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Post-nestling dependence period in the Bonelli's Eagle *Hieraaetus fasciatus*

Joan Real, Santi Mañosa & Jordi Codina

Real, J., Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 645, 08028 Barcelona, Catalonia, Spain
Mañosa, S., Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 645, 08028 Barcelona, Catalonia, Spain
Codina, J., Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 645, 08028 Barcelona, Catalonia, Spain

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The behaviour of five young Bonelli's Eagle *Hieraaetus fasciatus* was monitored from leaving the nest to dispersal in 1987 in three breeding sites in Catalonia (NE Spain), by means of radio-tracking techniques. On average, the young left the nests 63 days after hatching. The acquisition of flying ability was progressive, and was complete about 40–60 days after leaving the nest. The length of the dependence period (from leaving the nest to the end of parental food delivery) was 57–95 days. All the young suddenly left the natal area some days (11–36 days) after the last parental prey delivery was observed. The length of the post-nestling period (from leaving the nest to dispersal) was 77–113 days. Transition to independence involved a decline in parental investment. During the post-nestling period, some young were recorded up to 8.3 km away from the nest. A return of one young to its natal area three months after dispersal was also recorded.

1. Introduction

In large eagles, such as the Bonelli's Eagle, the fate of the nestling after leaving the nest is a much more important factor than production of young in determining population trends (Ferrer & Calderón 1990, Real & Mañosa 1997). The post-nestling dependence period, the period between leaving the nest to the end of parental investment and subsequent dispersal, may have important implications for the future survival of the young, since self-sufficiency and good physical condition for future life have to be acquired. Mortality of unskilled birds during their first days or weeks outside the nest may also be high, and may have some effects on population dynamics. Limited information exists on the length of the post-nestling period and post-nestling mortality in the Bonelli's Eagle (Cheylan 1972, Cugnasse 1985, Real & Mañosa 1986, Morvan & Dobchies 1986 and 1990, Real et al. 1989, Arroyo et al. 1992), a species which has experienced a sharp decline in Europe in the last decades (Rocamora 1994). The objective of this paper is to describe the development of flying ability and the transition to independence of the Bonelli's Eagle, and the role of adults and young in determining the length of the dependence period, which may be the result of a parent-offspring conflict of interest (Trivers 1974, Alonso et al. 1987, Bustamante 1990, Ferrer 1992).

2. Material and methods

We studied the post-nestling period of 5 young Bonelli's Eagles in three breeding sites (A, B and C thereafter) in El Vallès district (Catalonia, NE Spain, lat 41°40′N long 2°5′E) in 1987. All young birds were wing-tagged and banded in the nest (Young and Kochert 1987). Four young birds were also fitted with BIOTRACK back-pack transmitters when 50–60 days old, following Kenward (1987). The weight of the tags and transmitter including the harness was 61 g (2% to 3% of body mass, Kenward 1987), and were expected to last for nine months. The fifth bird (number 2) left the nest before the transmitter could be fitted to it. Behavioural data from this bird are not directly comparable to the radio-tagged birds, so only some descriptive information on the behaviour and fate of this one can be provided. The transmitters were equiped with an activity switch (Kenward 1987), which allowed the flight/rest activity of a young to be determined even when it was out of sight.

Observations at every site were conducted for periods of two consecutive days every 5–7 days, from fledging to dispersal (June–October). Observations were carried out by two observers using 8–10× binoculars and 20–60× telescopes, from 1–2 fixed points within the breeding area, 200–1000 m from the nest, and recorded on a tape. When a young bird left the area, one of the observers followed it by car. In some occasions, distant locations were established by triangulation. An aircraft was used to look for the young birds as soon as they were not located from the ground. An area of about 50 km around the nests was checked from the air. Observations ended as soon as a young bird was not found by any means for four consecutive observation days. Dispersal was then assumed to have occurred on the middle date between the last day the young bird was recorded and the first day that it was not found at all.

