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Source: Journal of Raptor Research, 48(3) : 248-256

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-11-70.1>

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POST-FLEDGING DEPENDENCE PERIOD IN THE EURASIAN KESTREL (*FALCO TINNUNCULUS*) IN WESTERN FRANCE

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ABSTRACT.—The post-fledging dependence period (PDP) of 25 Eurasian Kestrel (*Falco tinnunculus*) fledglings was studied in a coastal marsh in western France in 2002 and 2003. Body condition at fledging was the only parameter that had a positive effect on the length of the PDP, which averaged 18 d (range 3–31 d). Mean daily distance from the nest increased 15 m per day until independence, and mean area used during the PDP was 7.3 ha. Male kestrels provided food for fledglings during the PDP (though decreasing their delivery rate with time). Females stopped feeding their young 3 d after they fledged. First fledglings received more food than others and food per fledgling decreased with brood size.

KEY WORDS: *Eurasian Kestrel*; *Falco tinnunculus*; *body condition*; *fledgling*; *home range*; *post-fledging dependence*.

PERIODO DE DEPENDENCIA POST-EMPLUMAMIENTO EN *FALCO TINNUNCULUS* EN EL OESTE DE FRANCIA

RESUMEN.—El periodo de dependencia post-emplumamiento (PDP) de 25 volantones de *Falco tinnunculus* fue estudiado en un marisma costero en el oeste de Francia en 2002 y 2003. La condición corporal al momento del emplumamiento fue el único parámetro que tuvo un efecto positivo en la duración del PDP, el cual promedió 18 días (rango 3–31 días). La distancia media diaria desde el nido aumentó 15 m por día hasta la independencia, y el área promedio utilizada durante el PDP fue de 7.3 ha. Los individuos machos de *F. tinnunculus* proveyeron alimento para los volantones durante el PDP (aunque la tasa de entrega de alimento disminuyó con el tiempo). Las hembras dejaron de alimentar a sus pichones 3 días después del emplumamiento. Los primeros volantones recibieron más comida que los otros y la cantidad de alimento por volantón disminuyó con el tamaño de la nidada.

[Traducción del equipo editorial]

The post-fledging dependence period (hereafter, PDP) and subsequent stages of complete independence from parents are critical life-history periods when young develop foraging skills essential for survival (Bustamante and Hiraldo 1989, Wheathers and Sullivan 1989, Wheelwright and Templeton 2003, Castillo-Guerrero and Mellink 2006) and future fitness (Sunde 2008, Gruebler and Naef-Daenzer 2008). The post-fledging period is defined as the period between the first flight from the nest and independence from parents (Mock and Parker 1997, Arroyo et al. 2002). The length of this period likely reflects a balance between the ability of the young to hunt for themselves (Kitowski 2005) and

the parental reduction in food provision, or even their aggression toward fledglings (Alonso et al. 1987, Bustamante 1993, 1994a). In most raptor species, independence is thought to be induced by a reduction in parental investment (Bustamante 1993, Balbontin and Ferrer 2005, Vergara et al. 2010). However, in at least two species independence appears to be initiated by fledglings (Bustamante and Hiraldo 1990, Bustamante 1994a, Koga and Shiraishi 1994).

Aspects of PDP in Eurasian Kestrel (*Falco tinnunculus*) have been investigated (Komen and Myer 1989, Village 1990, Bustamante 1994b, Vergara and Fargallo 2008, Vergara et al. 2010). Recently, Vergara et al. (2010) experimentally examined the role of food supply, parent quality, and offspring dominance in explaining PDP duration. Here we

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assess the PDP of Eurasian Kestrel in a sedentary and semicolonial population in western France, using behavioral observations of fledglings. Using an observational approach, we evaluated factors that might influence independence in kestrel fledglings.

STUDY AREA

Our study was conducted in 2002 and 2003 in the Moëze's marshes, Charente-Maritime, western France, on the coast of the Atlantic Ocean (45°54'N, 01°03'W). The study site covered 1400 ha of crop fields and wet grasslands (65%) as well as old salt-marshes (35%), of which 214 ha were designated as a nature reserve.

