



## Parental investment and parent–offspring conflicts during the postfledging period in Montagu's harriers

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We studied factors influencing the length of the postfledging period in the Montagu's harrier, *Circus pygargus*. Fledging date influenced the date of departure, for both wild birds and captive-reared birds (for which food supply was constant throughout the postfledging period), suggesting that departure time was constrained by migration. However, this relationship was absent in good food years, when some birds had short periods of dependency even if fledged early in the season. The end of the postfledging period was associated with a decrease in the food provided by the parents, coinciding with an increase in the fledglings' flying and hunting abilities and in aggressive food solicitation. The postfledging period was shortest when food was scarcest (when controlling for fledging date), and was also shorter for younger siblings (when controlling for brood effects), even though the parents provided less food in poor food years, and for nestlings in larger broods, particularly the younger ones. These results suggest that departure time is an adult's choice. However, we also predicted that if fledglings control parental investment, they should attempt to prolong the period of dependency when they receive little food. Length of the postfledging period was affected by food abundance, with shorter periods in better food conditions for equivalent hatching dates. In addition, the postfledging period was longer for birds from larger broods (when controlling for hatching date and food abundance), and for wild birds than captive-reared birds except in peak vole years. These results suggest that fledglings try to compensate for a deficiency in the food supply with longer periods of dependence, provided there is enough time before migration.

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Parent and offspring interests may come into conflict over how much to invest in an individual offspring, because the optimal amount of care that a parent should give to one offspring will depend on the associated costs in terms of decreased production of other (including future) young (Trivers 1974). Parent–offspring conflict has been a central topic in evolutionary biology, especially with regard to reproductive effort and parent–offspring communication strategies (e.g. Charnov 1982; Harper 1986; Parker & Mock 1987; Mock & Parker 1997).

In altricial bird species, the postfledging period (i.e. the period between the first flight from the nest and the break-up of the family ties) is a period in which young depend partly, or entirely, on food from their parents. This period, which lasts several weeks (most passerines) to months (e.g. in large raptors), is an important stage in the development of birds, because energy is stored during this

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period, and young also develop foraging skills essential to survival (Weathers & Sullivan 1989). The critical nature of the postfledging period is reflected by high mortality rates of recently independent juveniles (Lack 1954; Sullivan 1989; Bustamante 1993). It is likely that conflicts between parent and offspring interests arise during the postfledging period, although relatively little attention has been given to this stage compared with the nestling period.

During the postfledging period parents and offspring may come into conflict over its length or the amount of food delivered. Fledglings would benefit from getting as much food as possible and remaining dependent on their parents for as long as possible. However, parents are expected to reduce their feeding effort, if prolonging the care of offspring may prejudice the success of the following reproductive cycle (see Verhulst & Hut 1996).

Among birds, raptors have been particularly well studied, partly because parent–offspring behaviour is easy to observe in these large birds. The postfledging period in raptors is critical for the completion of growth and the

maturation of flight skills (e.g. Simmons 1984; Alonso et al. 1987; Bustamante & Hiraldo 1989; Ferrer 1992; Bustamante 1993; Kenward et al. 1993). Independence in some raptors is thought to be induced by a reduction in parental investment (Simmons 1984; Wyllie 1985; Alonso et al. 1987; Bustamante 1993, 1994; Ceballos & Donazar 1990). However, in at least two species, it appears to be an offspring decision and thus an issue of little apparent conflict (Johnson 1973; Bustamante & Hiraldo 1990; Bustamante 1994; Frumkin 1994). Patterns may thus vary according to ecological or individual features.

Raptor brood sizes are variable and usually include more than one nestling. Thus, differences in food partitioning among siblings (in relation, for instance, to sex or to fledgling rank) may explain individual variation in either length of the postfledging period or the level of conflict between offspring and parents. In addition, variation in food availability during the dependency period may be pronounced, and this should have a strong influence on any parent–offspring conflicts, given that food abundance influences both the condition of the nestlings and the cost of reproduction for the parents. Parent–offspring conflicts should be particularly marked in poor food years. From the chick's point of view, the length of the postfledging period should be maximal in poor food years, as food supply is lower and potentially reduces offspring condition at fledging. In contrast, adults may minimize postfledging investment in poor food years: the cost of reproduction is presumably higher in such conditions, so maintaining the investment beyond a certain point may have a strong effect on future reproduction; furthermore, survival of offspring fledged in poor food years may be low, and parental investment may be adjusted to offspring survival prospects (e.g. Hakkarainen & Korpimäki 1994). No studies have specifically addressed the influence of food abundance on parent–fledgling relationships in raptors, but this is a factor known to affect the duration of postfledging care in other birds (Higuchi & Momose 1981; Byle 1990).

We studied the postfledging period in a ground-nesting migratory raptor, the Montagu's harrier, *Circus pygargus*. In this species, the postfledging period has been studied for fledglings released after captive rearing and which were fed ad libitum until departure (Pomarol 1994; Amar et al. 2000): the length of the postfledging period decreased with both hatching date and better chick body condition. These data indicate that, when fledglings receive a constant amount of food, independence is regulated by migratory urge and fledgling needs. In addition, the length of the dependency period (in a peak food year) did not differ significantly between released and naturally fledged birds when hatching dates were accounted for (Amar et al. 2000). This suggests that independence in wild birds was also under offspring rather than parental control, and should thus create little parent–offspring conflict.

