Natal dispersal, i.e., the movements performed between the departure from the parental territory and the settlement in the first breeding site (Greenwood & Harvey 1982), is an essential demographic process which influences ecological dynamics, spatial distribution, and genetic structure of populations (Johnson & Gaines 1990, Clobert et al. 2001, Bullock et al. 2002). To study natal dispersal in many bird species, remote-tracking systems have been frequently used, especially VHF radio-tracking techniques. However, continuous tracking of animal movements is difficult and logistically complex to carry out, especially in those cases in which long distance movements, large ranges and delayed reproduction are present (Kenward 2001). For these cases, satellite tracking techniques, though expensive, can be very helpful. Bonelli’s Eagle Aquila fasciata juveniles usually leave their parental territories suddenly and perform large movements during dispersal (Cheylan et al. 1996, Real & Mañosa 2001, Cadahía et al. 2005, 2007b) and, hence, the report of the distribution of the natal dispersal distances could be short-distance biased using conventional radio-tracking methods.

Bonelli’s Eagle is an ‘endangered’ raptor in Europe (BirdLife 2004). The strongholds of the European breeding population occur in the Iberian Peninsula, where the species is also considered ‘endangered’ both in Spain and Portugal (Marti & Del Moral 2003, Real 2004). Previous studies have described juvenile Bonelli’s Eagle...
movement patterns, the maximum distance juveniles can reach, the extent of their hourly and daily movements or the habitat they select during the initial phases of dispersal (Cheylan et al. 1996, Real & Mañosa 2001, Balbontín 2005, Balbontín & Ferrer 2005, Cadahía et al. 2005, 2007b). Here we provide a comprehensive account of the movements performed by two long-term tracked Bonelli’s Eagle juveniles throughout the natal dispersal period and describe the recruitment to the breeding population registered for one of them, after four years of satellite tracking.

Two nestling Bonelli’s Eagles, a male and a female, were tagged with solar-powered PTT-100s (Microwave Telemetry Inc. USA, 35g, 17.4 x 29.1 x 62.5 mm, antenna 17.8 cm) in eastern Spain (provinces of Valencia and Castellón), on 26 April and 9 May 2002, respectively. Both nestlings were removed from their cliff-located nests (distant 91 km) when they were ca. 50 days old, weighed, measured and fitted with the PTTs. These were fixed as back-packs to the birds’ body by a break-away, non-elastic, Teflon harness and were in both cases under 3% of the birds’ body mass (Kenward 2001). Gender of nestlings was established by molecular methods (Griffiths et al. 1998, Fridolfsson & Ellegren 1999) using a blood sample (around 0.5 ml) collected from the brachial vein and stored in ethanol 70%. During the nesting period, nestlings’ age was estimated according to feather growth and pattern (Torres et al. 1981, Gil-Sánchez 2000) using a spotting scope from a distant point. After tagging and measuring, exact age was computed as: age = 0.200 × tail length (central rectrix) (mm) + 16.262 (Mañosa et al. 1995).

Both PTTs were set to an 8-h on / 120-h off schedule. Estimation and initial management of the locations was made by Argos, a satellite-based location and data collection system (Argos 1996, Kenward 2001). Argos location classes (LC) 3, 2 and 1, with nominal accuracy < 150 m, 150–350 m and 350–1000 m, respectively, were used (Argos 1996, but see Keating et al. 1991, Soutullo et al. 2007). Lower quality locations (LC 0, A and B) were also employed, after filtering them according to Argos accuracy tests (see Soutullo et al. 2007) and the maximum speed per hour and per day calculated from Bonelli’s Eagle juveniles tagged with GPS (see Cadahía et al. 2007b).

