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Natal philopatry: local experience or social attraction? An experiment with Spanish imperial eagles

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We investigated juvenile dispersal strategy of a territorial long-lived species with deferred maturity, the Spanish imperial eagle, *Aquila adalberti*. Here we used a reintroduction programme as an experimental approach to test separately predictions of the two hypotheses about natal philopatry: social attraction and local experience. We determined the maximum juvenile dispersal distance of 90 young eagles in three different categories: (1) 31 translocated young released without adults in the area; (2) 29 translocated young released with adults breeding in the area; and (3) 30 wild nonmanipulated individuals. No differences between the sexes were found but there was a highly significant difference between the three categories, with longer distances in young released without adults in the area and similar distances in the other two categories. Our results thus showed that social attraction determined the juvenile dispersal strategies in this species.

Juvenile dispersal is a fundamental process affecting genetic flow, distribution, population dynamics and persistence of species (Clobert, Danchin, Dhondt, & Nichols, 2001; Dieckmann et al., 1999; Hanski & Gilpin, 1997). Nowadays most of the published information on juvenile dispersal behaviour of birds is based on the continuous following of tagged individuals (Ferrer, 1993a, 1993b; Muriel, Morandini, Ferrer, & Balbontín, 2015; Muriel, Morandini, Ferrer, Balbontín, & Morlanes, 2016; Sternalski, Bavoux, Burneleau, & Bretagnolle, 2008). A long-term database of this kind allows us to better understand the behavioural decisions, importance and factors involved in the period prior to settlement, known as juvenile dispersal (Whitfield, Douse et al., 2009; Whitfield, Duffy et al., 2009). Owing to the usual high mortality during juvenile dispersal, the costs associated with dispersal and settlement, and the resulting fitness, dispersal decisions must be under high selective pressure (Bowler & Benton, 2005; Stamps, 2001). The model species we studied here is a typical large raptor with around 84% juvenile mortality (Ferrer & Calderón, 1990), and consequently different strategies during dispersal movements would be under strong selection.

Typically, in birds with deferred sexual maturity, juveniles frequently tend to return to breed in their natal populations (e.g. Ferrer, 1993a; Ferrer, Morandini, & Newton, 2015; Sternalski et al., 2008). This widespread behaviour, called natal philopatry, has been interpreted under two mutually exclusive hypotheses. First, according to some authors, juvenile birds may show a natural tendency to return to the natal area for breeding because then they would be selecting familiar areas as future breeding territories where they know reproduction is possible (Greenwood, 1980, 1982). This is the 'local experience' hypothesis. Second, juveniles may also show a tendency to look for areas with breeding pairs of the same species as reliable indirect cues of intrinsic habitat quality for reproduction; this is known as the social (or conspecific) attraction hypothesis (Fletcher, 2006; Muller, Stamps, Krishnan, & Willits, 1997; Ray, Gilpin, & Smith, 1991). According to the social attraction hypothesis, juveniles should increase dispersal distances when they fail to find adults of their own species during their dispersal movements.

Local experience and social attraction have been shown to be the usual strategies that may lead to higher fitness benefits in terms

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of juvenile survival and postsettlement fecundity (Danchin, Heg, & Doligez, 2001; Doligez, Cadet, Danchin, & Boulinier, 2003; Fletcher, 2006; Stamps, 1988). These two strategies, however, cannot be studied separately in natural populations since juveniles always know their natal area and their own parents together, making the effect of each factor impossible to discern.

In the present study, we investigated juvenile dispersal strategy of a territorial long-lived species with deferred maturity, the Spanish imperial eagle, *Aquila adalberti*. Here we used a reintroduction programme (Muriel, Ferrer, Casado, Madero, & Calabuig, 2011) as an experimental approach to test separately predictions of the different hypotheses about juvenile dispersal movements. We examined the ontogeny of the movement behaviour of radiotagged juvenile eagles throughout their first 2 years of life under three different categories: (1) translocated young released without adults in the area; (2) translocated young released with adults breeding in the area; and (3) wild nonmanipulated individuals. In the first two categories, ad libitum food was provided for 6 weeks before the juveniles were released, potentially improving their nutritional condition. The wild juveniles were not given supplementary food.

According to the social attraction hypothesis we expected longer dispersal distances in young eagles released without adults in the area, and no differences in maximum dispersal distance in the other two categories (wild young and released young with adults breeding in the area). In contrast, under a local experience context, shorter distances would be expected in released juveniles without adults which would defend their territory and reject any young in the area.

