



Determinants and costs of natal dispersal in a lekking species

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Avoidance of competition and inbreeding have been invoked as the major ultimate causes of natal dispersal, but proximate factors such as sex, body condition or birth date can also be important. Natal dispersal is expected to be of particular importance to understanding the ecological and evolutionary implications of dispersal strategies, since 1) numerous evidences suggest that individual differences in dispersal strategies are expressed early in life (i.e. at the onset of dispersal movement), 2) ultimate and proximate factors are more likely to act during this stage and 3) this stage is associated with the highest mortality rates in most vertebrates. We analysed the natal dispersal (hereafter, dispersal) behaviour in 100 marked individuals of a lekking species, the North African houbara bustards *Chlamydotis undulata undulata*, during four years. We investigated the effects of proximate factors on dispersal pattern and distance, as well as the mortality cost associated with movement using multievent models, allowing uncertainty in sex assignment and mixture of live recaptures and dead recoveries. Overall, males exhibited longer dispersal distances than females, contrary to the common pattern in birds. Moreover, males in poorer body condition moved further than those in better condition, whereas distance was independent of body condition in females. Finally, survival rates during dispersal were lower for females than for males and were negatively correlated with the distances covered with a similar distance-survival slope in the two sexes. Collectively, our results suggest that 1) there is substantial dispersal cost in both sexes, 2) dispersal is strongly male-biased, 3) this bias is unlikely to be explained by differential movement costs of each sex, and 4) dispersal differences found across different categories of individuals are in broad agreement with both the inbreeding avoidance and intraspecific competition mechanisms for dispersal.

Dispersal directly affects the dynamics (Hanski 2001) and genetic diversity (Tallmon et al. 2005) of local populations, as well as the persistence (Hanski 1991) and genetic structure (Pannell and Charlesworth 2000) of metapopulations through effects on source–sink dynamics (Brawn and Robinson 1996), invasion and colonization (Shigesada et al. 1995), and gene flow. Besides these direct effects, dispersal rates and patterns are associated with two major components of fitness: reproduction and survival (Clobert et al. 2001), themselves strongly influencing species dynamics and having many implications in both evolutionary and conservation biology. Dispersal involves three successive behavioural stages: departure from the current patch, movement between patches (transfer) and settlement in a new patch (Bonte et al. 2011). Gaining greater knowledge of the factors affecting these three stages is critical in our understanding of the ecological and evolutionary consequences of dispersal (Ronce 2007, Clobert et al. 2009).

Numerous lines of evidence suggest that individual differences in dispersal strategies are expressed as early as the

pre-departure stage (i.e. before the start of dispersal; Bonte et al. 2011) and have a genetic basis (Dingemanse et al. 2003, Cote et al. 2010). Moreover, even though dispersal might be influenced by ultimate (inbreeding avoidance and intraspecific competition, Pusey 1987, Pusey and Wolf 1996) and proximate (e.g. sex, body condition at fledging, hatching date) factors, these factors appear most likely to act at the onset of dispersal movement (Haughland and Larsen 2004, Martín et al. 2008), while the settlement may be more driven by other environmental or social cues, such as nesting site or mate availability, habitat preference and quality (Verhulst et al. 1997, Clobert et al. 2009, Delgado et al. 2010).

During dispersal, individuals have to cope with new surroundings in which they must find food and avoid predators (Wiens et al. 2006, Bonte et al. 2011, Eraud et al. 2011). Thus, the onset of dispersal is generally associated with high mortality rates (Baker 1993), due to predation, stress, energy depletion, and more generally the lack of familiarity with novel environments (McNamara and

Houston 1990, Pärt 1995). Therefore, individuals moving longer distances and/or with a pronounced exploratory behaviour during dispersal may suffer higher dispersal cost in the form of especially low survival (Yoder et al. 2004). Relating mortality events to dispersal movements per se can provide direct estimates of the mortality that is associated with dispersal (Yoder et al. 2004). Overall, studying both the proximate factors associated with these movements and their consequence on survival can be particularly informative and bring new insights into the dynamics and balance of the costs and benefits of dispersal process (Yoder et al. 2004, Clobert et al. 2009).

