

FACTORS INFLUENCING LENGTH OF THE POST-FLEDGING PERIOD AND TIMING OF DISPERSAL IN BONELLI'S EAGLE (*HIERAAETUS FASCIATUS*) IN SOUTHWESTERN SPAIN

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ABSTRACT.—We studied factors influencing the length of the post-fledging period (from fledging to the start of dispersal) of Bonelli's Eagle (*Hieraaetus fasciatus*) nestlings in southwestern Spain, using 13 nestlings equipped with radiotransmitters. The age at fledging was negatively correlated with hatching date, but the duration of the post-fledging period was directly related to hatching date. This pattern could be explained by seasonal changes in prey abundance, especially that of wild rabbits (*Oryctolagus cuniculus*). Young increased their mobility throughout the post-fledging period, with a significant increase in the middle of the period. Dispersal began suddenly. The direction of dispersal was random, but most of the areas first used were located <25 km away and at lower altitudes than the nesting area.

KEY WORDS: *Bonelli's Eagle*; *Hieraaetus fasciatus*; *juvenile dispersal behavior*; *post-fledging period*; *Red-legged partridge*; *wild rabbits*; *Oryctolagus cuniculus*; *Alectoris rufa*.

Factores que influyen en el período de post-emplumamiento y el comienzo de la dispersión en jóvenes águilas perdiceras *Hieraaetus fasciatus*.

RESÚMEN.—Estudiamos los factores que influyen en la duración del período de post-emplumamiento, período comprendido entre el primer vuelo del joven hasta el comienzo de la dispersión, del águila perdicera (*Hieraaetus fasciatus*) en el sudoeste de España, mediante el radio-seguimiento de 13 águilas jóvenes. Pese a que hubo una correlación negativa entre la fecha de eclosión y la duración del período de emplumamiento, la duración del período de post-emplumamiento estuvo relacionada directamente con la fecha de eclosión. Este patrón podría ser explicado por los cambios estacionales en la abundancia de presas, especialmente de conejo silvestre (*Oryctolagus cuniculus*). Las jóvenes águilas fueron aumentando su movilidad a lo largo del período de post-emplumamiento, con un incremento drástico hacia la mitad de este período. El comienzo de la dispersión fue repentino. La dirección en la que ocurrió la dispersión fue al azar, pero la mayoría de las áreas utilizadas por vez primera estaban situadas a <25 km y a menores altitudes que las áreas de nidificación.

[Traducción de autores]

In most birds, young are dependent on their parents for some time after leaving the nest. For birds of prey, young usually stay within the natal

territory until initiation of juvenile dispersal. Waser (1985) suggested that later dispersing individuals would probably have less competitive abilities. However, the length of the period from fledging to the start of dispersal, referred to as post-fledging period, and factors that influence the onset of dispersal vary considerably (Donázar and Ceballos 1990, Ferrer 1992, Bustamante and Hiraldo 1993).

The length of the post-fledging period might be

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influenced by food availability, be a result of parent-offspring conflict (Trivers 1974), or a decision made by the young themselves. When food is abundant, young may stay longer within the natal territory (Walker 1988, Kennedy and Ward 1995) but, when food is scarce, they may leave earlier (Kenward et al. 1993). Some studies have suggested that when there is abundant food in the territory, young reach dispersal or migration condition sooner and, therefore, leave the natal territory earlier (Bustamante 1994a, Wood et al. 1998).

Factors influencing the timing of dispersal may be either environmental, endogenous, or a combination of both (Howard 1960). Young develop their flying and hunting skills prior to independence (Ferrer 1992, Real et al. 1998) and the endogenous component is reflected in increased exploratory behavior near the time of dispersal (Holekamp 1986).

Here, we evaluate the factors affecting the length of the post-fledging period in the Bonelli's Eagle, especially the influence of food availability, and describe the first movements involved in juvenile dispersal. For Bonelli's Eagles, an Endangered Species (Tucker and Heath 1994), this information is limited to two studies conducted by Morvan and Dobchies (1990) and Real et al. (1998). In order to discriminate whether young Bonelli's Eagles leave the parental territory as soon as possible or whether environmental factors determine the length of the post-fledging period, we related territory quality and temporal food availability with movement patterns of young. If individuals that disperse sooner have greater competitive abilities (Waser 1985), and environmental factors were not involved, we expected that young that fledged later or with good physical condition had a shorter post-fledging period. Likewise, young with good physical condition would move farther from nests at the end of the post-fledging period.