We tested the latter hypothesis with data from wild and captive-reared birds under contrasting food conditions. First, voles constitute the main prey of Montagu's harriers in western France, and their population cycles

(Salamolard et al. 2000) provide an extreme natural manipulation of food abundance. Second, data from captive-reared birds released in different food conditions provide a quasiexperimental approach to test the effect of food on the postfledging period, controlling for the effect of parental behaviour. Our predictions were as follows. If investment during the postfledging period is under parental control, independence should be associated with a decrease in parental investment and an increase in parent–offspring agonistic behaviour, and may occur earlier in years of low food abundance. In addition, if independence is forced when parents stop bringing food for the fledglings, siblings should become independent simultaneously. Alternatively, if independence is mainly under fledgling control, the postfledging period should be longer when there is less food, that is, in poor food years or for individuals receiving less food. It should also be longer in wild birds than in captive-reared birds in years when food is scarce. On the basis of these data, we discuss whether family break-up might arise from a generational conflict in this species.

## METHODS

### Study Sites

We carried out the study from 1996 to 1999 in two localities in central-western France, where Montagu's harriers have been monitored since 1994. The study sites are Marais de Rochefort (45.57°N, 0.55°W), covering 180 km<sup>2</sup> of pastured wetlands, and south of Deux Sèvres (46.11°N, 0.28°W), covering 350 km<sup>2</sup> of intensive agricultural landscape. They are separated by ca. 50 km. The main prey of Montagu's harriers in western France is the common vole, *Microtus arvalis* (Butet & Leroux 1993; Salamolard et al. 2000). We estimated vole density annually for each study site by line trapping (see Salamolard et al. 2000). We used live traps, without bait, water or bedding. Traps were provided by the Institute National de Recherche Agricole (INRA, National Institute for Agronomic Research) and the Service de Protection des Végétaux (Crop Protection Service). They were checked and removed 24 h after setting. We then released the mammals if alive (after determination of species, sex and weight). Those that died (ca. 1500, or ca. 40% of individuals trapped) were kept for dissection and were ultimately fed to the captive-reared harriers (see below). This technique is the standard way of quantifying vole abundance in France, and fulfils all regulations needed (no special licence is needed in France to trap voles, as they are classed as a crop pest). Different crop types were sampled (cereal, pasture land and fodder crops, rape seed and sunflower/corn). We obtained mean vole abundance each year in each study site by correcting for the overall surface of that crop type in each study area (i.e. multiplying the average number of voles in each crop type by the percentage of surface covered by that crop type). Trapping was carried out both in April and in July, because the research project evaluated the relationship between food abundance and reproductive strategies at different times of the breeding cycle but we only used July data for this paper as

postfledging occurs at this time. Vole abundance varies cyclically in both study areas, with peaks on average every 3 years (Salamolard et al. 2000, unpublished data). Food abundance in the years of study was thus high (peak years: 1996 and 1999), medium (1998) or low (crash year: 1997).

### Parent and Offspring Behaviour

We observed focal nests every year in Deux Sèvres (43 nests) and in the peak vole years (1996 and 1999) in Rochefort (19 nests). Each observation lasted on average 3 h (range 1.5–7 h), and these were made throughout the day at ca. 300 m from the nests (in Deux Sèvres) or from a hide (Rochefort), with binoculars and telescopes. We made 675 focal observations, of which 190 corresponded to observations before fledging, and 485 to observations after first flights. Each family was observed for an average of 29 h throughout the postfledging period (range 8–130 h). We noted all prey deliveries by male or female adults, whether food passes took place on the ground or in flight and, if the latter, whether the fledgling missed the prey. We also recorded fledgling hunting attempts, and agonistic behaviour by fledglings towards adults (which usually took the form of chases with soliciting calls), and by adults towards fledglings (chases and dives). In nests with wing-tagged fledglings (see below), food passes from adults to fledgling were attributed to an individual chick in 62% of all deliveries in families with broods of two or more ( $N=459$ ). The rest took place either on the ground, away from the observer or when all fledglings arrived at the same time, so that the final recipient could not be identified. The Montagu's harrier recognizes its own young, so between-brood parasitism or alloparental care in colonial situations is relatively rare (Arroyo & García, in press).

### Departure and Length of Postfledging Period

We wing-tagged 106 nestlings from 36 nests in both study areas. Licences for nest visits, ringing and wing tagging were given by the CRBPO (French National Ringing Scheme Office) to V. Bretagnolle. Wing tags measure ca.  $5 \times 3$  cm, and are attached to the patagium. They have been used on Montagu's harriers since 1988, and have no apparent effect on survival, mate choice or reproductive success (unpublished data). We observed these nests daily or every 2 days, which allowed us to determine the precise date of departure for fledglings and parents. Departure date was estimated as the day after the birds were last observed near the nest. Nests with wing-tagged nestlings included 31 nests (a random sample) out of the 62 focal nests described above, plus 18 nestlings in Rochefort in 1998 ( $N=6$  nests), which were observed for presence/absence of fledglings at particular dates, but for which no focal observations of prey deliveries were carried out. Six fledglings from two nests in 1997 (the low vole year) were depredated, and one nestling in 1999 died (undetermined cause) just after fledging; these were removed from analyses on the length of the dependency

period. Exact dates of first flights were available for only ca. 30% of nestlings (see Results). For consistency, we defined the length of the postfledging period from 30 days after hatching (the median age of first flights, see below) to the estimated departure date for all nestlings.