Each day, observations started at dawn and ended at dusk. We continuously recorded the location of the young birds, so the daily home range could be computed as the minimum convex polygon encompassing all the points where a young bird had been observed during a day (periods when a young bird was out of sight or a radio signal was lost were ignored), by using the RANGES IV suite (Kenward 1990). The arithmetic mean center of this polygon (irrespective of the time spent at each point) was taken as the daily activity center of a bird. The number, duration and pattern of flights, number and type of playing flights, and food deliveries were also recorded. Flights were classed into flapping (the bird flaps the wings continuously for more than 3 seconds), gliding (a no-flapping flight in which the bird losses height), and soaring (a circular flight, mostly with no flapping, in which a bird takes advantage of thermals to rise). We also recorded the number of times the young were observed performing begging calls or chasing an adult with prey. An index of the adult attendance towards the young was obtained as the time spent by one adult perched or flying in the vicinity of the young plus twice the time spent by two adults divided by total observation time.

Twenty-eight days of observation were completed at site A, 30 at site B and 22 at site C. A total of 851 h of field work yielded 959 h and 47' of contact with the young birds, which means the behaviour of some young was recorded. The hatching date and date of leaving the nest of the young were known to ± 2 days by regular inspections of the nests. The sex of the adults and the young was established according to their size and colour (Parellada 1984).

Statistics were conducted by means of SPSS (1990). Because developmental variables increased exponentially rather than linearly in relation to days after leaving the nest, they were log-transformed ($\log10(x + 1)$) before conducting regression analysis, to improve the linear fit between dependent variables and days since leaving the nest.

3. Results

3.1. The survival of the young and the length of the dependence and post-nestling periods

The young took their first flight at an average age of 63 days after hatching (± S.D. = 6 d, min. = 52 d, max. = 66 d). After leaving the nest, only two young birds were observed to come back to perch in the nest, which took place on 7 occasions spread over the post-nestling period. The young bird number 2 was killed by an Eagle Owl *Bubo bubo* when about 88 days old, 35 days after leaving the nest (Real & Mañosa 1990), so only 4 (80%) of the young survived to disperse. For these birds, the

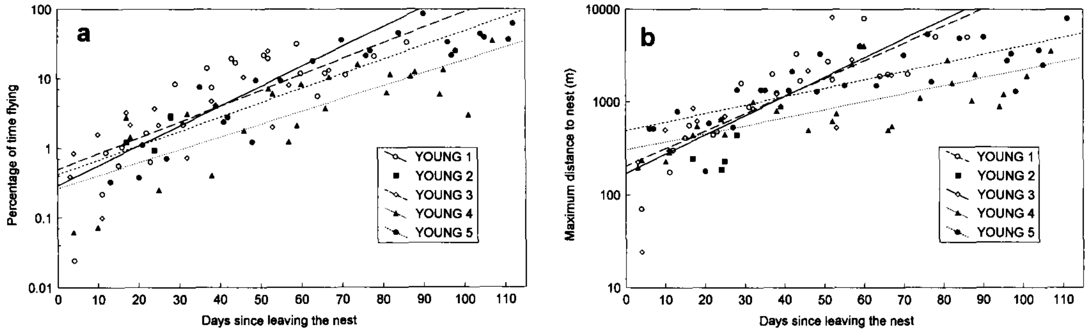

Figure 1. Change in (a) the percentage of time spent flying (PTF) and (b) the maximum recorded distance from the nest (MDN) during the post-nestling period. The Y axis is a logarithmic scale. A linear fit is drawn for every radio-agged young. Open symbols = females, black symbols = males

length of the dependence period (from leaving the nest to the last observed parental prey delivery) was 77 days (± S.D. = 15 d, min. = 57 d, max. = 95 d). A period of 21 days (± S.D. = 11 d, min. = 11 d, max. = 36 d) elapsed from the last observed prey delivery by the adults to dispersal of the young. The average duration of the post-nestling period (from leaving the nest to dispersal) was 98 days (± S.D. = 18 d, min. = 77 d, max. = 113 d), and the young dispersed at an average age of 163 days after hatching (± S.D. = 17 d, min. = 143 d, max. = 177 d). The dispersal of the young occurred between 22 August and 10 October (average 17 September, Table 1). A trend for males to have longer post-nestling periods than females was observed (Table 1).