STUDY AREA AND METHODS

We conducted the study in the provinces of Huelva, Cádiz, Málaga, and Sevilla, in southwestern Spain (Fig. 1). The study area is very heterogeneous comprising mountains, lowlands, and plains. The more mountainous areas supported Mediterranean woodlands and scrublands, while agricultural fields were prevalent in the lowlands.

We studied the post-fledging period of Bonelli's Eagle, from fledging to start of dispersion. We analyzed the length of the post-fledging period in re-



Figure 1. Study area in southwestern Spain, 1998. Grey circles represent territories of Bonelli's Eagles and black squares are the sites of prey availability counts.

lation to food availability, body condition, hatching date, and fledging duration.

During early February 1998, we searched known Bonelli's Eagle territories for accessible nests occupied by incubating adults. All nests were situated on cliffs, usually surrounded by Mediterranean woodlands (*Quercus ilex* and *Quercus suber*). The landscape in breeding areas was a mosaic of cleared woods, Mediterranean scrublands, and olive orchards. After egg laying, nests were checked every 10–20 d to estimate hatching dates. We estimated age of young based on morphometric measurements (Torres et al. 1981). In May–June 1998, when nestlings were 40–50 d old, we instrumented 14 young from 10 broods with solar ($N = 8$) and battery-powered ($N = 6$) transmitters, attached with backpack harness (Kenward 1987). One solar transmitter failed after the young eagle was released and was excluded from the analysis. Five unmarked siblings (three from a brood of two and two from a brood of three) flew from their nests during capture and were observed flying with their marked sibling during the post-fledging period.

When radio-tagging birds (on average 12 d before fledging, range = 1–22 d), measurements and blood extraction were performed to estimate body condition. We assessed body condition as the residuals of a linear regression of body mass against forewing length (Reist 1985, Krebs and Singleton 1993, Jacob et al. 1996). We used the concentration of urea in the blood to evaluate nutritional condition (Ferrer 1990, 1993) by extracting 2 ml of

blood from the radial vein of each marked nestling. Blood samples were collected in lithium-heparin tubes and were centrifuged (15 min at 3000 rpm) <12 hr after samples were drawn. Both the cellular fraction and the plasma samples were frozen. Analyses were carried out four months later using a Hitachi 705 multichannel automatic analyzer. To minimize circadian variations of the blood parameters, we extracted all blood samples between 1300–1800 H, except for one brood with two young which were not included in the analysis because blood was drawn later. We used the cellular fraction of the blood sample to sex young with primers 2945F, cR and 3224R (Ellegren 1996). Of the 13 nestlings, seven were females and six were males. Therefore, our results were not biased by sex.

We considered marked young to have fledged if they were observed flying or seen on a perch inaccessible from the nest. We searched for young in natal territories once every week using two vehicles equipped with roof-mounted, omnidirectional antennae to detect young and directional antennae to triangulate their location. Although the estimated territory size of Bonelli's Eagles in our study area averaged 3 km around nests (del Junco 1984, Gil et al. 1996, Mínguez unpubl. data), we considered young to have left their natal territories only when they roosted >4.5 km from their nests. This was the greatest distance we recorded young roosting and returning to nests a few days later. Dates of fledging and initiation of dispersal were considered as the middle of the interval between two visits. Because visits were made once a week, we assumed an error of ± 4 d.

To determine if seasonal changes of prey availability could affect fledging date and length of post-fledging period, we used data from a study on European rabbits (*Oryctolagus cuniculus*) and Red-legged Partridges (*Alectoris rufa*), the main prey of Bonelli's Eagles (Reál 1996, Ontiveros and Pleguezuelos 2000). From January–November 1998, we conducted monthly surveys of rabbits and partridges in six different sites (Fig. 1). Vehicle surveys were conducted along permanent roadside transects (10–14 km long) 1 hr before dusk at 10 km/hr (Villafuerte et al. 1993). Monthly indexes of rabbit and partridge abundance were computed for the entire study area as the mean number of rabbits and partridges seen per kilometer in each area. Prey abundance for each young eagle was considered as the mean of the monthly index of

prey abundance for the months of the fledging or post-fledging period. Thus, an average of rabbit and partridge abundance for the months during which fledging or post-fledging occurred corresponded to each young. Although these surveyed sites were not within Bonelli's Eagle territories, we related the post-fledging period with an average of prey abundance of all the surveyed sites, thus representing the general seasonal pattern of prey availability throughout the study area.