### Fledgling Characteristics

We determined nestling age (and thus hatching date) from biometric measures (Brignon 1997). Fledgling rank (oldest, intermediate or youngest) was estimated from nestling age. Nestlings were sexed by iris colour (Forsman 1999), which is very accurate (Leroux & Bretagnolle 1996). All nestlings were weighed at  $26 \pm 3$  days of age (range 20–33 days), when the asymptotic weight is already attained (Brignon 1997). We estimated condition of the nestlings as the difference between their measured weight and the asymptotic weight for their sex (315 g for males and 340 g for females, Brignon 1997).

### Captive Rearing Data

As a conservation measure in the Deux Sèvres site, eggs and young chicks were removed from nests in crop fields that were due for immediate harvesting when on-site conservation measures were not possible, or (as when harvesting occurred during the incubation period) they were known to be inefficient. Birds that were brought to be reared in captivity would thus have died from harvesting activities if left in the field. A special licence to allow keeping and rearing of harriers in the rearing centre at the laboratory was held by V. Bretagnolle. Chicks were reared in captivity and subsequently released by the method of hacking (see Pomarol 1994 and Amar et al. 2000 for further details). Birds were reared in groups of two to six, of approximately the same age, but not necessarily siblings, and were released at the hack site in groups. After release, 1-day-old dead chickens were placed each day within the hacking enclosure and on the roof of an adjacent farm building. The quantity of food placed each day was in excess of the amount actually eaten. The fact that released birds were fed ad libitum (cf. wild birds which are fed by their parents) allows us to test whether food influences the length of the postfledging period in controlled circumstances. The captive-reared birds behave, return and breed in similar proportions to wild ones (Amar et al. 2000).

Captive-reared fledglings were individually marked with patagial tags (identified by colour codes and numbers). We carried out observations at the hack site for 1 h before and 1 h after food placement (between 1600 and 1800 hours), daily or every 2 days. We conducted these observations from a car, parked no closer than 100 m from the hack site, using  $8 \times 42$  binoculars and a  $20\text{--}60 \times$  telescope. All birds in the vicinity of the hack site were identified by their individually numbered marks. As for wild birds, we defined the length of the postfledging period as 30 days after hatching to the date of the last recorded sighting of the bird at the hack site. A total of 79 birds were released. Two birds were found dead around

the hack site; another was retrieved ill (and released again 20 days later); five further birds disappeared before they were 35 days old and had probably died, although their corpses were not found. We removed these eight birds from the analyses. These losses represent 9–10% of the released birds, a figure comparable to the wild birds found dead during the postfledging period in our study area (7% of 106). Furthermore, some of the five released nestlings in our study that disappeared and were assumed dead might have been alive, so the 10% mortality figure is a maximum. Both figures are much lower than those found in another study with wild birds in Poland, where 17% of 51 young birds monitored were found dead (mainly depredated) during the postfledging period (Kitowski 1994, *in press*). In another hacking programme in Catalunya (Pomarol 1994), release was assumed to be unsuccessful (i.e. birds were never seen after 10 days after release, and thus were potentially dead) for 17% of 87 released birds. So, overall, postfledging losses in our study are apparently normal for the species, and not a result of manipulation.

### Statistical Analyses

We analysed the temporal variation in behaviour with each nest observation as a sample unit. Behaviours expressed as frequencies (feeding rates, hunting trials, agonistic behaviour) were log transformed, and those expressed as proportions were arcsine transformed for normalization before we used parametric statistical analyses.

For the analyses of the variation in food received according to year, fledged brood size or food abundance, we averaged all observations for a given family over the period 55–95 days after laying, to avoid pseudoreplication and biases from differences in observation regimes between pairs. We obtained a mean (but theoretical) prey delivery per nestling by dividing the latter mean by the number of fledglings in each family. For the analyses of the partitioning of food according to sex and rank, we calculated per brood the proportion of the identified prey each individual received (for the 28 observed broods with wing-tagged nestlings). We assumed that, if the null hypothesis (equal partitioning among siblings) were true, the proportion of prey individuals of a given sex received would be directly related to the proportion of siblings of that sex within the brood. Therefore we tested whether the slope,  $b$ , was different from 1. Similarly, if there were equal partitioning among siblings, we predicted that the proportion of prey each nestling within the brood received would equal 50% for broods of two, 33.3% for broods of three, 25% for broods of four and 20% for broods of five. Therefore, we tested for departure from  $b = -1$  for the log–log transformed relationships. For the analyses of partitioning of food according to rank, we excluded the five broods with a single nestling.