After dispersal was assumed, systematic observations of and searches for the young in the nest areas were stopped until the beginning of January 1988, when visits began again to the nest areas A, B and C to follow the next breeding attempt. During one of these visits, bird 5, which was assumed to have dispersed on 28 September 1987, was observed in its natal nest area (A) on 2, 7 and 8 January 1988, flying or perching with the adults, and subsequently disappeared. On two of these occassions the young was perched only several meters apart from the adults. No relevant interactions of any sort (agressions, chasings, food deliveries) were observed between the young and its parents.

3.2. Flight performance, playing, hunting, and ranging behaviour

The percentage of time spent flying (PTF) by the young increased during the post-nestling period (Fig. 1a), and was significantly related to the number of days after leaving the nest for the four radio-tagged individuals (Table 2). The number of flights initiated by the young per hour (NFH), the

Table 1. Hatching dates, age of first flight, age of first observed gliding, age of first observed soaring, age of last observed food delivery by adults, and age and date of dispersal of three male and two female young Bonelli's Eagles belonging to three different pairs, in 1987. Ages are given in days since hatching.

Young Sex Pair	Hatching date	Age at fledging	Age of first gliding	Age of first soaring	Age of last delivery	Age of disperse (date)
1 ♀ C	21/03	65	76	80	143	154 (22/8)
2 ♂ C	21/03	52	69	80	–	–
3 ♀ B	17/04	66	69	76	123	143 (7/9)
4 ♂ B	17/04	66	83	105	161	178 (12/10)
5 ♂ A	04/04	64	77	85	141	177 (28/9)

mean duration of flights (MFD) and the duration of the longest flight (DLF) followed similar trends, also significant for all the young (Table 2).

A shift from flapping to soaring flights occurred during the first half of the dependence period for all the young (Fig. 2). The first gliding flight was observed on average 11 ± 6 days after leaving the nest (N = 5, range: 3–17) at 75 ± 6 days of age (N = 5, range: 68–83). The first soaring flight appeared on average 23 ± 11 days after leaving the nest (N = 5, range: 10–39) at 85 ± 11 days of age (N = 5, range: 76–105), and this flying technique was regularly used from 30 days after the first flight onwards.

Acrobatic flights, flights while carrying objects in the talons or bill, or persecutions of potential prey, were first observed on average 28 ± 7 (range: 18–39) days after leaving the nest, 0–14 days after the observation of the first soaring flight (Fig. 2). Diving flights and low flights over the ground or vegetation appeared first and were observed on 379 occasions between 18–105 days after leaving the nest. They were followed a bit later by flights while carrying objects, which were observed on 40 occassions, between 28–104 days after the first flight. These usually involved grasping tree branches or pine-cones in the talons. Chasing after potential prey were recorded on 7 occasions, and were first observed 39 days after the first flight. None of the chased prey was caught. However, young bird number 3 killed a feral pigeon offered as bait to her 53 days after leaving the nest. No prey were offered to the young of pairs A and C.

The daily maximum distance from the nest reached by the young (MDN) remained below 1000 m during the first month after leaving the nest, and increased thereafter to as much as 8300 m two months after leaving the nest (Fig. 1b). That increase was significantly related to the number of days after leaving the nest for the four radio-tagged individuals (Table 2). The daily home range (DHR) followed a similar pattern, increasing from less than 100 ha during the first month after leaving the nest to as much as 4000 ha three months after the first flight. Simultaneously, the distance from the nest to the daily activity center of the young, which was initially low, became more variable as the center was moved farther away from the nest (Fig. 3).

3.3. Parent-offspring relationships

During the first week after leaving the nest, 11 out of the 119 adult-to-young flights recorded (9%) consisted of repeated flights around the perched young. The adult involved in this sort of flight was carrying a prey in its talons on eight occasions, and a piece of branch on another two.

Parents continued to deliver food to their young after these had left the nest. Only one out of 54 food transfers took place in the air. Both parents contributed to the deliveries, although the female did most of the food transfers (69% female, N = 32). The number of food deliveries de-

Table 2. Regression coefficients on days since dispersal of log-transformed variables NFH (daily number of flights per hour), PTF (daily percentage of time spent flying), MFD (daily mean duration of flights), DLF (duration of the longest flight on a given day), DHR (daily home range), MDN (daily maximum distance to the nest), and FDD (distance from the nest where food deliveries occurred). Sample size (number of days for NFH, PTF, MFD, DLF, DHR and MDN, or number of food transfers for FDD) given in brackets.