For the analyses, we used mean values of the length of fledging and post-fledging period for each brood, except for analyses regarding dispersal movements, when we considered young as independent observations. Because sample sizes were small, we used nonparametric tests (Norusis 1992). Spearman correlation coefficients were used to test the relationship between the length of fledging and post-fledging period with the different factors considered in the study (body condition, hatching date, fledging duration, and prey abundance) and to test the relationship between body condition and dispersal distance. We used comparisons between means for circular statistics to analyze the direction of dispersal from nests to the first known roosts, as defined by Batschelet (1981, cited in Upton and Fingleton 1989). We analyzed differences in the distance moved throughout the post-fledging period (dividing this period in groups of 20 d) with Levene's test for equality of variances, Wilcoxon paired tests and Friedman tests. Statistics were conducted using SPSS software.

RESULTS

Post-fledging Period. Young fledged between 15 May–22 June ($\bar{x} = 27$ May) and were between 44–69 d old at fledging ($\bar{x} = 59 \pm 8.2$ d, \pm SD, $N = 10$). The post-fledging period ranged between 43–131 d ($\bar{x} = 90 \pm 23.4$, $N = 10$). Age at fledging correlated negatively with hatching date ($r_s = -0.65$, $P = 0.04$, $N = 10$). However, length of the post-fledging period correlated positively with hatching and fledging dates ($r_s = 0.75$, $P = 0.01$, $N = 10$ and $r_s = 0.79$, $P = 0.006$, $N = 10$, respectively). No statistically significant relationship was found between age of fledging and availability of prey ($r_s = -0.15$, $P = 0.67$, $N = 10$ and $r_s = 0.15$, $P = 0.67$, $N = 10$, for rabbits and Red-legged Partridges, respectively). Length of the post-fledging period correlated negatively with seasonal rabbit abundance and positively with seasonal partridge abundance (Fig. 2). During the year of the study,

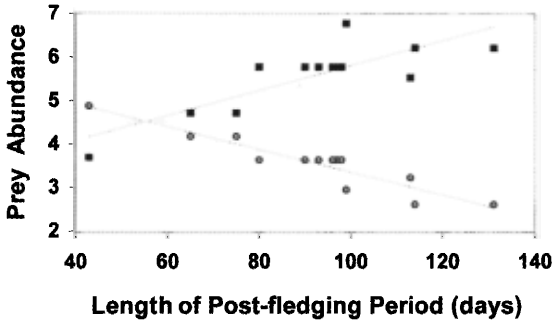


Figure 2. Relationship between prey abundance index (average of monthly prey abundance for the months of the post-fledging period) and length of post-fledging period of Bonelli's Eagles (number of days from fledging to the day that young roosted >4.5 km from the nest) in southwestern Spain, 1998. Grey circles represent rabbit abundance ($r = -0.93, P < 0.001, N = 13$) while black squares represent partridge abundance ($r = 0.76, P = 0.003, N = 13$).

rabbit abundance reached its highest level in June and July and declined thereafter, while partridge abundance reached its highest level in late summer. Peaks for maximum and minimum prey availability were in the same months throughout the study area, although the level of abundance was different in each surveyed site (Fig. 3). This strongly suggested that all of the study area had similar patterns of prey availability.

Neither urea concentration in the blood nor size corrected by body mass before fledging, showed a correlation with the length of the post-fledging period (Spearman correlation, $r_s = -0.15, P = 0.65, N = 11$ and $r_s = -0.04, P = 0.89, N = 13$, respectively).

During the post-fledging period, movements of young increased until about 80 d after fledging (Fig. 4, Levene's test for equality of variances, $F = 6.6, P = 0.001$). The development of mobility increased throughout the post-fledging period (Friedman test, $\chi^2_4 = 14.84, P = 0.005, N = 5$). Mean distance young moved from their nests increased significantly at about the middle of the post-fledging period (Wilcoxon paired test, 40 vs. 60 d after fledging, $Z = -2.20, P = 0.028, N = 8$). Distance moved increased gradually prior to the middle of the post-fledging period (Wilcoxon paired test, 20 vs. 40 d after fledging, $Z = -1.63, P = 0.10, N = 10$) and remained the same thereafter (Friedman test, comparing groups 60, 80, and 100 d after fledging $\chi^2_2 = 1.14, P = 0.56, N = 7$).