We analysed a large dataset detailing the dispersal movements of juvenile North African houbara bustards *Chlamydotis undulata undulata*. Our analysis was restricted to natal dispersal (i.e. dispersal from the natal to the first breeding site, hereafter simply referred to as dispersal). One hundred juveniles were individually monitored by telemetry at a large spatial scale in eastern Morocco. We investigated both the determinants and the cost, in terms of survival, of dispersal. Our general purpose was to test whether differential selective pressures shape different patterns of dispersal between sexes. A lekking species with strong sex-specific breeding habitat requirements (Hingrat et al. 2008) constitutes an ideal model for studying such aspects of dispersal.

We used two main metrics: the net dispersal distance (straight line between the departure point and individual location after movement) and the cumulative distance (overall path distance covered by the individual between these two points as a proxy of both the propensity to disperse and the exploratory behaviour). From these metrics, we produced six parameters characterising dispersal movements and tested the effects of the following proximate factors: 1) sex, 2) body condition, and 3) hatching date. We then estimated survival rates according to sex and age-classes and examined the cost of dispersal. We first hypothesized that the net dispersal distance will be related to individual reproductive decisions, whereas the cumulative distance is a compound of individual reproductive and survival decisions. We also hypothesised that movement patterns should be influenced by sex-specific dispersal strategies and by the costs and benefits associated with these strategies. In particular, we predicted that 1) dispersal is sex-biased (inbreeding avoidance hypothesis; Perrin and Mazalov 1999, 2000). In birds, female-biased dispersal is generally observed in non-lekking species (Greenwood and Harvey 1982), however owing to the high heterogeneity of sex-biased dispersal patterns observed among lekking bird species, we do not make prediction on which sex might disperse further. 2) If dispersal is sex-biased, stronger competition should be observed in the sex dispersing. The most competitive individuals (e.g. using a body condition index as a proxy) can benefit by remaining close to the natal area and expel less competitive individuals, resulting in shorter dispersal distances in the most competitive individuals (intraspecific competition hypothesis, Perrin and Mazalov 1999, 2000). 3) Dispersal is associated with mortality (Bonte et al. 2011), and this cost will differ between sexes, as asymmetries in the costs and benefits of dispersal between the sexes are expected (Pusey 1987). Our two metrics may also provide contrasting responses with respect to survival; in particular,

we predicted that cumulative distance is more related to survivorship than the net dispersal distance.

Methods

Species and study area

The North African houbara bustard (hereafter 'houbara') is a non-migratory and a sexually dimorphic species in which males are larger and heavier than females. It exhibits an exploded-lek mating system, where displaying males are less aggregated than in a classical lek (Hingrat et al. 2008). Males generally start reproducing later (2–4 year-old) than females (1–2 year-old). Females usually lay two to three eggs, occasionally four, from February to June with a peak in mid-March. The incubation period is about 23 days with only the female brooding and providing parental care. Juvenile houbaras are semi-precocial birds (i.e. they leave the nest quickly after hatching but are still fed by the dams for 10 days) that are fully fledged around 60 days after hatching (Saint Jalmes and van Heezick 1996). We assume here that the juveniles are able to start dispersing from 60 days-old (hereafter 'departure'). The houbara inhabit semi-arid desert areas composed of subshrub vegetation. The study was conducted from May 2006 to February 2010 in eastern Morocco (Fig. 1) over an area averaging 45 000 km². This study area is part of a wider conservation area, the management of which is led by the Emirates Centre for Wildlife Propagation (ECWP).

Capture and telemetry

We captured 100 wild born juveniles (28 in 2006, 29 in 2007, 18 in 2008, 25 in 2009) that were equipped with VHF transmitters and monitored from the ground and by aerial telemetry (details of the capture and monitoring procedure is given in Supplementary material Appendix A1). The period of individual monitoring averaged 414 ± 370 days (range: 3 to 2439 days).

