recognize their offspring after fledging; i.e., banded adults were able to find their offspring among other fledglings and fed them when away from the nest. On the other hand, fledglings frequently intruded in other nests and begged from any other kestrel, resulting in the possibility that adults might accidentally feed the wrong chick (as we observed in one occasion). Before young fledge adults do not seem to be able to recognize their own offspring. When nests are connected by ledges, chicks may move between nests and accidental adoptions during the nestling period may take place (Donazar et al. 1991). While there may be an evolutionary pressure for adults to recognize their offspring and not to feed unrelated young, individual recognition takes time to develop and this would explain why nestlings apparently are not recognized. On the other hand, fledglings may obtain extra food with hardly any risk by begging from unrelated adults, explaining the lack of selectivity in their begging behavior.

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