To describe the movements of both birds during natal dispersal we computed distance and range size variables. Since we were interested in modelling how the distancing and settlement patterns develop, we only used data after departure from the parental territories (see Cadahía et al. 2008). For a general description we calculated the annual ranges size, the median and maximum annual distance to natal nests, and, in the case of the recruitment we registered (the female), also the natal dispersal distance, i.e., the length of a straight line connecting the natal nest with the first breeding site (Greenwood & Harvey 1982). For annual computations, years were defined in relation to birds’ birth. For a more detailed description, we computed monthly distances to natal nests (ND) as the median of all distances calculated within each Gregorian month, and monthly range sizes (RS), using a 95% Minimum Convex Polygon of all the locations within a given month. In the recruitment case, we also computed the monthly distance to the first breeding site (BD). The spatial analyses were performed with ArcMap 9.2 (ESRI, Inc.).

To test whether autocorrelation existed in the monthly variables, we constructed autocorrelograms. All the distance data presented significant autocorrelation, and, to remove it, we used “autoregressive integrated moving-average” models (ARIMA models; Box & Jenkins 1976, Urios et al. 2007). Autocorrelation was eliminated using a first-order moving average process (an ARIMA (0, 0, 1) model) for the female’s ND and BD, and using a first-order autoregressive process (an ARIMA (1, 0, 0) model) for the male’s ND. Then, we fitted the (filtered) distance and range size variables to appropriate mathematical models to describe their general trend. Time series analyses were carried out with R 2.7.0 (R Development Core Team 2008). All other analyses were performed with SPSS 15.0 (SPSS, Inc.).

During the approximately four years of both birds’ tracking (until both PTTs ceased working), we collected 461 useful Argos satellite fixes for the female and 390 for the male, respectively. In general, the female reached more distant locations to its natal area than the male did, but, in the second and fourth year, covered smaller annual areas (Table 1, Fig. 1). The female’s monthly distance to the natal nest (ND) rapidly increased during the first months of life, but then became rather constant (Table 2, Fig. 2a). Similarly, both the monthly distance to the first breeding site (BD) and the monthly area (RS) covered by the bird decreased rapidly and, from the third month after dispersing on, remained relatively steady (Table 2, Fig. 2a).
This means that, soon after dispersing, the female settled in an area that, after being intensively explored during most of the whole dispersal period (1000 km² per month as an average), finally became its first breeding site (Fig. 1). In fact, considering an average Bonelli’s Eagle territory radius between 4.9 km (Sanz et al. 2005) and 11.9 km (Arroyo et al. 1995) in Spain, the female visited locations within its first breeding territory as soon as May 2005, i.e., already during the previous breeding season, and stayed within an average monthly distance of 13 km from its final nest location during the remaining time. In the male, the monthly distance to the natal nest (ND) indicated that the bird was already far away shortly after dispersing, but, after one year and a half, it moved to an area closer to its parental territory, just to move away once more after another one and a half years (Table 2, Fig. 2b). Despite these large movements, which made its annual range to be greater than that of the female on the second and fourth year (Fig. 1), the monthly range size (RS) decreased during the initial months after dispersing and became rather stable afterwards (Table 2, Fig. 2b). According to this, except for the large travelling episodes, the bird explored monthly

Table 1. Median and maximum annual distances (km) and annual range size (km²) covered by two Bonelli’s Eagle juveniles during their natal dispersal period (in this case, first four years of life) in Spain.

<table>
<thead>
<tr>
<th></th>
<th>Female</th>
<th></th>
<th></th>
<th></th>
<th>Male</th>
<th></th>
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<tr>
<td></td>
<td>1st year</td>
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<td>1st year</td>
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<td>Median annual distance</td>
<td>413</td>
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<td>434</td>
<td>441</td>
<td>236</td>
<td>201</td>
<td>97</td>
<td>117</td>
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<tr>
<td>Maximum annual distance</td>
<td>503</td>
<td>533</td>
<td>498</td>
<td>541</td>
<td>332</td>
<td>285</td>
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<td>Annual range size</td>
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<td>5730</td>
<td>3874</td>
<td>2468</td>
<td>16397</td>
<td>10308</td>
<td>2907</td>
<td>21244</td>
</tr>
</tbody>
</table>

