Sex-specific dispersal responses to inbreeding and kinship

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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, Arit, 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 conspecics) 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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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. Kellner & 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, & Waller, 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 (Ronc, 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 & Part, 2008). Compared with a dispersers versus nondispersers dichotomy, distances covered by individuals (e.g. Baguette & Schtickzelle, 2006; Murrell, Travis, & Dytham, 2002) have shown 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 el al., 2012, 2014). Captive-bred individuals provide a quasieperimental 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 (Ronc, 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 (Hoglund & 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 semi-arid desert areas occupied by shrub 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 bled via artificial insemination. Genetic management consisted of equalizing the founders’ genetic contributions and avoiding inbreeding (Charg 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,
prior to 2006, houbaras were tagged on the left tarsus with an aluminium ring (12.5 mm diameter) displaying a unique ID number and ECWP address. Starting in 2006, all individuals were subcutaneously microchipped (Trovan ID100 Implantable Transponder, Dorset Group, Aalten, The Netherlands) in the right tibia (injected via a single-use sterilized 25 gauge insulin syringe and stored in 100% ethanol). Microchips were implanted 1 month before release to control for any adverse effects such as infection, migration in the body or rejection. The release sites were selected for their high habitat suitability (see Monnet, Hardouin, Hingrat, Robert, & Jiguet, 2015). All of the released birds were transported in groups of six in crates used in animal production (model size 77 x 57 x 29 cm, Union Franco Suisse SARL, Evreux, France, http://www.ufs-aviculture.fr/caisse-a-volailles/866-cageot-2-portes-77x57x29-cm-3700724608595.html). The mean time of transport (by car or truck) from the aviaries to the release site was 105 min. Over the last 15 years, 80 000 houbaras have been released, and only one died during transport. Monitored individuals were fitted with a necklace power-powered VHF transmitters weighing 11 g or 20 g (models RI-2B-M and RI-2D-M respectively, Holohil System Ltd., Ontario, Canada), depending on their body mass. The lightest bird equipped with the 11 g transmitter weighed 640 g (transmitter weight equal to 1.7% of the body mass) and the lightest bird equipped with the 20 g transmitter weighed 900 g (transmitter weight equal to 2.2% of the body mass); thus, the transmitter weighed less than 3% of the bird’s body mass (as recommended by Withey, Bloxton, & Marzluff, 2001). Any potential problems with the radiocollar mounting were first tested in captivity. The collars were loose enough to allow the houbara to swallow large prey but tight enough so that the head of the bird could not pass through it. The feathers at the bottom of the neck in both sexes were long and were loose enough to allow the houbara to swallow large prey but tight enough (approximately 300 m) to continuously monitor the individuals that were monitored regularly (i.e. every 9 days on average between locations and 40 ± 20 locations on average per individual) from their release to first settlement were considered. Once they display in a lek, male houbaras are known to remain at the same site for years (breeding dispersal in houbara is female biased; Hardouin & Hingrat, n.d.); therefore, we assumed that displaying behaviour was a reliable proxy of natal dispersal in male houbaras. Although displaying behaviour serves only as evidence of sexual maturity and not reproduction, we use the term ‘settlement’ here for both males and females.

Bird Settlement

In total, 157 individuals (33 males and 124 females) were recorded breeding (by direct observation of nesting/brooding by females) or displaying (by males; hereafter, settlement). We conservatively ascertained that these events could indicate the first settlement of the individuals. Thus, (1) females that were unobserved for 1 month or longer between February and April (females’ breeding season) were excluded from the analysis because they might have engaged in reproduction (N=62 females were excluded) and (2) males that were unobserved between January and May (i.e. during the display period for males) were not included (N=16 males excluded). In total, 79 individuals (17 males and 62 females) were considered and only individuals that were monitored regularly (i.e. every 9 ± 4 days on average over 3 years) and without any evidence of sexual maturity and not reproduction, we use the term ‘settlement’ here for both males and females.