METHODS

Thirteen nest boxes were available for kestrels, and 7–20 pairs nested in the study area (in nest boxes and in old magpie [*Pica pica*] nests) each year between 1986 and 2003 (e.g., Boileau 1998). Nests were 150 to 300 m apart. Each breeding pair was monitored beginning at pair formation, and nest-boxes were visited every 3 to 7 d to determine laying and hatching dates. We monitored 25 fledgling kestrels, 13 from four nests in 2002 and 12 from five nests in 2003 (mean brood size: 3.58 ± 1.32 SD; range 2–5). We identified individual falcons either with radio-transmitters (Biotrack TW4 single button cell tag®, Biotrack, Stoborough, Wareham, U.K.) and color bands ($n = 8$ in 2002, $n = 10$ in 2003), or with color bands alone ($n = 5$ in 2002, $n = 2$ in 2003). Nestlings were fitted with radio-transmitters and color bands 1–2 d before fledging. In 2002, radio-transmitters were fitted on the two oldest nestlings from each brood (but all nestlings from the broods were banded), and in 2003, all nestlings from the broods were radio-tagged.

An estimated 1–2 d before the nestlings' first flights, we visited nests to collect blood samples and morphometric data to assess body condition. We collected 1 ml of blood from the brachial vein with a syringe for sexing of nestlings ($n = 18$) using molecular methods. We identified sex of kestrels by PCR amplification of part of two CHD genes present on the sex chromosomes (Fridolfsson and Ellegren 1999). We also measured wing length (± 0.5 mm) and body mass (± 0.1 g).

We monitored fledglings from 18 June to 25 July in 2002 and 24 June to 10 August in 2003. Once fledged, each bird was observed for ≥ 1 hr/d until dispersal from the study area. The fledging date was defined as the date when a nestling was first seen

outside the nest box; all fledglings from the brood left the nest within the next 2 d. The post-fledging period was defined as the period between the first flight from the nest and independence from parents (Arroyo et al. 2002); i.e., when parents no longer fed the young. Observations were made using a spotting scope (20–60 \times) and binoculars (8 \times 42) either from a blind or a vehicle located 50–300 m from the nest. To obtain precise locations, we searched for radio-tagged and color-banded individuals at least twice daily between 0800 H to 2000 H GMT, usually in the morning, but occasionally after 1600 H. Each fledgling was simultaneously observed for 1 hr by two observers, using a systematic approach to ensure that each nestling's observations occurred throughout the day. We noted the fledglings' behaviors (resting, flying, preening, hunting in flight, behaving aggressively toward conspecifics), as well as their duration. We defined "social activities" as all activities other than hunting or feeding. Parental investment was measured by the amount of time each parent was present during one hour focal observations and by the number of food deliveries to the young kestrels. Due to a lack of visual obstructions, we were able to monitor movements of the falcons that were color-banded up to 800 m from their nests. Falcons with color bands and radio-tags were classified as dispersed from the study area or dead when no observation occurred during one entire day in the study area.

We used the 95% fixed kernel method for calculating home ranges to reduce the influence of outlier locations (Kenward 2001), which were log-transformed to meet normality distribution. The smoothing parameter, h , was calculated with the least-square cross-validation technique (Seaman et al. 1999). Body condition was obtained using linear regression between wing length and body mass and interpreting the residuals as a measure of condition.

Statistical analyses were conducted using SAS 9.1 (SAS Institute 1988, North Carolina, U.S.A.). Data are expressed as mean \pm SD. We used nonparametric tests when sample sizes were small. Because fledglings within a brood were not independent statistical units, we used mixed models (PROC MIXED) with brood identity as a random factor. Food delivery (rate of delivery per hour) to fledglings by the adults was coded as a binomial variable and PROC GENMOD was used with a logit link function. For age at first flight and PDP, we ran exploratory analyses and tested the effects of being