Two standard monitoring protocols were defined: 1) from departure (i.e. 60 days-old) to the third months after the start of dispersal/departure (i.e. about 150 days-old \pm 10 days), juveniles were searched for twice a week and 2) individuals older than 150 days were searched for once a week. The first protocol was used to accurately estimate dispersal movement, and both protocols were used to build capture histories for survival analyses. Locations (accuracy \pm 5 m for terrestrial telemetry and \pm 200 m for aerial telemetry) were recorded using GPS.

Age and biometry

Body weight (\pm 1 g) and tarsus length (\pm 0.1 mm) were recorded at capture. Most birds were blood sampled ($n = 84$) and sexed using molecular sexing (D'Aloia and Griffiths 1999). When the date of hatching was known ($n = 14$ juveniles), juvenile ages were directly obtained. Otherwise, juvenile ages were estimated from the tarsus measurements with the following formula (ECWP captive breeding data):

$$\text{estimated age} = -0.0006 \times [\text{tarsus length}]^2 + 0.8143 \times [\text{tarsus length}] - 18.198$$

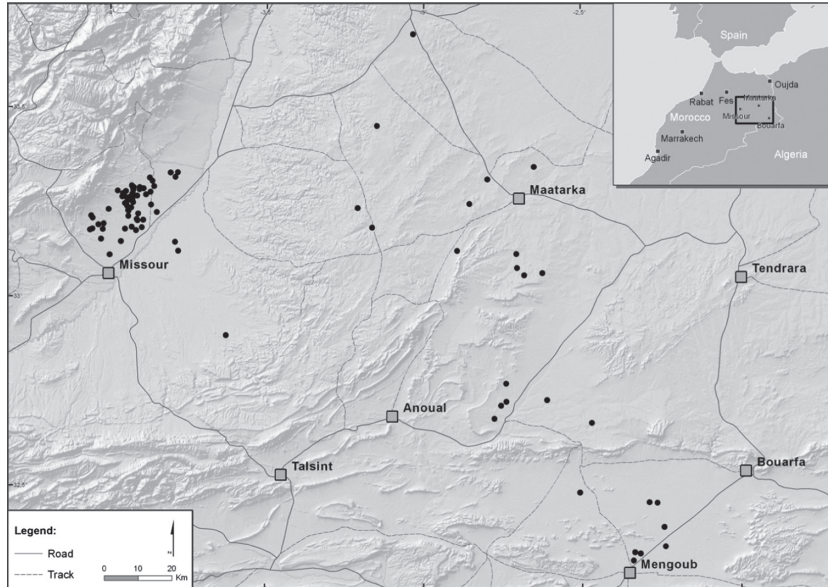


Figure 1. Map representing the capture sites of juvenile North African houbaras (black dots).

This equation was established using captive-bred juveniles reared by the ECWP. At this juvenile stage, the tarsus length is similar between males and females, is still growing and constitutes the best index to estimate the age of juveniles. We assessed his accuracy on the wild juveniles of known hatching date ($n = 14$ juveniles) and found that the differences between real and estimated age was on average of 5 ± 5 days (median = 3 days).

For each juvenile, an index of body condition was extracted using the residuals of the regression of the body weight against real/estimated age at capture ($F_{1,98} = 266.1$; Adj. $R^2 = 0.70$; $p < 0.001$; Jakob et al. 1996, Hardouin et al. 2009).

Definitions of movement parameters

In this study, we used two distinct metrics to describe dispersal movement and produced six different parameters.

Metric 1 corresponds to the direct distance from the individual's departure point to any of its locations that can be related to the propensity to disperse (Fig. 2). From this metric, we extracted three parameters. 1) Net dispersal distances (NDD) correspond to repeated measures of metric 1 along the monitoring of the individual. 2) The median net dispersal distance (NDD_{median}) was calculated from the NDDs. 3) The last net dispersal distance (NDD_{last}) is the distance from the departure point to the last localization of each individual.