Dispersal Movement Parameters

To quantify and characterize the movements of individuals, we used two different metrics and three main distance parameters to compare sex-specific responses to kinship and inbreeding. Metric 1 is the linear distance between an individual’s release site to a given location (Fig. 1) and is generally associated with geographical and environmental distances (Nekola & White, 1999), genetic isolation (Wright, 1943) and reduced competition, with or without respect to kinship (Lambin, Aars, & Pietrney, 2001; Ronce, 2007). Metric 2 is the distance between two successive locations (Hardouin et al., 2012, 2014, 2015). Sixty-five birds were recaptured in the wild before the end of their transmitters’ life span (1–3 years) and fitted with a new transmitter (20 g model RI-2D-M). Two trapping methods were used: snares at a male display site around a stuffed dummy female houbara from the ECWP captive breeding for trapping males or snares around a nest or wild-caught chicks for trapping females (Hardouin et al., 2012; Hingrat et al., 2004; Seddon, Launay, Van Heezik, & Al Bowardi, 1999). In the latter method, all of the chicks in the nest were captured (to avoid abandonment by the female) by hand and restrained in a fabric bag large enough to contain all of the chicks, and this bag was placed under a bush surrounded by snares. The trapped chicks called and attracted their mother. If the female did not return after 15 min, the trapping was cancelled and the chicks were released. The fieldworkers monitored the retrieval of the mother via telescope. No chicks were abandoned. For both male and female captures, fieldworkers remained close enough (approximately 300 m) to continuously monitor the individuals (targeted male or female and/or chicks in the bag) and snares via telescope until the end of the capture session. The snares were not left in place without surveillance. They were approximately 8–10 cm in diameter and set on the ground. Because houbaras are approximately 30–40 cm tall, they were always caught by the leg, not by the neck or wing, and nontargeted species were not captured. The captured houbaras were processed within several seconds of capture. A hood was placed over the birds’ heads throughout the handling process to keep them calm. None of the birds captured in this study were injured or obviously stressed by the capture. Note that from 1996 to 2014, the ECWP trapped 377 females with snares and experienced one death caused by stress and one caused by trauma (during bird handling). The ECWP also trapped 501 males and experienced two deaths caused by stress (myopathy). Thus, death occurred in 0.45% of cases. In addition, several birds exhibited limping after trapping and one had a skin injury (on a leg); however, these individuals recovered quickly, and none died.
is the release event, and location at time $t_x$ where $x$ corresponds to the number of the location), cumulative distance (CD; the full path distance between the location at $t_0$ and the location at $t_x$ and median of $d$ (direct distances between the location at $t_0$ and any of the locations $t_1$ to $t_x$) to obtain the net dispersal distance (NDD). Note that the time between locations can therefore vary. For details, refer to Hardouin et al. (2012).

From metric 1, we extracted the median net dispersal distance (NDD; repeated measures of metric 1 along the track of an individual) and the settlement distance (distance from the release site to the first nest or display location). From metric 2, we extracted the cumulative distance (CD), i.e. the full path distance covered by an individual between the release and settlement sites (Fig. 1). Although the CD and NDD were correlated ($r = 0.42$), they provide different information about dispersal movement. Whereas NDD is related to the propensity to disperse, CD is also related to the amount of exploratory movement undertaken on the route (Hardouin et al., 2012, 2014). To assess intraindividual variation in movement along the dispersal process, the entire dispersal movement was divided into two stages: early and late dispersal. Movement patterns during the early phase should be influenced by factors related to conditions at the time of departure, such as the presence, density and quality of members of the release group, whereas the late phase should be influenced by factors related to the settlement phase, such as sex-specific habitat requirements for reproduction. We calculated the rate of movement (m/day) during the early (i.e. from release until 50% of the time before settlement had elapsed) and late (i.e. from the 50% point until the effective time of settlement) stages of dispersal based on the NDD and CD. Finally, we used these four parameters to assess whether different patterns of dispersal occurred between the early and late stages by calculating the early-to-late-stage ratios of the median net dispersal ($NDD_{0.50}/NDD_{50-100}$) and cumulative distance ($CD_{0.50}/CD_{50-100}$). These ratios were log transformed to meet normality and homoscedasticity assumptions.