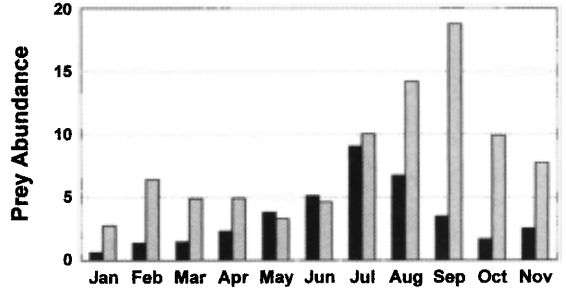


Figure 3. Monthly prey abundance of rabbits (black bars) and Red-legged Partridges (grey bars) for the six sites surveyed during the post-fledging period.

The Onset of Dispersal. All 13 instrumented young survived the post-fledging period, and the onset of dispersal occurred from 27 June–2 October ($\bar{x} = 21 \text{ August} \pm 25 \text{ d}$). Young from broods of two young ($N = 3$) did not start dispersal at the same time but with a delay of 16, 16, and 38 d between siblings.

The distance from the nest to the first-known roost site outside the territory averaged $33 \text{ km} \pm 25.7$ ($N = 13$). However, the sample differed from a normal distribution and the median distance was 23.8 km (Fig. 5). Distance to the first-known roost outside the territory was not related to condition of young (urea levels or size corrected by body mass; Spearman correlation, $r_s = -0.07, P = 0.85$,

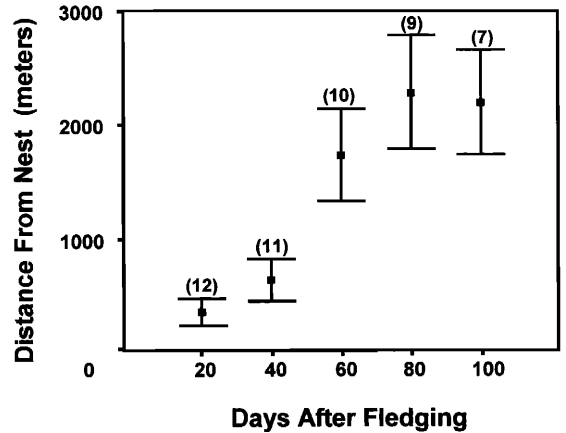


Figure 4. Mean distances to nest ($\pm \text{SE}$) moved by young Bonelli's Eagles by age during the post-fledging period in southwestern Spain, 1998. Data obtained by direct observations and short distance triangulations. Number of fledglings in parentheses. Sample sizes decrease by days as young started dispersal.

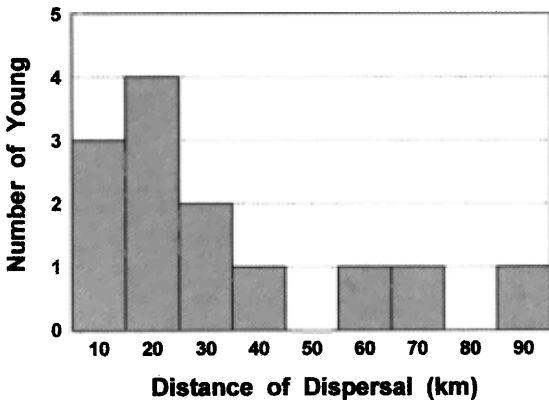


Figure 5. Distribution of dispersal distances for 13 young Bonelli's Eagles based on the first-known roost outside the natal territory in southwestern Spain, 1998.

$N = 11$ and $r_s = -0.03$, $P = 0.92$, $N = 13$, respectively).

Eleven of the 13 instrumented young dispersed to lower elevations. Mean elevation of the first-known roost sites was 281 m lower than nest sites (Wilcoxon paired test, $Z = -2.56$, $P = 0.011$, $N = 13$). Mean direction from the nest to first-known roosts outside the territory was 300.16° ($\text{var} = 1.21$). This direction did not differ from a uniform distribution as determined by the Rayleigh test ($P_{\text{RAY}} = 0.13$), modified by Wilkie (1983).

