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Sex-specific dispersal responses to inbreeding and kinship

Loïc A. Hardouin [a, b, *, †], Pierre Legagneux [c], Yves Hingrat [a, d], Alexandre Robert [b, †]

[a] Emirates Centre for Wildlife Propagation, Missour, Morocco
[b] Centre d'Ecologie et des Sciences de la Conservation (CESCO), UMR 7204, Sorbonne Universités, MNHN, CNRS, UPMC, CP51, Paris, France
[c] Canada Research Chair in Conservation of Northern Ecosystems and Centre d'études nordiques, Université du Québec à Rimouski, Rimouski, Québec, Canada
[d] RENECO for Wildlife Preservation, Abu Dhabi, U.A.E.

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Dispersal is a fundamental life history trait in animals that governs species distribution and population dynamics. However, the key mechanisms that promote dispersal are difficult to identify and remain unclear for most free-living organisms. Inbreeding avoidance is commonly invoked as a major driver of dispersal, but inbreeding can also be favoured by kin selection if inbred mating increases the inclusive fitness of the parents. Here, we investigated the relationships between inbreeding, kinship, sex and dispersal propensity in a carefully monitored population of captive-bred North African houbara bustards, *Chlamydotis undulata*, in Morocco. Over 8 years, 79 houbaras (of known pedigree) were released into the wild and radiotracked over a large spatial scale until settlement. Using several dispersal metrics, we confirmed that both inbreeding and kinship affect dispersal, with differential effects depending on sex. In males, settlement distance was associated with movements soon after release, whereas in females, later movements determined settlement distance. When released with close kin, females in female-biased release groups covered greater distances than when released with distant kin, suggesting that intrasexual kin competition governs dispersal in females. In males, dispersal was reduced when associated with genetically close relatives but increased with the individual coefficient of inbreeding. Overall, our results highlight complex (but consistent with theoretical expectations) sex differences in movement patterns that depend on inbreeding, kinship, group structure, type of movement and stage of the dispersal process.

Dispersal is a key life history trait that influences a species' range (Kirkpatrick & Barton, 1997) and the dynamics and genetics of populations (Clobert, Danchin, Dhondt, & Nichols, 2001; Stamps, 2001) and metapopulations (Robert, 2009). Although dispersal confers several benefits to individuals (Nevoux, Arlt, Nicoll, Jones, & Norris, 2013) and populations (Pannell & Charlesworth, 2000; Robert, 2011; Tallmon, Luikart, & Waples, 2004), it can also impose costs (Bonte et al., 2012; Ronce & Kirkpatrick, 2001). The decision to disperse through an unknown habitat can be risky because it reduces the time and energy available for self-maintenance (Cote & Clobert, 2010). Many studies have examined the costs of dispersal (reviewed in Bonte et al., 2012), but empirical studies investigating the benefits of dispersal are relatively scarce. Dispersal can be affected by multiple intrinsic and extrinsic factors (Dobson & Jones, 1985), such as body condition, inbreeding avoidance, mate competition, resource competition and habitat characteristics (Bowler & Benton, 2005; Clobert et al., 2001).

Intraspecific competition (between related or unrelated conspecifics) and inbreeding avoidance are the two major processes invoked to explain the evolution of dispersal (Ronce, 2007). Theoretically, inbreeding avoidance should favour divergence in sex-specific dispersal rates (Gandon, 1999); however, a theoretical framework is required that can account for the interacting effects of inbreeding depression, kin competition (competition among kin for mates or resources) and kin cooperation (cooperation among kin to acquire or defend mates or resources) on sex-biased dispersal (Lawson Handley & Perrin, 2007). Although studies have reported evidence for inbreeding avoidance through mate choice (Kempenaers, 2007, but see Keller & Arcese, 1998), certain authors consider sex-biased dispersal to be the main mechanism that reduces the risk of inbreeding (Gandon, 1999; Lebigre, Alatalo, & Siitari, 2010; Motro, 1991, 1994; Perrin & Mazalov, 1999, 2000).

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[*] Correspondence: L. A. Hardouin, Centre d'Ecologie et des Sciences de la Conservation (CESCO), UMR 7204, Sorbonne Universités, MNHN, CNRS, UPMC, CP51, 55 Rue Buffon, 75005, Paris, France.
E-mail address: loic.hardouin@gmail.com (L. A. Hardouin).
[†] These authors contributed equally to this paper.

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However, the evolution of sex-biased dispersal in response to inbreeding depends on the overall effects of inbreeding on fitness, which depend on the magnitude of inbreeding depression (Gandon, 1999). Less intuitively, inbreeding may also be favoured by kin selection (Kokko & Ots, 2006) if inbred mating increases the inclusive fitness of the parents (i.e. an individual who mates with a relative will help that relative to spread identical genes by descent, see Kokko & Ots, 2006). Current theory provides no clear predictions of the appropriateness of avoiding, tolerating or pursuing inbreeding (Szulkin, Stopher, Pemberton, & Reid, 2012), making general predictions of sex-biased dispersal patterns difficult and emphasizing the need for empirical studies on this topic.

Population genetic theory indicates that the benefit of interpopulation crosses (i.e. heterosis) increases when populations have small effective sizes and high average inbreeding coefficients (e.g. Whitlock, Ingvarsson, & Hatfield, 2000). If inbreeding partially results from small population size (e.g. Keller & Waller, 2002), the individual inbreeding coefficient of an individual is expected to reflect the average level of inbreeding in its population (and the potential benefit of dispersal, e.g. Tallmon, Luikart, & Waples, 2004). Based on this reasoning, we assumed that more inbred individuals (i.e. individuals exhibiting high individual inbreeding coefficients, equal to the kinship of their parents) will be more prone to disperse. Although no empirical study has investigated the relationship between the individual inbreeding coefficient and propensity to disperse, positive relationships between inbreeding and dispersal have been demonstrated at the population level (e.g. Willi & Fischer, 2005), in agreement with theory (Ronce, 2007; Whitlock et al., 2000).