	NFH	PTF	MFD	DLF	DHR	MDN	FDD
Young 1	0.004	0.018	0.019	0.027	0.035	0.019	24.7
	(22)**	(22)***	(22)***	(22)***	(22)***	(22)***	(9)***
Young 3	0.004	0.015	0.013	0.017	0.031	0.021	12.3
	(16)**	(16)***	(16)*	(16)***	(16)**	(16)***	(12)**
Young 4	0.005	0.012	0.010	0.014	0.024	0.009	6.0
	(26)***	(28)***	(26)***	(26)***	(26)***	(28)***	(6)***
Young 5	0.003	0.017	0.016	0.021	0.021	0.009	9.4
	(27)**	(27)***	(22)***	(25)***	(27)***	(26)***	(14)**

$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

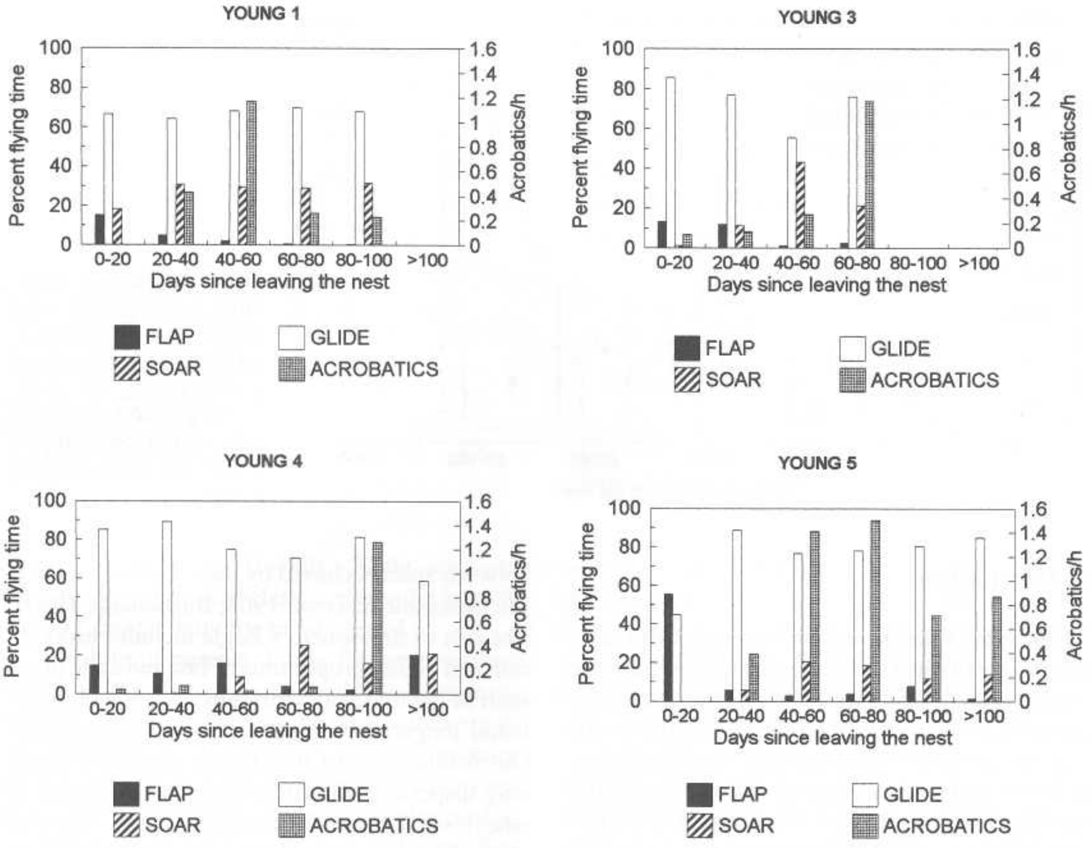

Figure 2. Changes in the percentage of flying time spent flapping, gliding or soaring, and the frequency of acrobatic flights by each radio-tagged young during the post-nestling period. Above = females, below = males.

clined progressively during the post-nestling period for all the young (Table 3). However, the total number of food deliveries per hour to the young was similar for all the pairs.