DISCUSSION

The length of the post-fledging period of Bonelli's Eagles was related to hatching date. This period was longer for young that hatched later, which contradicted results of studies on other species (Donázar and Ceballos 1990, Ferrer 1992). For some migratory species, length of the post-fledging period in later-fledged young might be reduced by the need to migrate (Bustamante and Hiraldo 1989, Donázar and Ceballos 1990, Bustamante 1994b). For a nonmigratory species such as the Spanish Imperial Eagle (*Aquila adalberti*), Ferrer (1992) suggested that in addition to physical condition of young, the physical condition of parents may determine the end of the post-fledging period.

Hatching date is generally considered to be a good indicator of territory quality and probably of high food availability (Korpimäki 1987, Cichon and Lindén 1995). Therefore, it seems unlikely that young Bonelli's Eagles that hatched early spent a shorter time in the natal territory as a con-

sequence of food scarcity. The main prey item, both in numbers and biomass, for Bonelli's Eagles in Spain is rabbits followed by Red-legged Partridges (Leiva et al. 1994, Martínez et al. 1994, Real 1996, Ontiveros and Pleguezuelos 2000). As in other Mediterranean ecosystems (Soriguer and Rogers 1981, Beltrán 1991, Villafuerte et al. 1997), our results showed that rabbits and partridges varied seasonally in abundance, with the highest abundance in late spring and late summer. These peaks in rabbit and partridge abundance coincided with the post-fledging period and the initial onset of dispersal of Bonelli's Eagles.

We found a strong negative correlation between temporal abundance of rabbits and length of the post-fledging period. We also found that young that hatched earlier took longer to fledge and had shorter post-fledging periods. This pattern may have been due to the fact that pairs that laid eggs early experienced low rabbit abundance during the brood-rearing period but high abundance during the post-fledging period. In contrast, pairs that laid eggs later in the season experienced high rabbit abundance during the brood-rearing period, but low rabbit abundance during the post-fledging period. Scarcity of rabbits during the latter period could have resulted in young needing more time to reach the necessary body condition for dispersal.

Length of the post-fledging period was directly related to partridge abundance. Therefore, young that fledged later and experienced a scarcity of rabbits would have had access to greater numbers of partridges. These young might have switched from rabbits to partridges thus resulting in the same total length of their post-fledging period as young that fledged earlier. The differences we observed could be explained by the preferences of Bonelli's Eagles for rabbits rather than partridges (Jordano 1981, Leiva et al. 1994, Gil et al. 1994, Ontiveros and Pleguezuelos 2000) that were observed as uneaten remains at nests. The lower biomass of partridges could also have been a factor, but because we assumed the same temporal prey abundance for all sites, we did not know what the real availability of prey was in each territory. There is need for more information on the effects of prey availability and the importance of each prey species on Bonelli's Eagles.

Young Bonelli's Eagles spent most of their time within 3000 m of their nests during the post-fledging period, which is within the estimates of the

mean radius of the natal territory (del Junco 1984, Gil et al. 1996). Distances moved by young from nests increased with age. In the middle of the post-fledging period, these distances increased significantly. Spanish Imperial Eagles exhibit a similar pattern with a significant increase in mobility midway during the post-fledging period when soaring flight starts to occur (Ferrer 1992).

The increase in distance moved from the nest as young aged, and the fact that young suddenly began to disperse, was caused by an increase in hunting effort by the young, as shown by Real et al. (1998), rather than by exploratory behavior or a behavior caused by the parents. Further, we observed no young returning to their natal territory during the first days of dispersal. Siblings seemed to leave territories in an independent manner, suggesting the existence of an endogenous factor to start dispersal. However, our data suggested that the time of dispersal was determined mainly by rabbit availability.

ACKNOWLEDGMENTS

We thank many people for their collaboration in the fieldwork, especially C. Aguilar, C. Fernández, S. Moran, R. Fernández, and J. Ayala. G. Janss and E. Revilla were indispensable for their support. G. Pino arranged a house in the field. F. Recio performed plasma analysis in the Valme Hospital in Sevilla. Special thanks go to R. Villafuerte and G. Jordán. We thank F.M. Jaksic, J.E. Jiménez, and an anonymous referee for their useful comments. This study was directed by M. Ferrer and it was supported by the regional Government (Junta de Andalucía). V. Siebering was funded by the Wageningen University, while E. Mínguez and E. Angulo were funded by the Estación Biológica de Doñana (CSIC).

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Received 27 July 2000; accepted 7 April 2001