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Juvenile dispersal behaviour and conspecific attraction: an alternative approach with translocated Spanish imperial eagles

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The transient stage prior to definitive recruitment, known as juvenile dispersal, is thought to be under great evolutionary pressure and subject to a trade-off between associated costs and long-term benefits for fitness. Conspecific attraction has been shown to be an adaptive mechanism driving dispersal behaviours that may lead to negative density-dependent dispersal patterns. However, conspecific attraction can be scarcely discernible from imprinting to the natal area in wild populations. Reintroductions in the absence of settled individuals can be used as alternative colonization-like contexts to investigate the relative role of conspecific attraction in juvenile dispersal behaviours. We examined the spatiotemporal development of dispersal movements in reintroduced juveniles of a long-lived species with deferred maturity, the Spanish imperial eagle, *Aquila adalberti*, in comparison with nonmanipulated juveniles from a nearby population. We found that reintroduced birds started dispersal earlier and were initially more philopatric, probably encouraged by the advantageous competitive environment in the release area. Conversely, they revealed a more expansive strategy as they matured and approached the time when settlement decisions would be made, especially in females. They returned less frequently, increased exploratory movements and dispersal ranges, and visited breeding areas, probably as a consequence of the relatively lower reproductive prospects in the release area than in nearby populations. Therefore, the singular social cueing in reintroductions may eventually lead to juvenile wandering behaviours characteristic of colonization contexts in this territorial long-lived species. Such dispersive strategies relying on conspecifics may have important consequences for population dynamics and management. They may hinder the initial settlement phase in reintroductions, although behaviours such as longer returns may enhance recruitment prospects. Translocation programmes should consider specific dispersal scenarios, as well as postrelease monitoring to increase philopatry and success probabilities.

The study of animal movement has received much attention as it has profound effects on population biology, ecology and evolution (e.g. Clobert, Danchin, Dhondt, & Nichols, 2001; Nathan et al., 2008; Swingland & Greenwood, 1983). In particular, natal dispersal (Greenwood, 1980) seems to play a key role in individual performance as a strategy aimed to increase lifetime reproductive success in spatiotemporally heterogeneous landscapes by optimizing settlement decisions (Bowler & Benton, 2005; Clobert et al., 2001; Johnson & Gaines, 1990; McPeek & Holt, 1992). Moreover, dispersal strategies affect population dynamics and persistence, abundance and distribution of species and genetic flow (Clobert et al., 2001; Dieckmann, O'Hara, & Weisser, 1999; Hanski & Gilpin, 1997). Natal dispersal has been a central topic in behavioural ecology with increasing theoretical work and empirical studies (e.g. reviews in Bowler & Benton, 2005; Greenwood, 1980; Paradis, Baille, Sutherland, & Gregory, 1998). However, the transient stage of wandering from the natal site to the definitive recruitment area, known as juvenile dispersal, has received much less attention. It is during this period that dispersers prospect their environment to gather information on habitat quality essential for movement and settlement decisions, which eventually determine the effective natal dispersal (Clobert et al., 2001; Clobert, Le Galliard, Cote, Meylan, &

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Massot, 2009; Danchin, Giraldeau, Valone, & Wagner, 2004; Reed, Boulinier, Danchin, & Oring, 1999). Dispersal behaviours are therefore thought to be under great evolutionary pressure and subject to a trade-off between associated costs and the resulting long-term benefits (Bowler & Benton, 2005; Penteriani, Ferrer, & Delgado, 2011; Stamps, 2001). Information on habitat quality can be acquired by direct interaction with the physical environment, known as personal information (Danchin et al., 2004), whereby individuals assess the availability of vital resources and their accessibility as a function of the competitive environment (Fretwell & Lucas, 1970; Murray, 1967). Dispersers can also rely upon proximate cues of intrinsic habitat quality provided inadvertently by other conspecifics, known as social information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin et al., 2004; Seppänen, Forsman, Mönkkönen, & Thomson, 2007), which are linked to the occurrence and density of conspecifics (i.e. conspecific attraction) or their performance (i.e. public information). Both direct and indirect strategies may result in density-dependent dispersal patterns (Matthysen, 2005). In this respect, conspecific attraction will promote negative density-dependent dispersal and aggregated distributions, with individuals being attracted by the presence of conspecifics, whereas higher density will increase intraspecific competition and dispersal under nonconspecific cueing.

Typically, studies on large philopatric birds with delayed sexual maturity show a notable tendency for juveniles to return to their natal populations (e.g. Ferrer, 1993a; Forero, Donázar, & Hiraldo, 2002; Sternalski, Bavoux, Burneleau, & Bretagnolle, 2008; Walls & Kenward, 1998). These returns can be interpreted under two nonmutually exclusive mechanisms. First, juveniles can show a natural inherited tendency to stay in or return to the natal area for breeding, so they would preferably select familiar areas as breeding territories where reproduction is known to be possible (Greenwood, 1980; Greenwood & Harvey, 1982; Shields, 1982). Second, juveniles may react positively to the social landscape, showing attraction to areas with conspecific breeding pairs as reliable indicators of suitable habitat for reproduction (Fletcher, 2006; Muller, Stamps, Krishnan, & Willits, 1997; Ray, Gilpin, & Smith, 1991). Both strategies have been shown to provide higher benefits to lifetime fitness by favouring less costly dispersal patterns in terms of juvenile survival and postsettlement fecundity (Danchin, Heg, & Doligez, 2001; Doligez, Cadet, Danchin, & Boulinier, 2003; Fletcher, 2006; Stamps, 1988).