Metric 2 corresponds to the distance between two successive locations (Fig. 2). From this metric, we calculated two parameters. 4) The cumulative distances (CD) correspond to repeated measures along the individual path of cumulative distances from its departure point to successive locations, 5) the full cumulative distance (CD_{full}) that corresponds to the final path distances covered by juveniles from the departure point to the last localizations. Although cumulative distance depends largely upon the last NDD

distance ($CD_{full} - NDD_{last}$; $r = 0.80$), it will also be influenced by the amount of exploratory behaviour on route. To provide an estimate of this exploratory behaviour and the search efficiency of individuals independently of the distances covered. We calculated for each individual ($n = 6$) a straightness index (ST) as $ST = NDD_{last} / CD_{full}$ (Almeida et al. 2010). The straightness index ranges from 0 to 1. Values close to 0 correspond to highly explorative individuals. ST was not correlated with NDD_{last} and was negatively correlated with CD_{full} ($r = -0.38$, $p = 0.009$). Both metrics were extracted using a geographical information system

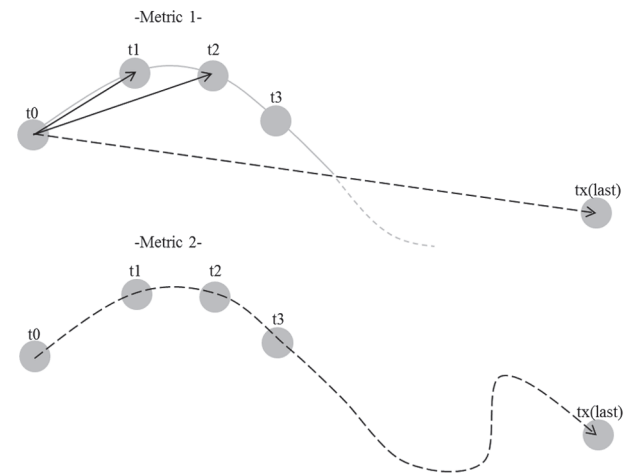


Figure 2. Schematic representations of the distances from the start of dispersal of an individual to any of its locations (metric 1) and the distances between successive locations (metric 2). Individual path is represented from the departure location (t_0) to the last location (t_x) with intermediate locations (t_1 , t_2 and t_3). For the metric 1, black straight arrows correspond to the repeated measures of the net dispersal distances (NDDs) and dashed straight arrow corresponds to the last net dispersal distance (NDD_{last}). For the metric 2, dashed curved arrow follows the repeated measures of the cumulative distances (CD) along individual's path until the full cumulative distance (CD_{full}).

(ArcGIS 9.2) and the Hawth's analysis tools for ArcGIS (Beyer 2004).

Influence of proximate factors on dispersal movement

To investigate the factors influencing movements, only birds with more than 10 localizations and at least one localisation per 30 days period were considered. When birds were located twice in the same day, we considered only one of these locations, favouring a ground-based location if available; otherwise the location was randomly chosen. Birds that were found dead or were lost during this period were discarded from our sample (see Discussion about the potential bias). Overall, 57 individuals of known sex were considered in the analysis with 21 ± 5 (mean \pm SD) localizations and 91 ± 12 days of monitoring per individual, and a total of 1213 localizations. We tested the influence of various proximate factors on the net dispersal distance, cumulative distances and straightness index using linear mixed effect models. The first two set models aimed at testing the effect of body condition (and its quadratic term), sex, hatching date and time (i.e. ages of juveniles at localizations) on NDD (first model set) and CD (second model set). The individual ID was considered as a random term (to account for the repeated measures of NDD and CD per individual) and nested into the broodID, which was itself crossed with the year factor.

In the third set of models, we tested the association between ST and the previous explanatory variables (except time). BroodID and year factor were added as random effect.