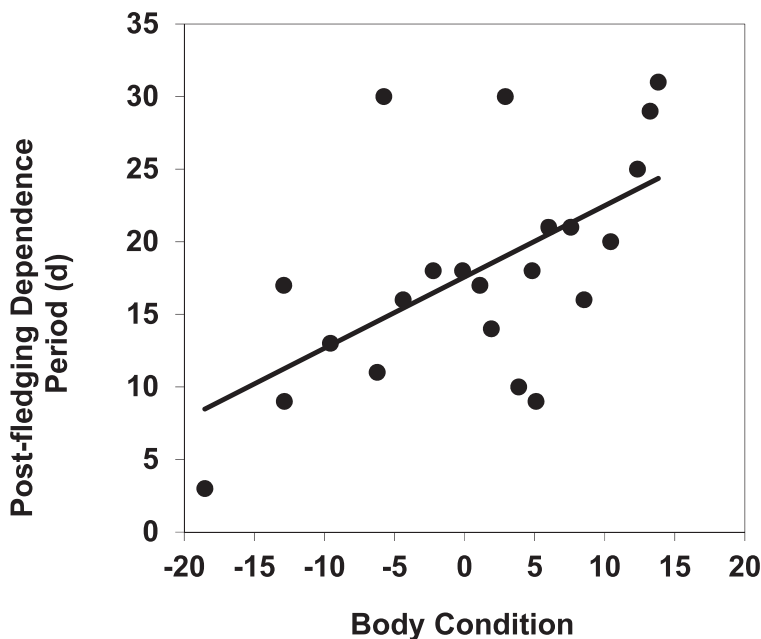


Figure 1. Relationship between PDP and body condition (residuals of wing length on body weight at age 31 d) in 22 fledglings of Eurasian Kestrels in western France.

fitted with a transmitter, sex, order within brood (categorical variable), brood size (categorical variable), hatching date (continuous variable), and body condition (continuous variable).

RESULTS

PDP duration was highly variable among individuals in the same brood. The mean difference in PDP among siblings was 5.7 d (range 2–14 d; $n = 6$ broods with more than one fledgling). Three birds from one nest were found dead 1–3 d after fledging. Another bird disappeared 3 d after fledging but was considered dispersed. Mortality rate during the dependence period was estimated at 12% ($n = 25$).

First flights were observed at 30.0 ± 2.52 d after hatching (range 26–34 d, $n = 25$ nestlings). Fledglings became independent at 18.0 ± 7.6 d after leaving the nest (range 3–31 d; $n = 22$).

There was no effect of year on either age at first flight (mixed model with nest as a random factor, $F_{1,17} = 0.01$, $n = 25$, $P = 0.99$) or PDP ($F_{1,14} = 0.01$, $n = 22$, $P = 0.91$), and year was not included in subsequent analyses. Age at first flight was positively related to fledgling order within brood (mixed model, nest as a random factor: $F_{4,13} = 4.31$, $P = 0.02$), whereas PDP did not differ between sexes

($F_{1,6} = 2.38$, $P = 0.17$) although females (18.1 ± 8.17 , $n = 12$) stayed about 40% longer than males (11.0 ± 2.16 , $n = 6$). In addition, there was a significant positive effect of body condition on PDP ($F_{1,13} = 5.96$, $P = 0.03$); i.e., fledglings in better condition stayed longer, irrespectively of sex (Fig. 1). There was no effect of transmitter on age at first flight (29.6 d, $n = 18$ vs. 30.7; $n = 7$, with or without transmitters respectively; $F_{1,5} = 0.11$, $P = 0.75$). Lastly, there was no relation between PDP and age at first flight (mixed model, $F_{1,13} = 0.52$, $P = 0.48$).

Daily distance from the nest increased significantly with the number of days after fledging (mixed model, with fledgling identity nested within brood identity as a random effect, $F_{406} = 12.54$, $P < 0.0001$; Fig. 2). Mean distance from the nest at the end of PDP was 372 ± 243 m (range 50–1000 m, $n = 22$). After accounting for the effect of date, only age at first flight had a significant effect (negative; mixed model, $F_{406} = 4.12$, $P = 0.04$), although its magnitude was small compared to the effect of relative fledging date. After independence, fledglings dispersed several kilometers from the nest, and thus we rapidly lost their signals: only three birds could be located at 41–48 d after fledging (20–30 d after independence) at a distance of 3–7 km.