We used univariate or multivariate general linear model analyses. In these, hatching date, fledging age, brood size, vole abundance or fledgling condition were considered continuous variables, whereas sex, rank

within the brood or year were considered categorical variables. For the analysis of the factors affecting the length of the postfledging period in wild birds, each fledgling is not an independent observation (because departure could be simultaneous for all siblings, see Results). Therefore we used general linear mixed models, with the procedure GLIMMIX within SAS 8.0, with year and brood as random variables. This procedure allowed us to analyse hierarchical designs (Littell *et al.* 1996). The overdispersion factor was fixed at 1, and type III analyses for the effects are presented.

Data are expressed as mean  $\pm$  SD (except when stated otherwise). All tests are two tailed.

## RESULTS

### Fledgling Condition and Behaviour

Condition at fledging did not vary according to sex ( $F_{1,85}=2.09$ ,  $P=0.15$ ) or vole abundance ( $F_{1,85}=0.04$ ,  $P=0.84$ ). It varied significantly between years ( $F_{3,82}=10.60$ ,  $P=0.0001$ ), but differences arose only in 1997, the low vole year (Tukey test between 1997 and all other years:  $t=4.7$ – $5.6$ ,  $P<0.05$ ; all other comparisons: NS). In that year, the majority of fledglings did not reach asymptotic weight (condition  $-52 \pm 41$  g,  $N=11$ ). Fledgling condition also decreased with hatching date ( $F_{1,85}=31.02$ ,  $P=0.0001$ ) and varied with rank within the brood ( $F_{2,78}=3.36$ ,  $P=0.040$ ), being lower for the youngest nestlings (Tukey test: last–first:  $t=-2.5$ ,  $P=0.05$ ; last–intermediate:  $t=-2.3$ ,  $P<0.05$ ).

First flights were observed  $32 \pm 4$  days after hatching (range 25–47, median 30,  $N=36$  chicks), a figure possibly overestimated given that flights were rare early in the postfledging period, and 2-h observations might have missed nestlings able but unwilling to fly. First flights were significantly later in 1997, the low vole year, than in any other years (Table 1). No significant differences in age at first flight were found according to sex ( $F_{1,34}=0.01$ ,  $P=0.9$ ), rank within the brood ( $F_{2,32}=0.33$ ,  $P=0.8$ ) or hatching date ( $F_{1,34}=0.08$ ,  $P=0.8$ ).

The proportion of aerial prey deliveries to the fledglings also increased with fledgling age ( $F_{1,232}=104.9$ ,  $P<0.0001$ ), and were common (>75% of prey deliveries) from 40 days of age (Fig. 1a). At the same time, the proportion of dropped deliveries (where the fledgling failed to catch the prey in flight) decreased ( $F_{1,176}=6.58$ ,  $P=0.011$ ; Fig. 1a). The frequency of hunting attempts increased with fledgling age ( $F_{1,402}=23.7$ ,  $P<0.001$ ; Fig. 1b) but were rare, even near to independence. In addition, captures by nonindependent fledglings were observed only twice (both in a peak vole year).

Fledglings frequently chased the adults (an agonistic form of food solicitation) when they were present in the nest area, and the frequency of this behaviour increased throughout the postfledging period ( $F_{1,359}=8.00$ ,  $P=0.005$ ), remaining high until independence (Fig. 1b). Conversely, agonistic behaviour by adults towards fledglings was marked when fledglings were 40–50 days old, when it averaged  $0.30 \pm 1.56$  attacks/h ( $N=217$

**Table 1.** Age at first flight in wild harriers and length of the postfledging period in wild and captive-reared harriers in the years of the study

	1996 (peak)	1997 (low)	1998 (intermediate)	1999 (peak)	df	F	P
Age of first flights	30.2±1.9 (9) <sup>a</sup>	35.7±7.2 (9) <sup>b</sup>	31.5±3.1 (8) <sup>a,b</sup>	30.9±2.5 (10) <sup>a</sup>	3,22	3.05	0.043
Postfledging period: wild birds	28.4±5 (29) <sup>a</sup>	17.8±6 (5) <sup>b</sup>	27.5±5 (32) <sup>a</sup>	20.6±4 (33) <sup>b</sup>	3,95	15.03	0.0001
Postfledging period: captive birds	22.7±12 (45) <sup>a</sup>	— (17) <sup>b</sup>	14.4±6 (9) <sup>a,b</sup>	19.7±9	2,68	3.79	0.028

Means are given±SD. Sample sizes (number of nestlings) are given in parentheses. *F* and *P* values are for one-way ANOVA analyses. Letters next to the sample sizes refer to 2×2 comparisons (similar letters refer to nonsignificantly different values). The stages of the vole cycle are indicated below the years.

focal observations), but was rare afterwards ( $0.04 \pm 0.24$  attacks/h,  $N=81$ ).

### Feeding Rates

Feeding rates varied throughout the nestling and postfledging period (Fig. 1b). There was a decrease in feeding rates preceding the first flights, followed by a significant increase in the early postfledging period. Prey deliveries became progressively scarcer during the late postfledging period (>40 days after hatching;  $F_{1,317}=35.26$ ,  $P=0.0001$ ).