METHODS

Study Species

The Spanish imperial eagle is a large (2500–3500 g) raptor breeding only in the Iberian Peninsula with a conservation status of 'vulnerable' (IUCN Red List, BirdLife International 2008). With around 500 breeding pairs in 2015 (National Working Group, 2015) it is one of the rarest eagles in the world. The species is long-lived (21–23 years), with a mean annual productivity of 0.75 chicks/pair, sedentary and territorial, (Ferrer & Calderón, 1990). The reproductive cycle lasts around 8 months (from February to October), and independent juveniles show long-distance dispersal behaviour (Ferrer, 1993a), including exploratory movements, temporary settlement and visits to breeding populations to gather information on breeding prospects. The age of first breeding is around 4–5 years old on average (Ferrer et al., 2015). Temporary settlement areas are selected by high prey density (wild rabbits), avoiding the presence of other large breeding eagles (Ferrer & Harte, 1997).

Study Area and Data Collection

We studied 105 birds hatched in 14 nonconsecutive years from 1986 to 2013. These birds were from the population of Doñana National Park (1049.7 km^2; 36°56′N, 6°30′W), a reinforcement project in the same area and a reintroduction project in the province of Cádiz (≈36°20′N 5°48′W, around 87 km from Doñana National Park), in southern Spain. Data from wild birds were obtained from 1986 to 2010, data from young released without adults in the area were obtained from 2002 to 2009 and data from young released with adults in the area were obtained from 2005 to 2013. We monitored the birds over a large area of the southern Iberian Peninsula, a mix of dry-humid Mediterranean forest, scrubland and wetlands (for a more detailed description see Muriel et al., 2015). Hatching dates of the young were accurately known due to previous checks of the nests. The mean hatching date for all the young was 25 April ± 8 days.

The Spanish imperial eagle reintroduction programme in the province of Cádiz started in 2002 (Muriel et al., 2011). Between 2002 and 2013, young eagles were translocated when 47.8 ± 6.1 days old to the hacking facilities in three nearby locations, and released after 28.8 ± 6.2 days. They were fed ad libitum until the last one left the release area (for more details see Muriel et al., 2011). Young eagles do not learn any special flight skill from their parents during the dependence period (Ferrer, 1993a), so no differences in dispersal abilities between wild and translocated young were expected.

All nestlings were ringed and equipped with backpack radiotransmitters when they were 45–70 days old. Radiotransmitters (three models: TW-3, Biotrack Ltd., Dorset, U.K.; HSPB 14003, Wildlife Materials Inc., Murphysboro, IL, U.S.A.; and 5/XOB 17-04, Wagener Telemetrieanlagen, Koeln, Germany) did not exceed 2.5% of the body mass of the young at fledging (Kenward, 2001). The sex of the young was determined from the forearm measurement (Ferrer & De le Court, 1992) as well as molecular methods (Fridolfsson & Ellegren, 1999) using blood samples between 2006 and 2013.

Dispersal Monitoring

Radiotagged juveniles were radiotracked from the beginning of dispersal to the end of their second year of life (i.e. 700 days old) or until transmitter failure/loss. We considered the beginning of dispersal as the first day the individual was located over 6.5 km from the natal population (mean internest distance; González, 1991), i.e. from any active nest belonging to the natal population for nonmanipulated juveniles, or from the hacking site for translocated individuals. At least two simultaneous teams tracked birds by car using portable receivers (Stabo, GFT Technologies SE, Bonn, Germany; and R1000, Communication Specialist Inc., Orange, CA, U.S.A.), nondirectional antennas and three-element Yagi antennas. Searches were conducted at least 5 days per week by each team, using high observation points regularly distributed over the dispersal area. We always tried to locate the bird visually; otherwise location by triangulations was carried out. Occasionally, we searched from light aircraft within a radius of 150 km around the Doñana population and hacking sites to look for nonlocated individuals. In total, we devoted 3150 days for the field work and searched an area of 44 243 km^2 (kernel 95% of spotting sites used). Young eagles reach their maximum dispersal distance (Dmax) from their natal nest within 2 years of their departure (Ferrer, 1993b). Consequently, in the present study we only considered those juveniles that we were able to track for more than 700 days after dispersal. The final data set for Dmax analyses included 90 young eagles (50 males and 40 females); 31 translocated young released without adults in the area (all in Cádiz), 29 translocated young released with adults breeding in the area (14 in Doñana and 15 in Cádiz), and 30 wild nonmanipulated individuals (20 in Doñana and 10 in Cádiz).

Statistical Analysis

We explored variations in Dmax among the three categories considered (released young with and without adults and wild young). We fitted a generalized linear model (GLM) with normal distribution to analyse Dmax including 'categories' and 'sex' and first-order interactions as factors. We also investigated potential differences between the two populations (Doñana and Cádiz) selecting the two common categories they share: wild young and released young with adults in the area. All tests were two-tailed