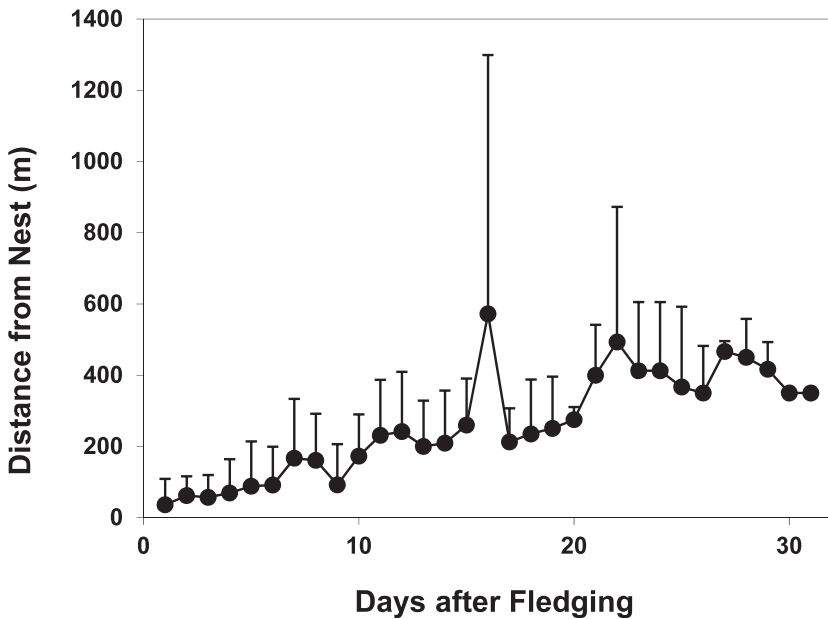


Figure 2. Average (\pm SD) dispersal distance from the nest in relation to time after fledging for 22 fledglings during PDP in Eurasian Kestrels in western France.

On average, fledglings used a spatial area around the nest of 7.3 ± 2.7 ha (range 1–57) before independence. This area varied marginally within broods ($F_{1,12} = 2.47$, $df = 7$, $P = 0.07$), so subsequent analyses included nest identity as a random factor. There was a slight positive tendency for home-range size to increase with PDP ($F_{1,12} = 3.62$, $P = 0.08$). No other factor (sex, rank, brood size, body condition, hatching date or age at first flight) had a significant effect (all $P > 0.35$).

Siblings stayed together during the PDP, with little sign of aggressiveness (four aggressive interactions during $n = 217$ hr of observation). Fledglings almost never chased adults that were present in the nest area (14 instances of food-solicitation behavior, involving 7 of 25 fledglings, during 217 hr of observation). Fledglings spent most of the time resting and preening during the first 14 d after fledging (ca. 60% of the time), with very few hunting activities during the first 11 d (Fig. 3). After 11 d post-fledging, time spent in hunting activities increased rapidly to an average level of 40% at day 14.

Parental investment varied by sex of the parent: based on our observations of 1 hr per day, females apparently abandoned the brood after 2.4 ± 1.8 d (range 0–5), while males fed fledglings for as long as 31 d after fledging (Fig. 4). Males provided, on

average, 0.6 prey/hr during the first 12 d, after which the delivery rate fell to 0.1 prey/hr. Prey delivery rate by males decreased significantly with date (mixed model, male identity as a random effect, $F_{1,361} = 5.63$, $P = 0.02$), and when date was accounted for, male delivery rate differed significantly by brood size ($F_{1,360} = 19.12$, $P < 0.0001$; Fig. 5): feeding rate per brood increased with brood size. However, the slope of the relation (0.035 ± 0.025) was significantly less than 1 ($P < 0.001$), hence food per fledgling decreased with fledging order (Fig. 6). On average, each fledgling received 0.17 ± 0.13 prey/hr during the post-fledging period, or two food items per day for a 14-hr day. Rank within the brood at fledging had an effect on food distribution: first fledglings received a higher proportion of food than siblings that fledged later (Fig. 6), with a negative relationship between rank at fledging and average delivery rate by the male during post-fledging dependence ($r_s = 0.34$; $P < 0.001$).