Conspecific attraction cannot be studied separately from imprinting to the natal area in natural populations because juveniles usually disperse between already occupied breeding areas where these factors are scarcely discernible. This is not the case during colonization, characterized by the initial absence of settled breeders and the extremely low conspecific density (Gray, Crawley, & Edwards 1987). In this sense, the reintroduction of animals into new areas with initial null or very low conspecific density can provide unique opportunities to investigate dispersal strategies (Sarrazin & Barbault, 1996), allowing the discrimination of the relative role played by conspecific attraction in the dispersive response of founders prior to their first reproductive settlements regardless of tenacity to the natal area.

Density-dependent dispersal strategies mediated by conspecific attraction may also be secondarily conditioned by the intrinsic individual state (Bowler & Benton, 2005; Clobert et al., 2009). In this respect, age- and sex-related dispersal may reflect state-specific sensitivity to dispersal environments and in particular to social cueing. For instance, young individuals tend to be subordinate in competitive scenarios and thus prone to dispersal, while individuals approaching sexual maturity are subjected to reproductive-related pressures that can promote strategies that increase early recruitment in optimal habitats and/or prevent inbreeding (Bowler & Benton, 2005). Dispersal strategies may also differ between the sexes, with females usually dispersing more frequently and further than males in territorial birds (Dobson, 2013; Greenwood, 1980). Female-biased dispersal has been explained by multiple mechanisms such as asymmetry in reproductive and resource defence strategies (Clarke, Saether, & Roskaft, 1997; Greenwood, 1980), competitive effects (Perrin & Mazalov, 2000; Waser, 1985) or inbreeding avoidance (Pusey, 1987; Pusey & Wolf, 1996).

In the present study, we investigated how the juvenile dispersal behaviour of a territorial long-lived species with deferred maturity, the Spanish imperial eagle, *Aquila adalberti*, responds to the conspecific landscape under an induced colonization context. We applied an alternative quasiexperimental approach by using an existing translocation programme of the species to an unoccupied area of southwestern Spain (Muriel, Ferrer, Casado, Madero, & Calabuig, 2011), characterized by the absence of settled dominant conspecifics, but with breeding populations within the dispersal range. The Spanish imperial eagle has a relatively long juvenile dispersal period which has been previously described in detail (Ferrer, 1993a, 1993b; González, Heredia, González, & Alonso, 1989; see Methods for details). It is considered a philopatric facultative species with a tendency to recruit within or close to the natal population (Ferrer, 1993a; González et al., 2006), although it may also emigrate to other breeding nuclei according to the metapopulation structure. Here, we examined the development of spatiotemporal behaviours of young translocated Spanish imperial eagles, in comparison with nonmanipulated individuals from a nearby breeding population during the juvenile dispersal period, in order (1) to determine the relative role played by conspecific attraction in dispersal onset and movement patterns throughout their first 2 years of life, (2) to assess whether the perception of social features is dependent on age and thus varies as individuals approach sexual maturity, and (3) to account for possible sexual differences in dispersal behaviours related to sex-specific sensibility to conspecific cueing. In the context of conspecific attraction, we expected an increase in longer exploratory movements and larger accumulated ranges of translocated juveniles, particularly in females, searching for breeding opportunities as they matured, since the likelihood of mating and occupying reproductive vacancies is initially lower in the release area than in existing breeding populations. In contrast, if individuals did not rely on conspecifics we expected a delayed dispersal, an increasing frequency and/or duration of natal returns and smaller dispersal ranges of translocated juveniles driven primarily by the attraction to the release area and the reduced intraspecific competition. Therefore, a trade-off between large-scale dispersive behaviours searching for breeding populations and a philopatric response with individuals staying relatively close to the release sites is expected in this alternative scenario. The resulting patterns will rely on how female and male juvenile eagles perceive conspecific cues and dispersal landscape as they reach maturity.

METHODS

Study Species

The Spanish imperial eagle is considered one of the rarest raptors in the world (Vulnerable in the IUCN Red List; BirdLife International, 2013) with 407 breeding pairs in 2013 (National Working Group, 2013). It is a large (2500–3500 g), long-lived endemic bird of prey from the Iberian Peninsula. The species is monogamous, sedentary and territorial, with a low annual productivity of 0.75 chicks/pair (Ferrer & Calderón, 1990). Although the species typically acquires adult plumage from the age of 5 years on average, individuals reach sexual maturity before then and can breed at 3 or even, but rarely, 2