Fig. 1. Annual home ranges of two juvenile Bonelli’s Eagles during natal dispersal in Spain, computed using the 95% Minimum Convex Polygon. Autonomous Communities (Spanish administrative units) are shown. a) to d) indicate first to fourth year of life. Light grey: female; dark grey: male. Stars designate natal nests. The broken arrow represents the female’s natal dispersal distance, i.e., the distance from the natal nest to the first breeding place.
It is well known that Bonelli’s Eagle juveniles can perform large movements during natal dispersal (Cheylan et al. 1996, Real & Mañosa 2001, Cadahía et al. 2005, 2007b), a phase which may last several years until birds reach sexual maturity. Hitherto, recruitments of Bonelli’s Eagles reported natal dispersal distances ranging from 50 km to 320 km in southeastern France (Cheylan et al. 1996) and from 5 km to 120 km in southern Spain (Balbontín & Ferrer 2009). In comparison, our female was recruited in a more distant location (441 km, Fig. 1d), which implies that it cannot be considered philopatric, i.e., it did not return to its natal area or nearby to attempt breeding. In addition, if the male we monitored for four years were actually breeding, it should also be considered non-philopatric, but, as we could not find the bird, this statement must be taken with caution. In any case, all these individual differences make it difficult to clarify the real distribution of the natal dispersal distances in the western European population of Bonelli’s Eagle. Several factors, like geographical

Table 2. Regression models used to describe the movement patterns of two juvenile Bonelli’s Eagles during natal dispersal in Spain. ND: monthly distance to natal nest (km); RS: monthly range size (km²); BD: monthly distance to first breeding site (km); ‘time’ indicates months. The regressions of the distance variables are computed on the residuals of ARIMA models used to remove autocorrelation from the original data. a — In the male’s ND the regression model was calculated using the original data, despite the existing autocorrelation, to illustrate the general tendency of the bird’s movement, since the residuals of the ARIMA model did not show any straightforwardly informative pattern.

<table>
<thead>
<tr>
<th></th>
<th>Regression model</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>R²</th>
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<tr>
<td>Female</td>
<td>ND = 14.54 - 139.16/time</td>
<td>1.43</td>
<td>49.359</td>
<td>0.001</td>
<td>0.534</td>
</tr>
<tr>
<td></td>
<td>RS = 709 + 8088/time</td>
<td>1.40</td>
<td>19.324</td>
<td>0.001</td>
<td>0.326</td>
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<tr>
<td></td>
<td>BD = -17.35 + 163.51/time</td>
<td>1.43</td>
<td>58.020</td>
<td>0.001</td>
<td>0.574</td>
</tr>
<tr>
<td>Male</td>
<td>ND² = 230.67 + 5.70 × time - 0.84 × time² + 0.02 × time³</td>
<td>3.42</td>
<td>26.643</td>
<td>0.001</td>
<td>0.656</td>
</tr>
<tr>
<td></td>
<td>RS = 446 + 9981/time</td>
<td>1.39</td>
<td>9.316</td>
<td>0.001</td>
<td>0.479</td>
</tr>
</tbody>
</table>

areas of approximately similar size (800 km² as an average) during most of its dispersal period. At the beginning of the breeding season in 2006, the female’s movements were confined to a restricted area in central Spain. After three field trips, we confirmed that the bird was attending an active nest located 441 km from its natal nest (i.e., natal dispersal distance; Fig. 1d) and that both it and its unbanded mate retained juvenile plumage features. Egg laying took place in the first fortnight of April 2006 but the breeding failure was confirmed on 6 June. During the following breeding season the pair was observed successfully raising a chick that probably hatched in the second fortnight of April 2007. As to the male we also tracked for four years, we could not confirm any breeding attempt before losing contact, but its last locations were assembled in a breeding area around 260 km south from its natal territory.