**Characteristics of Released Birds**

The 79 individuals (62 females and 17 males) were released at an average age of $269 \pm 92$ (mean $\pm$ SE) days and a body weight of $1128 \pm 140$ g (females) and $1675 \pm 164$ g (males) (release group size $= 55 \pm 79$, range 6–498). For each individual, an index of body condition was extracted using the residuals of the regression of body weight as a function of release age (body weight linearly increased with age at the time of release: inflexion point of the growth curve $= 44 \pm 8$ days for males and $38 \pm 6$ days for females), with sex as a covariate ($F_{2,76} = 107.6$, adjusted $R^2 = 0.73$, $P < 0.001$; Hardouin et al., 2012). Males and females settled an average of $527 \pm 283$ and $346 \pm 234$ days after release (time of settlement), respectively.

Based on the available pedigree information on the captive population ($N = 45163$ over the 1996–2009 period), the kinship coefficients of all pairs of released individuals considered in our sample of release events ($N = 5147$ individuals) and individual inbreeding coefficients were calculated using PEDIG software (Boichard, 2002). The inbreeding coefficient of an individual is defined as the probability that the two alleles of a locus are identical (derived from the same ancestral gene), and the kinship coefficient between two individuals is the probability that two alleles sampled at random from each individual are identical. For each of the 79 continuously monitored individuals, in addition to the inbreeding coefficient, we derived an average kinship coefficient between the individual and the rest of its release group.

**Statistical Analysis**

Because patterns of dispersal may have heritable components, next of kin might exhibit more similar patterns of dispersal distances than distant kin or unrelated individuals (e.g. Doligez, Gustafsson, & Part, 2009). To investigate similarities in dispersal or morphology components between kin, we constructed a genetic distance matrix (i.e. $1 –$ kinship) and performed Mantel tests on NDD, CD and body condition (genetic distance matrix versus Euclidean distance matrix or the matrix of differences in body condition between individuals).
We performed sex-specific analyses of movement parameters during the full dispersal process (NDD and CD) as well as the early and late stages of dispersal. Our main approach was based on linear mixed-effects modelling and the response of male and female dispersal metrics (NDD and CD) to inbreeding and kinship. The initial global model included the time of settlement and two second-order interactions: (1) individual inbreeding and intrarelase group kinship and (2) intrarelase group kinship, sex, and sex ratios. This global model revealed significant interactions primarily according to sex; therefore, to investigate sex-specific responses, two submodels (one for each sex) were performed. Both included the time of settlement and two first-order interactions: (1) individual inbreeding and intrarelase group kinship and (2) intrarelase group kinship and sex ratio. For all of the models, two random-slope effects were retained: year of settlement and release site, which account for the variability between years and between release sites, respectively. Note that preliminary analyses were performed on the data; in particular the release group size (as a proxy of the competition level) had no influence on both metrics (see Hardouin et al., 2014 for similar results) either as a single factor or in interaction with other factors (including sex ratio and kinship).

For all model sets, we started from the global model, comparing its performance via the corrected Akaike’s information criterion, AICc, to all submodel combinations, the latter of which were generated automatically using the function ‘dredge’ (library ‘MuMIn’, Barton, 2013). NDD was log transformed and CD was square-root transformed to satisfy normality and homoscedasticity assumptions. The freeware R 2.10.1 (R Development Core Team, 2009) and the libraries lme4 (Bates & Maechler, 2010) and languageR (Baayen, 2009) were used for statistical analysis.