Total feeding rate per brood during the postfledging period increased significantly with brood size ( $F_{1,60}=5.51$ ,  $P=0.022$ ), but the slope ( $0.057 \pm 0.025$ ) was significantly less than 1 ( $P<0.001$ ), hence food per fledgling decreased with brood size ( $F_{1,60}=3.82$ ,  $P=0.05$ ; Fig. 2a). Feeding rate per fledgling increased significantly with increasing food abundance, when brood size is taken into account (multiple regression: vole abundance:  $F_{1,59}=4.64$ ,  $P=0.035$ ; brood size:  $F_{1,59}=7.53$ ,  $P=0.008$ ; Fig. 2a). On average, each fledgling received  $0.17 \pm 0.13$  prey/h during the postfledging period, or two prey/day for a 14-h day. However, in good food years, a fledgling in a brood of one received twice as many prey per day as an average fledgling in a brood of four or five (Fig. 2a).

Food partitioning among fledglings of the same brood was independent of sex: the proportion of prey received by each sex was equivalent to the proportion of siblings of each sex within each brood (linear regression:  $F_{1,25}=77.97$ ,  $P<0.0001$ ). The slope of that relationship ( $b=1.149 \pm 0.186$ ) was not significantly different from 1. In contrast, rank within the brood had an effect on food partitioning according to brood size. Oldest fledglings within the brood received an increasingly higher than expected proportion of the total prey delivered to the brood in larger broods (Fig. 2b). The slope of the relationship between the proportion of prey received and brood size ( $b=-0.183 \pm 0.335$ ) was significantly different from  $-1$  ( $t_{19}=2.43$ ,  $P<0.05$ ). The opposite was observed for youngest nestlings within the brood, which received a lower proportion of the total prey in larger broods ( $F_{1,19}=10.41$ ,  $P=0.004$ ; Fig. 2b). In addition, the oldest fledglings received overall a higher proportion of the food than intermediate ones ( $F_{1,32}=4.52$ ,  $P=0.041$ ).

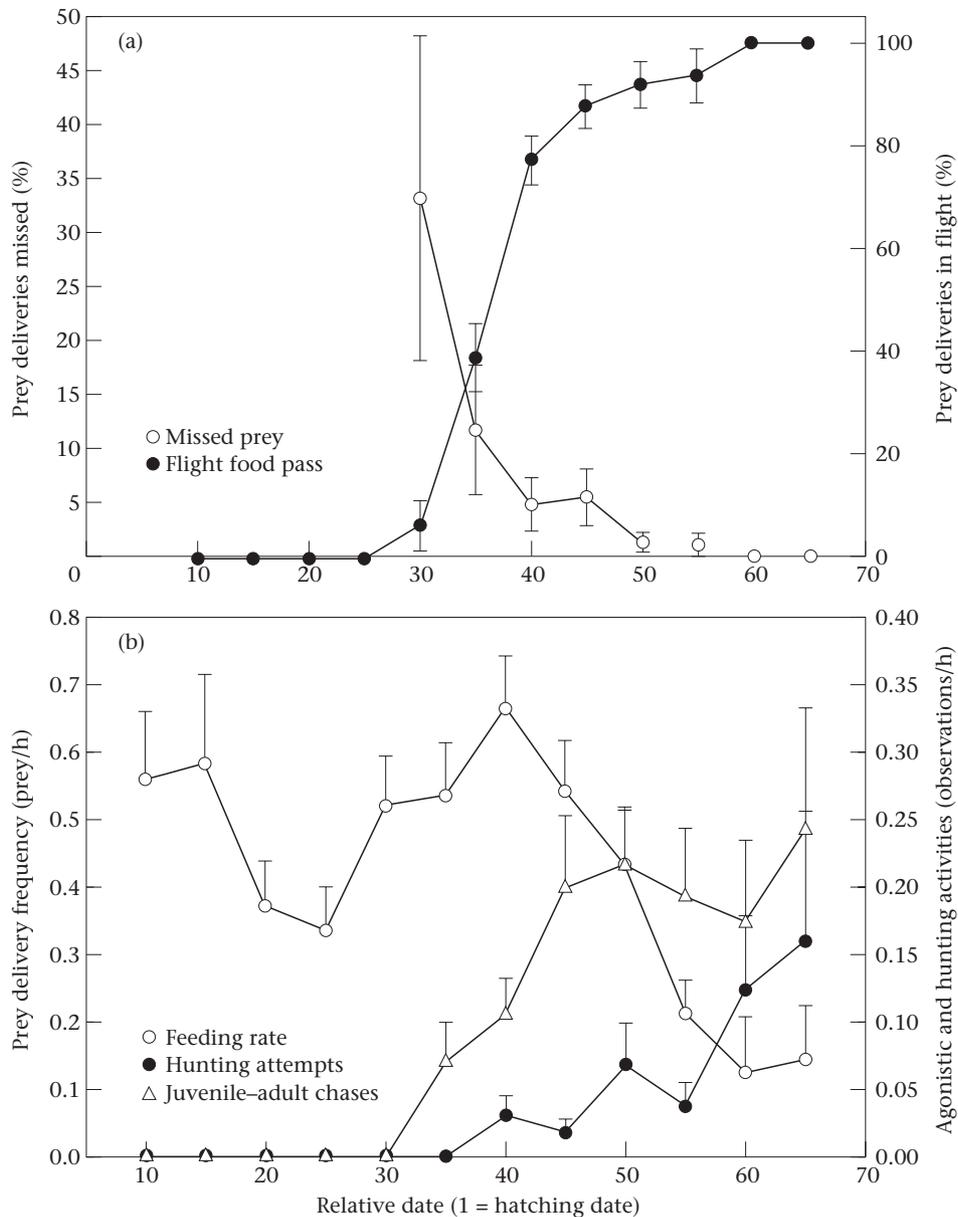
### Departure and Length of Postfledging Period