DISCUSSION

The PDP of Eurasian Kestrels in our study area averaged 18 d, which at 37% of the total time between hatching and independence represents a substantial amount of parental investment. The length of the PDP in our study was shorter, compared to

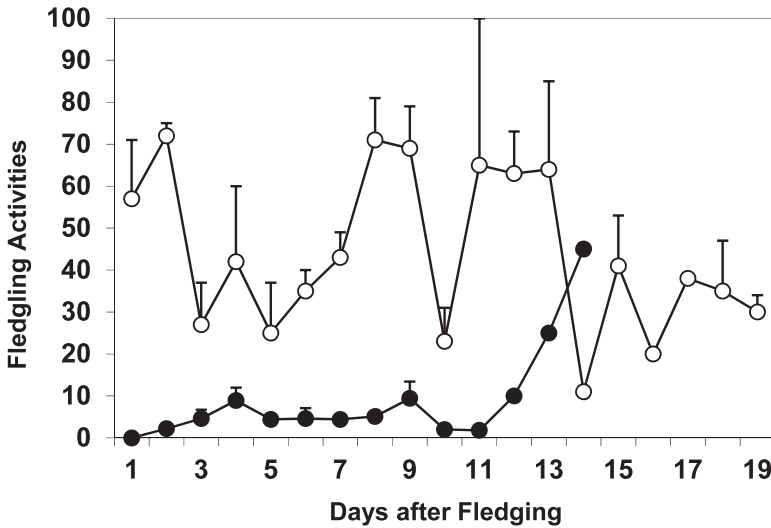


Figure 3. Social (white) and hunting (black) activities of Eurasian Kestrel fledglings as percentage of total observation time (\pm SD).

other studies on the same species (20–25 d: Tinbergen 1940, 30 d: Masman in Komen and Myer 1989), but similar to those reported by Bustamante (1994b) for a colonial population of kestrels in Spain (determined using radio-tracking). Recently, Vergara et al. (2010) reported a PDP which varied between 12.7 and 18.5 d, according to year, although they started their survey when fledglings were 32 d old. We likely overestimated age at first flight, because we rarely observed flights early in the

post-fledging period, and some first flights may have been missed because we observed nestlings only 1 hr/d. The proportion of 37% cited above is similar to that for other raptor species (Bustamante and Hiraldo 1989, Ceballos and Donazar 1990, Bustamante 1993, 1995, Arroyo et al. 2002).

In this sedentary population of kestrels, the fledging date had no effect on the length of the post-fledging period (see Bustamante 1994b). In contrast, a decrease in the length of the period with

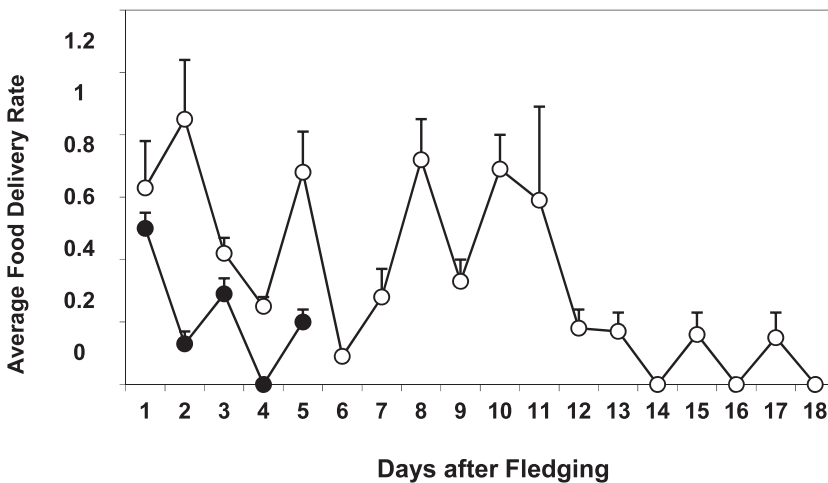


Figure 4. Average food delivery rates of males (white) and females (black) to Eurasian Kestrel fledglings (prey/hr \pm SD) during the first 18 d of PDP.