For all models, we started from the global model (all explanatory variables and first order interaction) and compared it with submodels from which we sequentially deleted non-significant terms until we arrived at the minimal model. We based our model selection on the fixed effects using likelihood ratio tests (Lewis et al. 2010). Because the appropriate number of degrees of freedom to use in assessing the statistical significance in mixed-effects models is controversial, we present model coefficients with estimates of highest posterior density (HPD) intervals, which are Bayesian's equivalent to confidence intervals, calculated at the 95% level using Markov chain Monte Carlo (MCMC) sampling with 100 000 samples. In this case, a coefficient is deemed significantly different from zero when the HPD interval does not include zero. Second, we used the MCMC sampling to calculate p-values based on the posterior distribution. The NDDs were log-transformed and the CDs were squared root transformed to meet normality and homoscedasticity assumptions. All statistical analysis were conducted with the freeware R 2.10.1 (R Development Core Team), specifically using libraries lme4 (Bates and Maechler 2010) and languageR (Baayen 2009).

Relationship between dispersal and survival

To investigate the relationships between mortality and dispersal, data from all 100 captured individuals were used: 36 males, 43 females and 21 non-sexed individuals. Movements were calculated from departure to death or up

to 90 days (± 10 days) resulting in 14 ± 8 (mean \pm SD) localizations and 80 ± 30 days of monitoring per individual with a total of 1684 localizations. Monitored hunting occurred in the study area and 4 birds from our sample were hunted at 200 ± 39 days-old.

We used multievent capture–recapture modelling (Pradel 2005) to estimate survival of radio-tagged individuals, which enabled us to account for imperfect detectability and uncertainty in the assignment of states to individuals (here sex; Pradel et al. 2008). We examine survival variation between sexes from departure to adult life following three age-classes: a1 = the third months after departure, a2 = 3 to 6 months after departure, a3 = more than 6 months after departure). We tested the influence of covariates such as NDD_{median} , NDD_{last} , CD_{full} , ST and body condition at capture on survivorship at the different age-classes. Details about the model structure are described in supplementary materials (Supplementary material Appendix A2). Briefly, we considered four states to code individual sex and whether it was alive or dead (states 1 to 4 respectively corresponded to alive male, alive female, newly dead male and newly dead female). We also considered seven events to code for the observed fate and sex of an individual at each occasion (event 0: not observed, events 1 to 3: alive male, female and non-sexed individual, events 4 to 6: dead recovery of a male, a female and a non-sexed individual). A step-down model selection (Supplementary material Appendix A3–A5) was performed using program E-SURGE (Choquet et al. 2009a) based on the Akaike information criterion corrected for sample size (AICc), the AICc weights (w_i) were also given. The selection of the models with covariates (five covariates and their first order interactions) is given in Supplementary material Appendix A5. The best model was also presented with model coefficients and associated lower and upper confident interval (CI at $\pm 95\%$; Supplementary material Appendix A6). A coefficient is deemed significantly different from zero when the CI does not include zero.

We verified the fit of the general, time dependent model. Because there is no test available to assess the goodness-of-fit (GOF) of the general model when combining live telemetry locations and dead recoveries, we separately performed GOF tests on recaptures and recoveries (with program U-CARE ver. 2.3.2 (Choquet et al. 2009b). Unless indicated otherwise, survival rates are presented as mean \pm standard error (SE).

Results

Basic statistics of the dispersal parameters are given in Table 1.

Influence of proximate factors on the net dispersal distances

From the first set of models, the selected model (AIC = 2734, DF = 10, $R^2 = 0.58$; Table 2) was significantly different from the null model (AIC = 3049, $\chi^2 = 325.4$, DF = 5, $p < 0.001$) and revealed that body condition, sex and time were all related to the NDDs. More precisely, the NDDs increased with time in interaction with sex, where males covered greater distances when compared to females

Table 1. Description of the dispersal movement parameters (over the third months after the start of dispersal) according to sex (n = 30 males and n = 27 females).