In 80% of the broods ( $N=34$ ), at least one adult (usually the female) left the area before all fledglings were independent. In 58% of cases, the last observation of the nestlings and of the adults coincided. In only 23% of cases were adults observed in the area after the fledglings had left. In 51% of multinestling broods ( $N=29$ ), estimated departure date was the same for all fledglings. In the remainder, the oldest fledglings left first in eight cases, the intermediate left first in four and the youngest in two.

The average length of the postfledging period (first flight to independence) in wild birds was  $25 \pm 6$  days ( $N=99$ ), but it varied significantly between years (Table 1). The length of the postfledging period decreased with increasing hatching date (Fig. 3), so birds hatching later in the season became independent at younger ages. There was, however, a significant interaction between year and hatching date (Table 2). The latter arose because no significant relationship between hatching date and length of the postfledging period was found in the two peak vole years ( $r=0.122$  and  $r=0.038$  for 1996 and 1999, respectively). In these years, some individuals had short postfledging periods even when they hatched early in the season (Fig. 3).

Vole abundance itself also had an influence on the length of the postfledging period, when taking into account hatching dates: independence was attained earlier in better food conditions for birds with equivalent hatching dates (Table 2), except in very poor food years (Fig. 4). Because of the shorter periods observed in the vole crash year, the relationship between vole abundance and the residuals of the relationship hatching date-length of the postfledging period fitted a quadratic relationship ( $F_{2,96}=8.12$ ,  $P=0.001$ ,  $R^2=12.7\%$ ) better than a linear relationship ( $F_{1,97}=9.76$ ,  $P=0.002$ ,  $R^2=8.2\%$ ; Fig. 4).

When controlling for hatching date and vole abundance, there was also a significant effect of brood size (with longer periods in nestlings from larger broods), nestling rank (with shorter periods for younger siblings) and sex (with shorter periods in males) on the length of the postfledging period (Table 2). In contrast, no differences were found in the length of the postfledging period



**Figure 1.** Mean  $\pm$  SE percentage of prey deliveries to the fledglings that were aerial food passes and the percentage of these deliveries that failed (where the prey was dropped to the ground) and (b) mean  $\pm$  SE feeding frequencies per brood, hunting attempts by the fledglings and chasing flights by juveniles towards adults according to relative date. First flights occur at ca. 30 days.

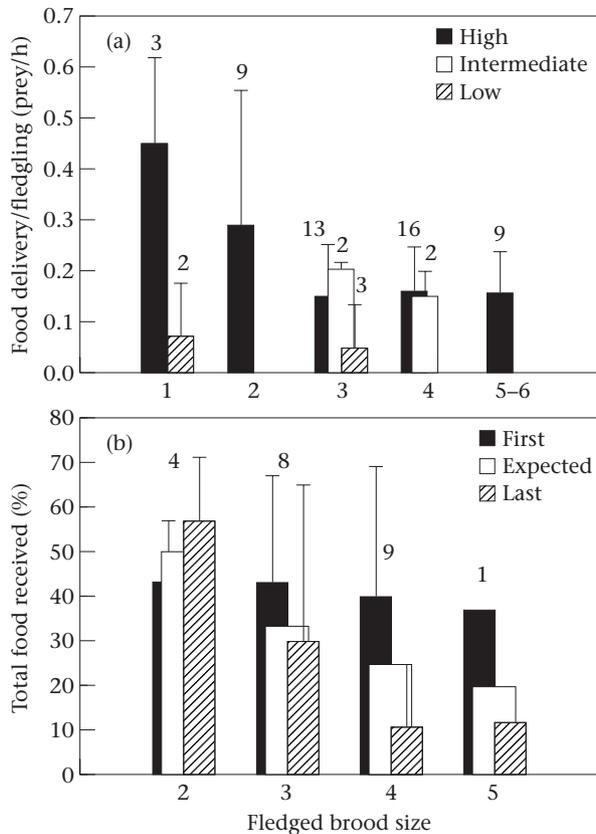
according to condition at fledging, after the effect of the other variables was taken into account (Table 2).