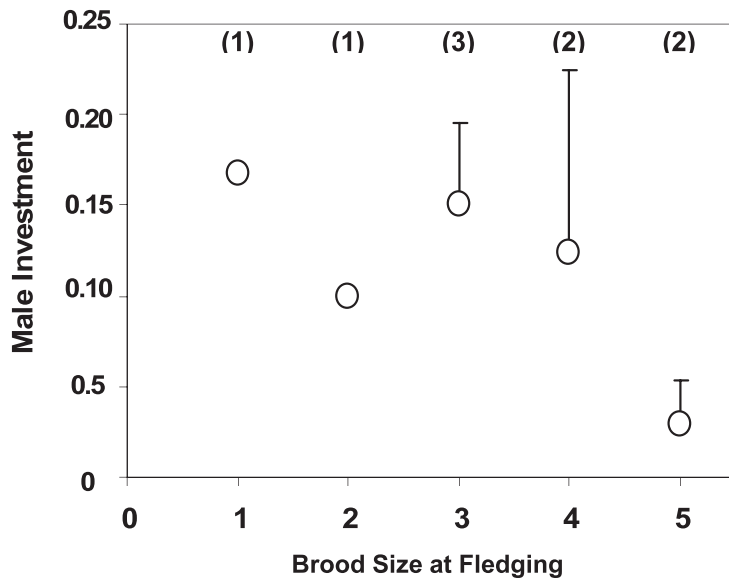


Figure 5. Male investment in food provisioning of fledgling Eurasian Kestrels (prey/hr \pm SD) during PDP by brood size at fledging in western France. Number of broods of each size is in brackets at the top of the graph.

fledging date has been found in other nonmigratory species of raptors, such as the Spanish Imperial Eagle (*Aquila adalberti*; Ferrer 1992), the Red Kite (*Milvus milvus*; Bustamante 1993) as well as in migratory raptors that become independent well prior to migration, such as the Lesser Kestrel (*Falco nau-*

manni; Bustamante and Negro 1994) or Montagu's Harrier (*Circus pygargus*; Amar et al. 2000). Fledging date was the variable that most influenced the length of the post-fledging period in the Montagu's Harrier, with birds fledging later in the season becoming independent at a younger age (Arroyo et al.

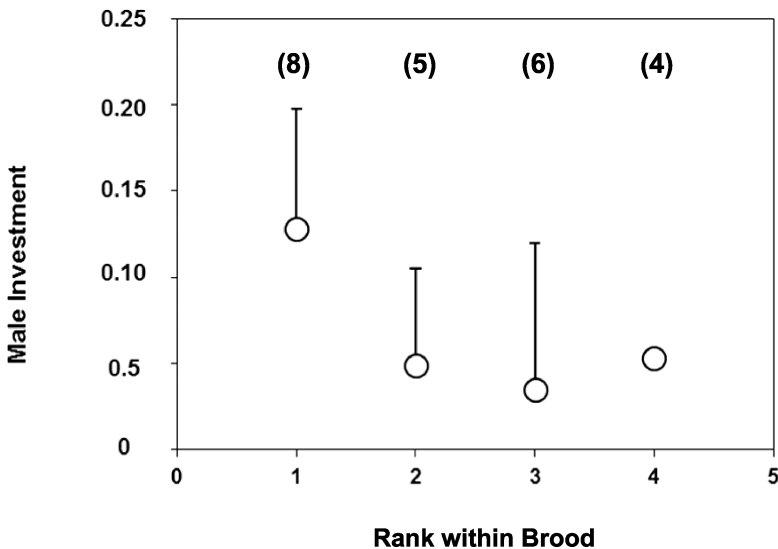


Figure 6. Male investment in food provisioning of fledgling of fledgling Eurasian Kestrels (prey/hr \pm SD) during PDP by rank within brood in western France. Rank is defined as hatching order. Number of fledglings of each rank is in brackets at the top of each graph.

2002). Migratory urge has been proposed to explain this temporal pattern in another migratory species, the Black Kite (*Milvus migrans*; Bustamante and Hiraldo 1990). In such cases, the need for adults to start recovering before the next reproductive cycle has been proposed to account for the pattern in departure dates (Ferrer 1992).

Eurasian Kestrel fledglings at our study site did not show aggression to their parents, their siblings, or fledglings from other broods. A similar result was found by Bustamante (1994b) on the same species, but our study contrasts with others on kestrels (e.g., Vergara and Fargallo 2008), in which high within-brood and within-sex competition for food delivered by parents was observed. These differing patterns may result from differences in prey size and/or quality, leading to differences in within-brood competition. In our study, as well as in others on small falcons, family break-up took place without apparent conflict (Bustamante and Hiraldo 1990, Bustamante 1994a, Koga and Shiraiishi 1994, Dronneau and Wassmer 2005).