**RESULTS**

We did not observe any similarity in movement components among kin (all $P > 0.05$; Mantel tests). However, NDD was sex biased (Fig. 2, Table 1), with males having a higher propensity to disperse and settle further from the release point than females. This overall sex difference was explained only by the early stage of dispersal (Table 1, Appendix Fig. A1). In contrast to net distance, no sex bias was observed in CD (Table 1, Fig. 2), although the movement rate based on CD was significantly higher in females than in males in the late stage of dispersal (Table 1).

We observed a strong decrease in the movement rate from the early to the late stage of dispersal in males; in females, the

![Figure 2](image-url)
movement rate tended to be stable or increase (Table 1). In addition, we observed only one weak significant correlation in movement rates (based on the settlement distance) in females between the early and late stages at the intraindividual level (Table 1). Finally, the relative contributions of the early and late stages of dispersal to the overall distance covered were strongly related to the interaction between settlement distance and sex. Males that dispersed further tended to cover longer distances during the early stage than during the late stage, whereas females that dispersed further covered longer distances in the late stage than in the early stage (interaction settlement distance × sex: estimate ± SE = 5 × 10⁻² ± 2 × 10⁻¹, P = 0.02; Fig. 3).

We then focused on responses to inbreeding and kinship and specifically tested the effects of inbreeding coefficient, intrarelase group kinship coefficient, sex ratio, sex, time of settlement and interactions on NDD and CD (see Methods). The selected models of NDD (R² = 0.34, χ² null = 17.3, df = 4, P = 0.001; Appendix Table A1) and CD (R² = 0.80, χ² null = 85.7, df = 8, P < 0.001; Appendix Table A1) both revealed highly significant interactions between individual inbreeding and sex (Appendix Table A1). For CD, the selected model also revealed an interaction between the average kinship of the focal individual and its release group and the sex ratio of the release group (Appendix Table A1). As most of the interaction terms involved sex, we employed one submodel for each sex, starting with the full model. In all models (except for NDD in males), time of settlement was positively and significantly related to NDD and CD (see Appendix Table A1 for the global model and Table 2 for sex-specific models).

The analysis of the submodels revealed that the average kinship of the focal individual to its release group had significant and opposite effects in the two sexes. In males, CD was negatively related to kinship with the release group (i.e. when released with close kin, males tended to cover shorter distances than when released with distant kin; Table 2, Appendix Fig. A2). In females, the opposite relationship between CD and kinship was observed, although this relationship was dependent on the sex ratio of the release group (Table 2): kinship positively influenced female dispersal in female-biased release groups only (Fig. 4). Finally, individual inbreeding had a positive and significant effect on NDD (Table 2, Fig. 5) and CD (Table 2) in males only, with the most highly inbred males dispersing the furthest.

**DISCUSSION**

Overall, our results demonstrated (1) sex differences in the patterns of movement between the early and late phases of dispersal, with males moving primarily during the early phase and females during the late phase, (2) contrasting sex-specific patterns of NDD and CD and (3) independent and contrasting effects of kinship and individual inbreeding levels in male and female dispersal. In males, dispersal distance was positively related to individual inbreeding, whereas in females, particularly when the release group was female biased, dispersal distance increased among focal individuals released with close kin, compared to those released with more distantly related kin.

**Sex-biased Dispersal and Dispersal Metrics**

We did not observe a strong significant correlation at the intraindividual level between the early and late phases of movement within each sex. However, in accordance with our predictions, we observed strong differences in dispersal patterns between the sexes. First, although males did not travel further than females (in terms of CD), their net distance covered (in terms of geographical distance from their release site) was twice that of females. This finding contrasts with the general pattern of female-biased dispersal observed in most avian species (Clarke, Sæther, & Røskaft, 1997; Greenwood & Harvey, 1982) but is consistent with the pattern observed previously in wild houbaras (Hardouin et al., 2012) and in the great bustard, Otis tarda (Alonso, Martín, Alonso, & Morales, 1998). Unfortunately, to our knowledge, great bustards and houbara bustards are the only two birds that exhibit an exploded lek mating system for which natal dispersal biases have been investigated, thus making generalizations difficult. Nevertheless, this lekking structure might have played an important role in the evolution of male-biased patterns of dispersal (Martín et al., 2008). However, the relationship between kinship, inbreeding and sex-biased dispersal remains unclear (Lebigre et al., 2010).