The length of the postfledging period in captive-reared birds decreased with both hatching date and condition at fledging (multiple regression: hatching date:  $F_{1,65}=28.8$ ,  $P<0.0001$ ; condition:  $F_{1,65}=7.60$ ,  $P=0.008$ ). Condition at fledging in captive-reared birds did not change with hatching date ( $F_{1,66}=0.12$ ,  $P=0.7$ ), in contrast to wild birds. Wild birds were in better condition than captive-reared birds if hatched early in the season, but lower if hatched late in the season. Captive-reared birds had shorter periods of dependency than wild birds, when controlling for hatching date (hatching date:  $F_{1,167}=28.76$ ,  $P=0.0001$ ; wild/captive:  $F_{1,167}=9.01$ ,  $P=0.003$ ; interaction:  $F_{1,167}=1.48$ ,  $P=0.22$ ). Differences arose

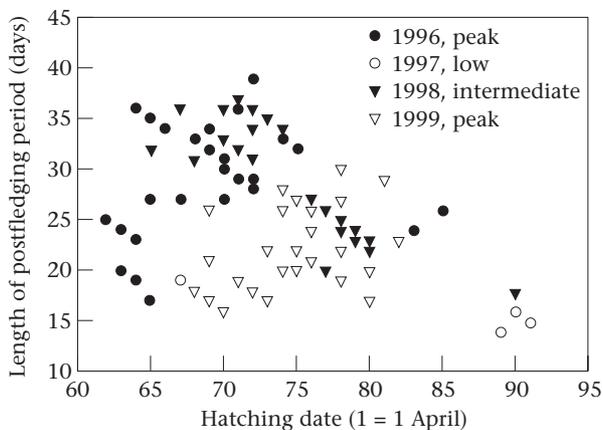
mainly in 1998, the intermediate year (Table 1), whereas in peak vole years both captive-reared and wild birds had similar postfledging periods.

## DISCUSSION

The average length of the postfledging period in the Montagu's harrier was 25 days, a comparable figure to those found in other studies (Kitowski 1994; Pandolfi 1996), and thus represented 45% of the total time between hatching and independence. This proportion is similar to, or slightly larger than, that found in other raptor species (Simmons 1984; Bustamante & Hiraldo 1989; Ceballos & Donazar 1990; Village 1990; Ferrer



**Figure 2.** (a) Mean±SD feeding rates per fledgling according to fledged brood size and vole abundance; and (b) mean±SD percentage of identified prey deliveries that each fledgling received according to fledged brood size and rank within the brood. Sample sizes (number of broods observed) are given above the histograms.



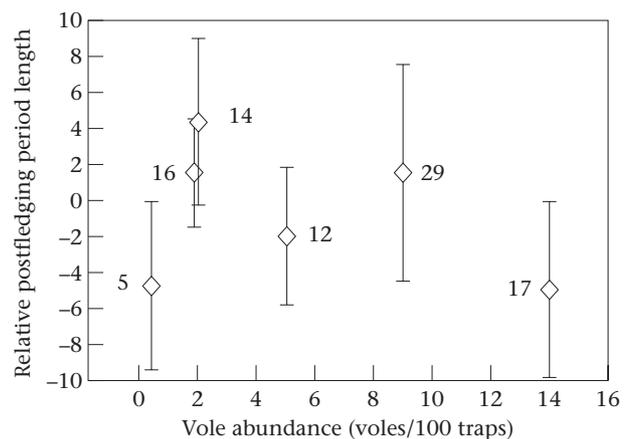
**Figure 3.** Length of the postfledging period according to hatching date, year and the stage of the vole cycle.

1992; Bustamante 1993, 1995; Frumkin 1994). The postfledging period in raptors thus represents a significant part of the investment of parents in offspring and might interfere with later reproductive cycles (Verhulst & Hut 1996). However, survival probabilities and future reproduction depend on conditions experienced at fledging or

**Table 2.** Results of the generalized linear mixed model of the effect of hatching date, vole abundance, their interaction, brood size, sex, rank within the brood and condition at fledging on the length of the postfledging period for wild harriers

	df	Type III F	P	Slope
Hatching date	1,79	24.06	<0.0001	—
Vole abundance	1,79	42.95	<0.0001	—
Year×hatching date	1,79	39.51	<0.0001	+
Brood size	1,79	10.72	0.002	+
Condition	1,79	0.54	0.460	—
Sex	1,79	5.01	0.028	—
Rank within the brood	1,79	28.43	<0.0001	—

The model included year and brood as random variables. The sign of the slopes is given for continuous variables.



**Figure 4.** Mean±SD residuals of the relationship between length of the postfledging period and hatching date, according to vole abundance. Sample sizes (number of fledglings) are indicated.

at independence in many birds (e.g. Perrins 1965; Alatalo et al. 1990; Linden et al. 1992; Gaston 1997; Merilä & Svensson 1997; van der Jeugd & Larsson 1998). In species where the postfledging period is very long, condition at independence is likely to depend on condition at fledging, but also on the amount of food received during the postfledging period and the length of this period, which might have a strong additive or compensatory effect over condition at fledging.