	Male				Female			
	Mean ± SD	Median	Max	Min	Mean ± SD	Median	Max	Min
Net dispersal distance (km)	5.9 ± 6.2	5.9	27.6	0.4	4.1 ± 2.9	4.4	12.1	1.0
Last net dispersal distance (km)	16.2 ± 23.6	8.9	111.9	1.1	9.1 ± 6.6	6.7	29.9	2.1
Full cumulative distance (km)	123.5 ± 134.4	95.3	710.5	7.3	76.3 ± 43.8	56.8	186	27.7
Straightness Index	0.086 ± 0.060	0.069	0.31	0.02	0.080 ± 0.056	0.064	0.21	0.004

(Table 2, Fig. 3). Similarly, the NDDs appeared to be differently affected by body condition according to the sex of the individual, as suggested by the significant interaction between body condition and sex (Table 2, Fig. 3). That is, body condition was negatively associated with NDDs in males, indicating that males in better condition dispersed shorter distances while there was no such relationship present for females.

Influence of proximate factors on the cumulative distances

From the second set of models, the selected model (AIC = 12149, DF = 10, $R^2 = 0.41$; Table 2) was significantly different from the null model (AIC = 13710, $\chi^2 = 1570.2$, DF = 5; $p < 0.001$) and indicated that body condition, sex and time were related to cumulative distance. Males exhibited higher cumulative distances than females through time and individuals in better body condition travelled lower cumulative distances than those in poorer body condition (Table 2). Contrary to the net dispersal distance, no interaction between body condition and sex was uncovered.

Influence of proximate factors on the straightness index

Finally, from the third set of models, none of the models testing the effect of the body condition, sex and hatching date on the straightness index were significantly different from the null model (model with the lowest AIC = -137 vs null model AIC = -141; $\chi^2 = 4.6$; DF = 5; $p = 0.46$); suggesting that exploratory behaviour was not influenced by these proximate factors.

Relationship between dispersal and survival

The goodness-of-fit and model selection procedures are detailed in Supplementary material Appendix A3 (goodness-of-fit and encounter probabilities), 4 (survival rates) and 5 (individual covariates). Ultimately, we selected as the best fitting model the one assuming age- and sex-dependent survival rates (model 6 of Supplementary material Appendix A4). The survival rate was particularly low for females in the first age-class and increased in the second age-class (Fig. 4). For males, we observed a decrease in survival rates in the second age-class (Fig. 4). In the third age-class, survival rates were high for both males and females (Fig. 4).

We next tested the influence of body condition, NDD_{median} , NDD_{last} , CD_{full} , ST and their first order interactions on survival probabilities (Supplementary material Appendix A5). The models with CD_{full} as covariates (model

13, 15, 19, 20, 21, 22, 23 and 24) were generally preferred over models with other covariates. Models including ' CD_{full} ' had a total sum of weights of 0.99. We concluded that there was some evidence of an influence of the full cumulative distance on survival rates. In particular, we found that full cumulative distance was negatively related to the survival rates of males and females of age-classes 1 and 2 (model 22; Supplementary material Appendix A6), indicating that individuals that covered longer distances had a lower probability of survival. Given that survival is likely to differ between sexes and age-classes, we considered models with age- and sex-specific intercepts and similar slopes among age-classes (sex effect only, model 23, Supplementary material Appendix A5) or sexes (two first age-classes effect only, model 24, Supplementary material Appendix A5), in order to explicitly test whether the intensity of the effect of CD_{full} was similar between age-classes or sexes, respectively. We found that model 24 was 12 times more likely than model 22 (w_i -model 24/ w_i -model 22 = $0.90/0.07 = 12.8$; $\Delta AIC_c = 5.1$; Supplementary material Appendix A5). Therefore, we concluded that while the effect of the CD_{full} differed among age-classes, it similarly affected male and female survival rates.