The distance from the nest to the point where food deliveries occurred (FDD) increased during the post-nestling period (range 0–2350 m) and was related to the number of days after leaving the nest for all the young (Table 2). Bill-to-bill feeding by the parents was observed until 25 days after fledging. When food deliveries were grouped according to who took the initiative (parent or young) in the transfer, we found that parent-initiated transfers decreased from 70% between 0–20 days (N = 17) to 45% between 20–40 days (N = 11) and 12% after 40 days since fledging (N = 8), and were progressively replaced by young-initiated food transfers.

The time spent by the adults in the proximity of the young declined significantly during the post-nestling period for all the pairs (Fig. 4). Overt aggressive behaviour of the adults towards the young was never observed. Adults were observed performing undulating territorial flights (Cramp & Simmons 1979) on 38 occasions, but these occurred at any time during the post-fledging period and no seasonal pattern emerged.

The number of occasions for which the young was recorded begging for food per hour increased during the post-nestling period for three of the four radio-tagged birds. Female young begged more often than males (Table 4). In spite of the adults reducing the amount of time spent near the young, the percentage of total time spent by the young flying with adults increased for all the young during the post-nestling period (Fig. 5).

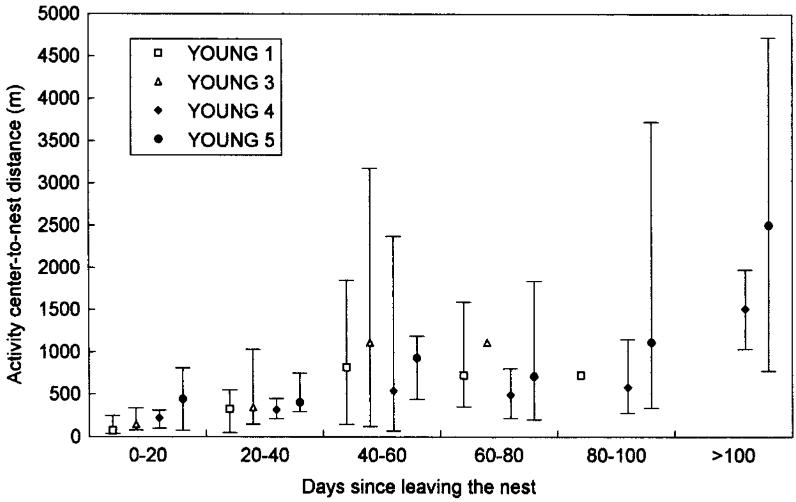

Figure 3. Changes in distance between the nest and the daily activity center for every radio-tagged young during the post-nestling period (median ± max, min). Open symbols = females, black symbols = males.

4. Discussion

The length of the dependence period (from leaving the nest to the end of parental feeding) and the post-nestling period (from leaving the nest to dispersal) in the Bonelli's Eagle are similar to the values expected based on its body size (Bustamante 1990), and are in agreement with previous studies (Real & Mañosa 1986, Real et al. 1989, Morvan & Dobchies 1990). However, the periods seem to be proportionally longer than values reported for larger raptors such as *Aquila adalberti* (Alonso et al. 1987, Ferrer 1992) or *Aquila chrysaetos* (Walker 1987, 1988). This might be attributed to different criteria employed in determining the length of the post-nestling period, but also to different food availability situations, which facilitates early transition to independence (Walker 1988, Kenward et al. 1993), or real differences between species caused by their different way of life (Ashmole & Tovar 1968, Bustamante 1990). The diet of the Bonelli's Eagle includes less carrion and higher proportions of fast and agile prey, such as pigeons and partridges, which would demand longer learning and dependence periods. Our results suggest that female Bonelli's Eagle may disperse earlier than males, as observed in other birds of prey (Kenward et al. 1993), but more evidence is needed to confirm this trend. This could be the result of the higher food requirements of the larger sex, reflected by higher begging rates in female than male young. The inability of the parents to provide enough food would lead to earlier dispersal of this sex.

Table 3. Change in the frequency of prey deliveries (number of deliveries per hour of young control).