### Is There Generational Conflict After Fledging?

There was considerable variation between individuals in relation to the length of the postfledging period in the Montagu's harrier (CV=24%). This variation was significantly related to fledging date, with birds fledged later in the season becoming independent at younger ages, although the relationship was modulated by food abundance: in good food years some birds had short dependency periods even if fledged early in the season. This suggests that in good environmental conditions the length of the postfledging period may be adjusted

according to individual variables. In contrast, when birds fledged late in the season, postfledging periods were relatively short regardless of food conditions, which indicates that departure time is constrained by migration needs (Bustamante & Hiraldo 1990). A decrease in the length of the period with fledging date has also been found in other nonmigratory species of raptors, such as the Spanish imperial eagle, *Aquila adalbertii* (Ferrer 1992), or the red kite, *Milvus milvus* (Bustamante 1993), as well as in migratory raptors that become independent at a much earlier date than migration time, such as the lesser kestrel, *Falco naumanni* (Bustamante & Negro 1994). In such cases, the need for adults to start recovering before migration or the next reproductive cycle may explain the pattern in departure dates (Ferrer 1992). If this were the case, it would be mainly the adults that benefited from shortening the postfledging period late in the season, whereas fledglings would improve their condition by being fed by their parents instead of hunting for themselves. Nevertheless, the fact that such an effect was also observed in captive-reared fledglings suggests that there is also a cost for fledglings starting migration late in the summer.

We predicted that if investment during the postfledging period is mainly under parental control, independence should be associated with a decrease in parental investment and an increase in parent-offspring agonistic interactions. These predictions were supported by our data. First, the end of the postfledging period was associated with a decrease in parental investment in feeding, which declined gradually after the fledglings were 40 days old. This decrease coincided with the moment when the majority of prey were successfully delivered in flight, reflecting the increasing flying ability of the fledglings, and also with the appearance of hunting by the fledglings. However, the hunting success of offspring was very low at the moment of independence, as observed in other raptors (Bustamante & Hiraldo 1989; Ferrer 1992; Bustamante 1993; Bustamante & Negro 1994). Furthermore, agonistic behaviour by fledglings towards adults was frequent, and peaked mainly after parents decreased their feeding rates, suggesting that the reduction in parental investment was not due to a decrease in fledgling interest in prey delivered by the parents but to the adults' choice. The fact that in the majority of broods at least one adult had left the breeding area before the fledglings also supports the hypothesis that departure is forced by the adults. Siblings departed simultaneously in 50% of broods, which probably would not have been the case if independence was the result of individual fledglings' decisions: given that the division of food among siblings was not equal, with younger fledglings receiving proportionally less food, the relative advantage of prolonging parental care should vary according to rank (with younger fledglings trying to extend their dependency period). In fact, the negative relationship between the length of the dependency period and rank within the brood implies that fledglings do not have complete control over determining departure time according to their needs. In addition, the postfledging period in low vole years was shorter than expected from the relationship

with vole abundance when correcting for differences in hatching date (Fig. 4). Fledglings may move to areas where prey may be more abundant rather than stay and wait for the scarce food delivered by parents. However, that is probably not an advantage for the harrier fledglings, given that both condition at fledging and food received during the postfledging period (thus condition at independence) were significantly lower when food was scarce, and that hunting success for the fledglings is also likely to be low in these conditions. In contrast, reducing the investment in offspring when breeding is most costly and offspring survival prospects are probably low might be a benefit for the parents in terms of future reproduction (Verhulst & Hut 1996). The latter also implies that departure time is probably tuned to benefit parents rather than fledglings, and is thus regulated by parents.

However, we also predicted that if independence were under fledgling control, fledglings should try to maximize the length of the postfledging period when the amount of food received was low (i.e. in poor food years or for individuals receiving less food) or if they were in poor condition at fledging. Several results support that prediction. First, food abundance influenced the length of the postfledging period, with a trend for longer periods in poorer food conditions for equivalent fledging dates. This suggests that departures were, at least partly, condition related, as found for captive-reared birds (Amar et al. 2000; this study). The latter may be a consequence of fledgling decisions, but it is also of benefit to the parents to enhance the condition of their young under difficult conditions, provided that it does not interfere with future reproduction. The fact that condition itself did not have a significant effect on postfledging period length was probably due to this variable being absorbed by hatching date and vole abundance, given that condition at fledging decreased significantly with hatching date in wild birds. Second, individuals from larger broods (which received proportionally less food) had relatively longer postfledging periods. Finally, wild birds had longer periods of dependency than captive-reared birds (which were fed ad libitum), at least when food abundance was not at its peak. These results suggest that fledglings and/or adults try to compensate for a deficiency in food supply with longer periods of dependency, provided delayed departure dates do not interfere with migration.

In conclusion, our results suggest that fledglings have some control over departure time, as suggested by Amar et al. (2000), although the regulation of the length of the postfledging period in the Montagu's harrier is probably mainly under parental rather than fledgling control, particularly when food is scarce (and presumably costs of breeding high). The amount of care (in terms of food) given to the fledglings seemed to be mainly under the control of the parents, who reduced their investment as soon as fledglings could fly well enough to make hunting attempts. Fledglings tried (by chasing and soliciting the parents) to get as much food as possible from the parents, and to adjust the time of departure according to their needs in terms of food, but that was possible only when food was relatively abundant and fledging occurred early in relation to migration time.

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