Discussion

This study aimed to investigate both the determinants and mortality costs associated with natal dispersal. Overall, we found that movement has a stronger sex specific component, suggesting sex difference in individual reproductive strategies as one of the underlying causes of dispersal patterns. Furthermore, individual body condition modulated the dispersal behaviour of houbaras, in interaction with sex. Finally, we found that the distance-dependent component of dispersal is costly in the houbara (this corresponds to the risks and energy costs during the transfer phase, Bonte et al. 2011), and this cost does not differ between sexes.

Drivers of dispersal

Phenotypic traits such as body condition or body size have been shown to modulate individual dispersal behaviour in mammals, birds and reptiles (Meylan et al. 2002, Legagneux et al. 2009). In birds, for instance, the rate of dispersal can decrease (Ekman et al. 2002), increase (van der Jeugd 2001) or even have a quadratic relationship with individual quality (Barbraud et al. 2003).

We found that the net dispersal distance was influenced by sex and for males at least, their body condition. Males exhibited longer net dispersal distances than females.

Table 2. Effect of proximate factors on the net dispersal distances (NDDs) and the cumulative distances (CDs) in North African houbara bustards. The results of the selected linear mixed-effects model is given with NDDs/CDs as response variables and body condition, sex, time and their interactions as explanatory variables. Parameter estimates (i.e. fixed-effects estimates), HPD intervals, MCMCmeans and the p-values based on the posterior distribution (pMCMC) for the fixed-effects table are given. For random effects, the estimates of the residual standard deviation, the standard deviation of the random effects (intercept), HPD intervals and MCMCmeans are provided.

Fixed terms	Net dispersal distances (NDDs)					Cumulative distances (CDs)						
	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC		
Intercept	6.61	6.62	6.11	7.13	< 0.001	-111.2	-110.9	-139.3	-82.2	< 0.001		
Body condition	0.0018	0.0017	-0.0014	0.0047	0.26	0.36	0.34	0.15	0.54	< 0.001		
Sex	-0.64	-0.64	-1.11	-0.18	0.006	-46.2	-46.5	-78.1	-15.5	0.004		
Age (Time)	0.011	0.011	0.009	0.014	< 0.001	2.53	2.53	2.37	2.68	< 0.001		
Sex × Time	0.007	0.007	0.003	0.01	< 0.001	0.62	0.62	0.42	0.82	< 0.001		
Body condition × Sex	-0.006	-0.006	-0.009	-0.001	0.005	-0.004	-0.004	-0.006	-0.003	< 0.001		
Random terms	Std. Dev.	MCMCmean	HPD95lower	HPD95upper	Std. Dev.	MCMCmean	HPD95lower	HPD95upper	Std. Dev.	MCMCmean	HPD95lower	HPD95upper
Individual : Brood	0.44	0.36	0.23	0.51	26.80	25.90	17.60	34.30	26.80	25.90	17.60	34.30
Brood	0.48	0.33	0.12	0.52	57.50	30.90	22.40	39.30	57.50	30.90	22.40	39.30
Year	0.16	0.30	0.00	0.75	0.00	11.15	0.00	36.70	0.00	11.15	0.00	36.70
Residual	0.74	0.75	0.72	0.78	44.80	46.10	44.10	48.10	44.80	46.10	44.10	48.10