Days since leaving nest	PAIR A	PAIR B	PAIR C
0–20	0.13	0.07	0.14
20–40	0.06	0.07	0.08
40–60	0.10	0.04	0.03
60–80	0.05	0.02	0.05
80–100	0.00	0.02	0.00
> 100	0.00	0.00	–
Global	0.06	0.05	0.06

Young Bonelli's Eagles acquire full flight proficiency well before becoming independent. Flight playing is commonly observed in young Bonelli's Eagles, as in many other raptor species (Bustamante 1993), as soon as soaring appears, which suggests that this behaviour indicates the full acquisition of flying ability, and may initiate training for hunting. By 40–60 days after the first flight, the young are proficient at flight and are responsible for initiating most food transfers. As previously described (Real & Mañosa 1989), the young were able to catch live prey offered as bait to them during the post-nestling period. This indicates that they are skilled enough to hunt well before dispersal. Although none of the young was observed catching natural prey on their own, in contrast to what is found for other birds of prey (Bustamante 1993), the capture of wild prey might not be rare

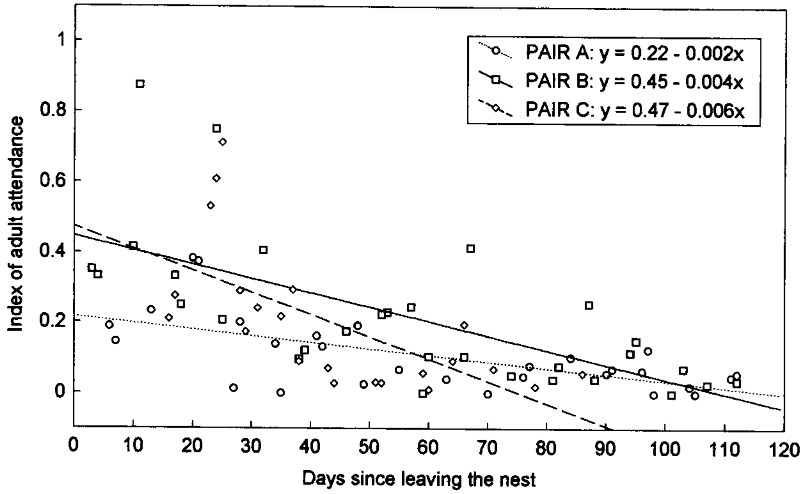

Figure 4. Changes in the index of adult attendance on the young (see text) during the post-nestling period. The linear trend for every pair is shown. All trends are significant ($P < 0.001$).

before dispersal in the Bonelli's Eagle, owing to the long period of time elapsing from the last observed parental delivery and dispersal.

The role of parents during the post-nestling period is not only to provide food to the young. In the first days after leaving the nest, adults try to encourage the young to fly or to move to safer perches, a behaviour also reported by Morvan and Dobchies (1990), and similar to that observed in the Black Kite (*Milvus migrans*) to hasten first flight, perhaps to reduce nest predation risks (Bustamante & Hiraldo 1990). Although the decline of parental attendance on the young may be a consequence of the reduction in the need for this sort of investment, the frequency of food deliveries declined in spite of a constant or increasing begging behaviour of the young which indicates the existence of a parent-offspring conflict of interest. This suggests that the end of the dependence period (from leaving the nest to the end of parental feeding) in the Bonelli's Eagle is the consequence of adult birds halting their investment, rather than the young stopping their demands (Alonso et al. 1987, Bustamante & Hiraldo 1990).

Although food deliveries have finished before dispersal, adult-offspring relationships are not totally broken by the time of the departure of the young. Just before dispersal, the young continue to spend a significant proportion of time flying in the company of their parents. The exact time of dispersal may be caused both by a reduction of parental investment and a decision of the young to disperse. As observed in pair B, young birds from the same brood may disperse independently: while one young bird has already left the parental area, parents continue to feed its sibling. So the

Table 4. Change in the frequency (number per hour of young control) of begging of the young during the post-nestling period.