Fig. 2. Changes in time of monthly distances and home range sizes of two juvenile Bonelli’s Eagles during natal dispersal in Spain. a: female; b: male. Open circles: monthly range size (RS); empty triangles: monthly distance to natal nest (ND); filled triangles (only female): monthly distance to first breeding site (BD).
origin, population density, foraging opportunities, etc., are likely to influence the natal dispersal distance in each particular case and account for the observed variation.

The different evolution of range size and movement patterns in the two studied birds might reflect different dispersal strategies regarding how and when individuals decide to settle in a potential first-breeding site. During almost the entire natal dispersal period the female moved around an area within which it finally attempted breeding (Fig. 1, Fig. 2a). This juvenile took advantage of previously built nests in the area, forming a new pair in a marginal area by reconciling an old territory (J. Cisneros, P. González, pers. comm.). In contrast, the male alternated long-distance travelling episodes with settlement in particular areas during the four years. This enabled him to explore areas spread along the south-east region of the Iberian Peninsula, both distant and close to his natal territory (Fig. 1, Fig. 2b). With this strategy the juvenile might be checking different breeding territories, monitoring the availability of breeding opportunities, as it has been suggested for other eagle species, like Spanish Imperial Eagle Aquila adalberti (Ferrer 1993, 2001) or Golden Eagle A. chrysaetos (Urios et al. 2007). In fact, this dissimilar behaviour has already been suggested as a sex-related difference in the dispersal strategy of Bonelli’s Eagle (Balbontín & Ferrer 2009).

This complicated scenario of dispersing strategies and natal dispersal distances is also noticeable when looking at genetic data. Cadahia et al. (2007a) studied mitochondrial DNA sequences in Bonelli’s Eagles from the Iberian Peninsula and Morocco and found no evidence of significant genetic structure. To account for this result, the authors proposed the occurrence of gene flow among different areas of the distribution range through long natal dispersal events. However, when using microsatellites as molecular markers, the results obtained revealed the existence of significant genetic structure in some Bonelli’s Eagle populations within the Iberian Peninsula (Mira 2006). In this case, the philopatric behaviour of the species was put forward as the most likely explanation. These apparently contradictory results, along with the diverse natal dispersal distances reported, point out the need to collect more data, both genetic and ecological, to disentangle how this process really occurs, including its implications for the demography and conservation of the western European population of the species.

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REFERENCES


STREZCZCENIE

[Dyspersja natalna orzelka południowego] Aby określić odległości przebywane przez młode orzelski południowe pomiędzy opuszczeniem gniazda a przystąpieniem do rozrodu dwa młode ptaki — samca i samice wyposażono w 2002 w nadajniki telemetrii satelitarnej zasilane baterią słoneczną. Oba ptaki pochodziły z gniazd położonych we wschodniej Hiszpanii.

Samica przeleciała na dość znaczną odległość i dość szybko (po ok. 3 miesiącach — Fig. 2a) osiedliła się na terenie zajmowanym następnie przez kolejne 4 lata, gdzie przystąpiła do pierwszego lęgu (Tab. 1, Fig. 1). Odległość między miejscem, w którym się wyklucza a własnym gniazdem wyniosła w linii prostej 441 km. Natomiast samiec w ciągu czterech lat od oznakowania nie był przywiązany do jednego terenu (Fig. 1, 2b). Autorzy sugerują, że w tym okresie prawdopodobnie przebywał na wielu różnych terytoriach lęgowych, sprawdzając możliwości gniazdowania, gdyż podobne strategie są obserwowane np. u orła iberyjskiego. W ciągu czterech lat obserwacji nie zanotowano próby lęgowej podjętej tego osobnika.

Odległość między miejscem wyklucia a własnym gniazdem stwierdzona dla badanej samicy jest jedną z najwyższych zanotowanych do tej pory.

SHORT NOTES