Second, our analysis uncovered strong qualitative differences between the sexes: males covered greater net distances in the early phase of movement and females tended to accelerate their rate of movement during the late phase of movement. As a result, the overall variation in settlement distance among individuals within each sex was related to distinct phases of the movement process in the two sexes: the early phase for males and the late phase for females. This pattern is similar to that observed in Belding’s ground squirrel, Urocitellus beldingi, a mammal exhibiting both polyandry and polygyny (Smale, Nunes, & Holekamp, 1997); in this species, males disperse further than females and arrive at their breeding grounds 2 years before sexual maturity.

Although most predictions of the evolution of dispersal in the theoretical literature address the rate and not the timing or distance of dispersal (Lawson Handley & Perrin, 2007), most classic hypotheses of dispersal rates in patchy habitats are generalized to movement patterns with potential application to noncolonial species living in continuous habitats (e.g. Debarre & Gandon, 2010). Our results revealed that dispersal distance and timing should be considered in tandem in future research because distinct temporal patterns of movement can occur during dispersal that may have major implications for the genetics and dynamics of metapopulations (Baguette & Schtickzelle, 2006; Johst et al., 2002; Murrell et al., 2002).

**Kinship and Sex-biased Dispersal**

Current theory suggests that the strength of selection for inbreeding avoidance strategies (e.g. through dispersal or mate
choice) might depend on the costs of avoiding inbreeding, e.g. the costs of dispersal or mating with kin (Bonte et al., 2012). A recent study of the houbara bustard (Hardouin et al., 2012) indicated that (1) dispersal is indeed costly (in terms of survival), (2) this cost is higher for males than for females and (3) this higher cost to males is not due to sex differences in the costs per unit distance travelled but rather to the longer distances covered by males. These findings indicate that the longer distances covered by males are not merely the result of their adjustment to lower costs but indicate different benefits of dispersal and different strategies between the sexes.

Sex-biased dispersal (Greenwood, 1980) is common and is usually considered one mechanism of inbreeding avoidance that evolves in response to inbreeding depression (Clutton-Brock, 1989; Pusey, 1987). However, recent results and reviews (Szulkin et al., 2012) have suggested that animals may avoid, tolerate or pursue inbreeding, depending primarily on the relative strengths of two opposing forces: kin selection (Kokko & Otis, 2006) and inbreeding depression (Keller & Waller, 2002). Based on this assumption, strategies are expected to vary among species depending on the potential benefits of kin selection and the deleterious effects of inbreeding. In species in which the two sexes invest differentially in reproductive events, such as the houbara bustard, male and female strategies involving inbreeding may differ or even oppose each other. For example, in polygynous/promiscuous species, males may tolerate inbreeding mating, whereas females will avoid it (Pizzari, Lø, & Cornwallis, 2004).

In addition to revealing such strongly divergent strategies between the sexes, our results indicate that when released with close kin, females cover greater distances (both net and cumulative), particularly when the release group is female biased, suggesting an influence of intrasexual kin competition (e.g. Gandon, 1999).

The houbara bustard mating system meets the definition of exploded leks (leks with large intermale distances), in which males exhibit high fidelity to their display areas between years (Hingrat et al., 2008) and an absence of male reproductive skew (i.e. low variance in reproductive success; Lesobre et al., 2010); these features may favour the cooperation of related males during reproduction. Although there is no clear evidence of male aggregation with close kin in leks (Lesobre, 2008), genetic relatedness measured at the population level is higher in males than in females (Lesobre et al., 2010), suggesting higher philopatry in males. This result apparently contradicts the greater dispersal distance of males observed in several studies (e.g. Spong & Creel, 2001), including the present one (Hardouin et al., 2012, 2014). However, our results indicate that, although males disperse further than females on average, they disperse to a lesser extent when genetically related to their group.