Days since leaving nest	Females		Males	
	Young 1	Young 3	Young 4	Young 5
0–20	0.11	0.03	0.00	0.00
20–40	0.31	0.15	0.04	0.02
40–60	0.25	0.25	0.02	0.06
60–80	0.18	0.39	0.08	0.09
80–100	0.08	–	0.12	0.15
> 100	–	–	0.00	0.00
Global	0.22	0.16	0.04	0.06

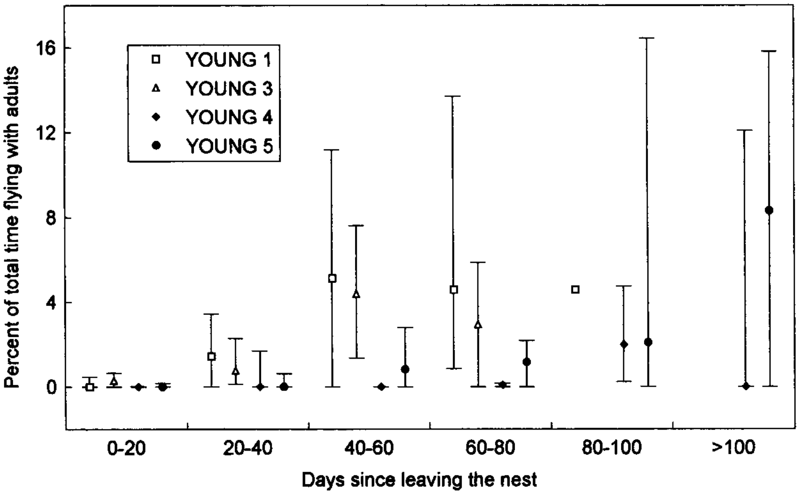

Figure 5. Changes in the percentage of total time spent by the young flying with some adult during the post-nestling period (median ± max, min). Open symbols = females, black symbols = males.

length of the post-nestling period would depend on a decision by both a young bird and its parents, as observed in other birds of prey (Ferrer 1992, Kenward et al. 1993).

Although the increase in home range and flying ability was progressive, dispersal seem to be a sudden event, as reported for other birds of prey (Bustamante & Hiraldo 1989, 1990, Donázar & Ceballos 1990, Kenward et al. 1993). Since the transmitters were expected to last for nine months and the shooting season does not begin until mid-October, a very low probability exists of attributing the loss of the signal to transmitter or battery failure, or to the birds being killed. Although the radio-signals of birds still in the nest area were easily found from the aircraft, we never managed to locate from the plane the radio-signals of the birds that were not found within the nest area from ground. This indicates that loss of signal was the result of a sudden long-distance move of the young away from the natal area for more than four days, and shows that the young behaved more as dispersers than as drifters (Walls & Kenward 1995). In spite of that, some young came back to the parental area after dispersal was assumed, as shown by the observation of one of the young in its natal area in the company of its parents several months after dispersal, as has been reported in other eagles (Ferrer 1993).

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Selostus: **Vuorikotkan poikasten itsenäistyminen**

Kirjoittajat tutkivat Kataloniassa, Koillis-Espanjassa viiden radiomerkityn vuorikotkan poikasen käyttäytymistä ja riippuvuutta vanhemmistaan pesästä lähdön ja syntymäreviiriltä poistumisen välisenä aikana. Poikaset lähtivät pesästä keskimäärin 63 vuorokautta maalis–huhtikuussa tapahtuneen kuoriutumisen jälkeen (Taulukko 1). Lentotaito kehittyi 40-60 vuorokauden aikana pesästä lähdön jälkeen (Kuva 1 ja 2). Vanhemmat ruokkivat poikasia 57–95 vuorokautta pesästä lähdön jälkeen (Taulukko 1). Kaikki poikaset jättivät syntymäpaikkansa 11–36 vuorokautta sen jälkeen kun vanhemmat viimeisen kerran ruokkivat poikasiaan. Lentopoikasajan pituus pesästä lähdöstä syntymäpaikalta lähtöön kesti 77–113 vuorokautta. Tänä aikana vanhempien ruokinta-aktiivisuus (Taulukko 3) ja poikasten vartiointiin käytetty aika (Kuva 4) laskivat. Lentopoikasaikana poikaset liikkuivat jopa 8.3 km etäisyydellä pesästään ja etäisyys pesään kasvoi iän myötä (Kuva 1b ja 3). Yhden poikasen havaittiin palanneen syntymäalueelleen 3 kk itsenäistymisen jälkeen.

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