Contrary to findings by Bustamante (1994b), adult female Eurasian Kestrels in our study showed relatively low involvement in feeding their broods. Food delivery rates by males were higher, but then decreased. Differences in parental investment during the PDP by sex have been observed in diurnal raptors (e.g., Balbotin and Ferrer 2005), though it is sometimes females that invest more than males (MacDonald 2004). In the Eurasian Hobby (*Falco subbuteo*), adult females stay with fledglings at least 21 d after fledging; females are fed by the males and consequently sometimes compete with fledglings for food (Dronneau and Wassmer 2005). In our study, the rate of prey delivery was positively correlated with the number of fledglings and decreased at the end of PDP. We also found a positive relation between feeding rate and rank within the brood, whereas Bustamante (1994b) suggested that adults do not preferentially feed fledglings. Thus, first-ranked fledglings are probably more demonstrative to parents, and more rewarded. Interestingly, Vergara and Fargallo (2008) found that, within broods, male fledglings were more successful in obtaining larger prey from their parents.

Fledgling kestrels gradually moved away from the nest in a manner similar to that of Eurasian Sparrowhawks (*Accipiter nisus*; Wyllie 1985). Due to a very flat and open landscape, kestrel fledglings were presumably able to observe their parents almost continuously because home ranges of males are quite small

(1.8 km² on average) and localized around the nest (Boileau et al. 2006). We suggest that these landscape features allowed a gradual increase in dispersal distance in contrast to the colonial kestrels nesting on cliffs, whose average distance during post-fledging dependence was only 37 m from the nest (Bustamante 1994b), contrasting with the value of 372 m in average in our study. Similarly, in the Common Buzzard (*Buteo buteo*), birds coming from nests in open areas like grasslands disperse farther than birds from more forested nesting areas, possibly because they can more easily stay in contact with adults (Tyack et al. 1998).

Mortality of fledglings in our study was estimated at 12% during the PDP, which was similar to the value of 9% reported by Bustamante (1994b). In American Kestrels in central Iowa, United States, mortality rate of radio-tagged fledglings was 26% (Varland et al. 1993). Birds perching on cliffs are probably less exposed to terrestrial predators than those in open and forested landscapes (Fargallo et al. 2001), at least assuming that predation risk is associated with conditions at the nest site and terrestrial predators, rather than risk occurring during flight. As mass at fledging is not related to mortality in some raptor species, fledgling survival during post-fledging period is possibly not influenced by parental investment during the nestling period (Masman et al. 1989, Tolonen and Korpimäki 1996) or food availability (Dijkstra et al. 1990, Korpimäki and Rita 1996, but see Amar et al. 2000 and Arroyo et al. 2002). However, Adriansen et al. (1998) suggest that the most crucial phase in terms of food availability for young kestrels in Belgium occurs in the period after fledging, around the time the young become independent.

To conclude, length of the PDP in kestrels in our study area seemed similar to those already observed in previous studies in Spain (Bustamante 1994a, Vergara et al. 2010). Body condition of fledglings was the only parameter which had an effect on PDP duration in our study area, although food availability and parent quality are important factors elsewhere. Unlike in other studies, we detected no intra-brood competition for food deliveries during the dependence period. Because brood size at fledging, rank within the brood, and the males' food delivery rate all influence the length of the PDP in various locations and studies, we believe that the PDP is mainly under parental control in Eurasian Kestrels.

ACKNOWLEDGMENTS

We are very grateful to S. Lefevre, M. Holthoff, C. Chau-baroux, E. Pineau, J. Gautier, M. Tellier, F. Corre, P. Delaporte, and L. Brucy for help during fieldwork. L. Strenna, P. Delaporte, L. Rejt, and P.M. Wright made useful comments on an earlier draft of the manuscript. In addition, P. Vergara, D.E. Varland, and J.B. Buchanan made many helpful comments. The ringing program of kestrels is a personal ringing scheme (N.B.) conducted with the agreement of the *Centre pour la Recherche sur la Biologie des Populations d'Oiseaux (M.N.H.N. Paris)*. This work was part of a study program on the relation between small mammals and kestrels, funded by a grant from the *Fondation Electricité de France* and *Réserves Naturelles de France* (2001–2006).

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Received 22 September 2011; accepted 22 March 2014
Associate Editor: Joseph B. Buchanan