### Individual Inbreeding and Sex-biased Dispersal

Despite a relatively small sample size (especially for males), we found that male dispersal distance increased with the individual inbreeding coefficient (independent of kinship). We are unaware of any other empirical study reporting nonrandom dispersal with
respect to individual inbreeding. Indeed, previous studies of the importance of kinship in individual dispersal decisions have largely focused on nonrandom mate choice or the difference in dispersal strategy between a focal individual and the rest of the release group. From a metapopulation perspective, in an approximately panmictic local population (i.e. under random mating), the inbreeding coefficient of a particular individual should reflect the local population level of inbreeding. Thus, the inbreeding coefficient may be considered a reliable internal indicator of either a reduction in the local population fitness or the average level of kinship with the other individuals in the local population (both parameters are expected to increase with isolation and decreasing local population size, Whitlock et al., 2000). In this context, dispersal could improve individual fitness through heterosis (see studies on population rescue effects, e.g. Madsen, Uijvari, & Olsson, 2004; Tallmon et al., 2004; Willi & Fischer, 2005; and theoretical approaches in Roze & Rousset, 2009; Whitlock et al., 2000). Alternatively, changes in dispersal patterns in inbred individuals may be direct results of inbreeding depression (Keller & Waller, 2002), which has been shown to induce behavioural responses in several bird species, such as changes in exploratory behaviour patterns (Garten, 1977) or a reduced ability to compete for territories (Höglund et al., 2002), leading inbred individuals to disperse further.

**Conclusion**

Existing eco-evolutionary literature emphasizes the complexity of the dispersal behaviour process itself (Clobert et al., 2001) as well as the diversity of its ultimate causes (Ronce, 2007). Our results further emphasize this complexity in an in situ bird population study by revealing separate and interaction effects of inbreeding, kinship, group structure and sex in different types of dispersal movement (cumulative versus net distance). Overall, our results are in agreement with the most popular and general evolutionary movement (cumulative versus net distance). Overall, our results are leading inbred individuals to disperse further.

**References**


APPENDIX

Table A1

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<th>Effects of factors on NDD and CD in houbarabs</th>
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<tbody>
<tr>
<td>Net dispersal distance</td>
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<tr>
<td>Estimation±SE</td>
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<td>P</td>
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<tr>
<td>Inbreeding group kinship</td>
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<td>Inbreeding</td>
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<td>Time of settlement</td>
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<td>Sex</td>
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<td>Inbreeding group sex ratio</td>
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<td>Kinship sex</td>
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Starting full models included time of settlement and second-order interactions: (1) individual inbreeding, inbreeding group kinship, sex and (2) inbreeding group kinship and sex, and the. The results of the selected linear mixed-effects model are given, with NDD (R² = 0.34) as the response variable: sex, individual inbreeding and time of settlement and first-order interaction as explanatory variables. With CD (R² = 0.80) as response variable: sex, individual inbreeding, inbreeding group kinship, time of settlement and first-order interactions. Parameter estimates (i.e., fixed-effects estimates) SE and P values for the fixed-effects table are given.
Figure A1. Box plot of the two metrics (NDD and CD) by sex and early/late phases of dispersal. Boxes show the median (straight line within the box), mean (dashed line), 25th and 75th percentiles. Whiskers (error bars) indicate the 10th and 90th percentiles. Black dots refer to the outliers.

Figure A2. Effect of intrarelease group kinship coefficient on cumulative distances. Dashed line represents the predicted values of the significant relationship in males. Males are represented by black squares, females by white circles. Log-transformed data were back-transformed.