Despite broad interest in dispersal in the evolutionary ecology literature, quantitative, individual-based approaches to animal dispersal and movement remain rare (e.g. Nevoux et al., 2013), mainly because of logistical and spatial-scale limitations (Doligez & Pärt, 2008). Compared with a dispersers versus nondispersers dichotomy, distances covered by individuals (e.g. Baguette & Schtickzelle, 2006; Murrell, Travis, & Dytham, 2002) have strong evolutionary ecology implications because (1) in most noncolonial species, individuals do not remain at their exact birthplace, making the distinction between dispersers and nondispersers somewhat arbitrary, (2) although movement is only one component of the entire dispersal process, individual movement is shaped not only by the dispersal strategy but also by factors such as exploratory behaviour and individual morphology (Cote, Clobert, Brodin, Fogarty, & Sih, 2010) and (3) the distributions and costs of dispersal distances have major implications for the genetics and dynamics of metapopulations (Johst, Brandl, & Eber, 2002; Robert, 2009).

In the present study, we examined the patterns and strategies of natal dispersal and movement characteristics of both sexes of captive-bred North African houbara bustards, *Chlamydotis undulata* (of known genetic pedigree) released into the wild and tracked until their first breeding event. Although dispersal is not fully comparable between wild-born and captive-bred individuals (i.e. the behaviour of captive-bred individuals can be affected by captive breeding and release protocol factors, including the timing of releases and the density of birds at release; e.g. Le Gouar, Mihoub, & Sarrazin, 2012), the evolutionary mechanisms that drive dispersal may persist in captive-bred generations (e.g. the repeatability and heritability of exploratory behaviour: Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; the consistency of individual personality across captive and wild environments: Herborn et al., 2010; sex-biased dispersal in wild-born and captive-bred houbaras: Hardouin et al., 2012, 2014). Captive-bred individuals provide a quasiexperimental opportunity to investigate the effects of environmental (e.g. density and sex ratio of the release group) and individual factors (e.g. sex, kinship, inbreeding and body condition) on dispersal. Several authors have emphasized that the factors affecting dispersal decisions are likely to differ across the three stages of dispersal (departure, movement, settlement, Bowler & Benton, 2005; Clobert, Galliard, Cote, Meylan, & Massot, 2009; Cote et al., 2010). Monitoring the same individual across these three stages remains a very difficult technical problem. To assess whether the movement patterns of males and females vary throughout the dispersal process, we divided the movement into two distinct (early and late) independent movement phases. Assuming that movements during the early and late phases are affected by different extrinsic factors (respectively related to the departure and settlement stages of dispersal, Clobert et al., 2009), we anticipated distinct movement patterns between the two phases. Another nonmutually exclusive hypothesis is that a positive or negative correlation between the early and late phases may occur within individuals if both phases are similarly affected by intrinsic factors (physiology, morphology, personality, Cote et al., 2010). Thus, our study was focused on the potential differences in male and female movement patterns (distances, early- and late-phase contributions to overall movement) and potential contrasting responses to inbreeding and kinship (Lebigre et al., 2010). For the entire dispersal process, we expected that (1) interindividual similarity in movement patterns would increase with genetic relatedness and (2) dispersal distance would increase with both individual inbreeding and average kinship with the release group (Ronce, 2007).

METHODS

Study Species, Study Sites and Radiotracking Procedure

The North African houbara bustard exhibits an exploded lek sociosexual structure (Hingrat, Saint Jalme, Chalah, Orhant, & Lacroix, 2008). In a lek mating system males defend small, clustered courts that females visit solely for mating (Höglund & Alatalo, 1995). In an exploded lek, males can be separated by considerable distances. In such a lower level of aggregation, females can potentially forage and even nest within a lek (Morales, Jiguet, & Arroyo, 2001). Houbaras usually inhabit semiarid desert areas occupied by subshrub vegetation (Hingrat, Saint Jalme, Ysnel, Le Nuz, & Lacroix, 2007). This study was conducted from 2001 to 2009 in eastern Morocco (2°13′W, 33°55′N), where the Emirates Centre for Wildlife Propagation (ECWP) released 20 652 houbaras onto different release sites. The released birds were reared at the ECWP's captive-breeding facilities in Missour (4°5′W, 33°0′N) and Enjil (4°32′W, 33°6′N). Individuals of known pedigree were bred via artificial insemination. Genetic management consisted of equalizing the founders' genetic contributions and avoiding inbreeding (Chargé et al., 2014). Prior to release, each individual was caught by an expert bird keeper, weighed (±1 g), blood sampled (for molecular sexing purposes) and tagged. From 2001 to 2009, 957 individuals were fitted with necklace battery-powered VHF transmitters (see Ethical note below). Individuals were monitored at least bimonthly from the ground and by aerial telemetry (see Hingrat et al., 2004 and Hardouin et al., 2014). Bird locations were recorded via GPS and estimated with an accuracy of ±20 m by terrestrial telemetry and ±150 m by aerial telemetry.

Ethical Note

The birds used in the present study were bred in captivity and released into the wild in agreement with Moroccan authorities: Ministère de l'Agriculture, Développement Rural et des Pêches Maritimes, Direction Provinciale de l'Agriculture de Boulemane,