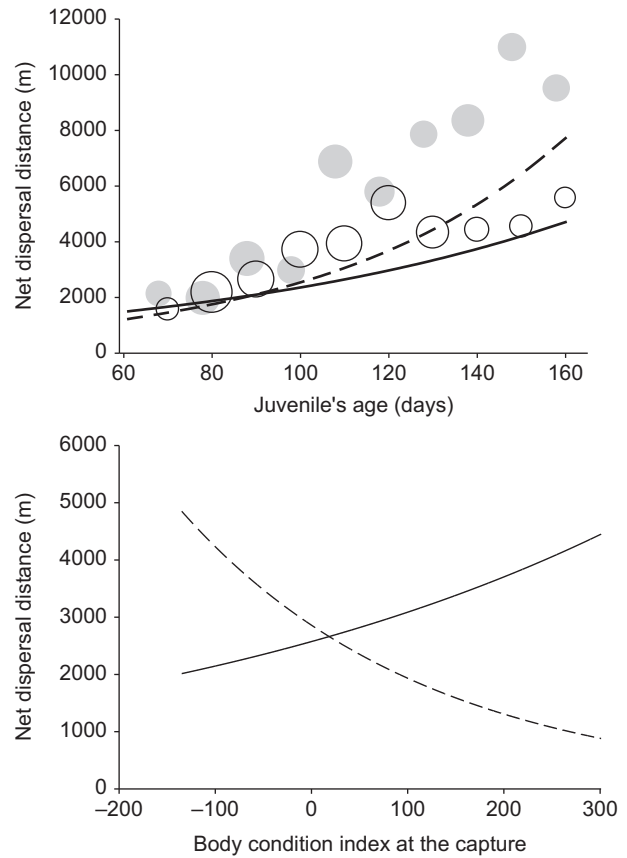


Figure 3. Partial effect plots (with back-transformed data) describing the net dispersal distance of juvenile North African houbara bustards according to time and sex (upper part) and the interaction between body condition and sex (lower part). Male juveniles are represented by the dashed fitted curve and female juveniles by the plain curve. We included in the upper part plot, the original data (means of NDDs are calculated on a time-step of 10 days) that are represented by grey circle for males and blank circles for females. The size of the circles is proportional to the sample size.

This could suggest male-biased natal dispersal in the North African houbara bustard, which would contrast with the general pattern of female-biased dispersal found in most avian species (Greenwood and Harvey 1982, Clarke et al. 1997), but be consistent with the pattern observed in some other lekking species. Indeed, male-biased natal dispersal has been observed in the great bustard *Otis tarda* which exhibits an exploded lek socio-sexual structure that is similar to the houbaras. From this, it seems plausible to suggest that this lekking structure may have played an important role in the evolution of male-biased patterns of dispersal (Martín et al. 2008). Indeed, as males do not defend any significant resource for females and do not participate in the rearing of their offspring, philopatry does not seem to offer a clear evolutionary advantage in terms of reproductive success (Greenwood and Harvey 1982, Martín et al. 2008). In contrast, females might obtain reproductive benefits from remaining close to their natal site, because of their familiarity with the breeding site (Clarke et al. 1997, Martín et al. 2008). Additionally, female philopatry can also be promoted by kin cooperation mechanisms (Armitage et al. 2011). Although few data are currently

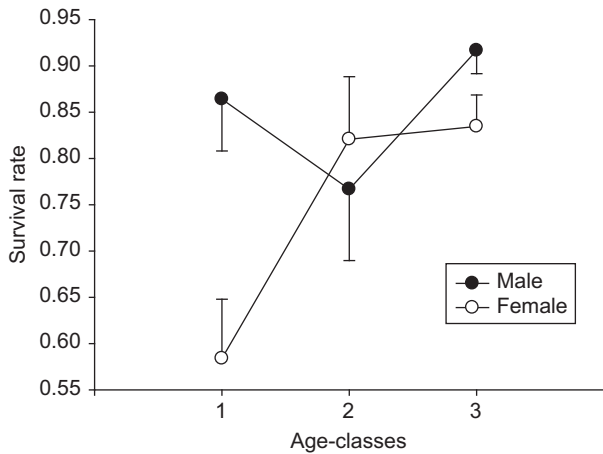


Figure 4. Age-specific survival rates (\pm SE) of juvenile North African houbara bustards (three age-classes such as 1 = the third months after departure, 2 = from 3 to 6 months after departure, 3 = more than 6 months after departure).

available in houbaras, natal dispersal distances (i.e. from departure to first settlement for reproduction – display site for males and nest site for females) range from 19.4 ± 12.8 km ($n=4$, median = 13.7 km) for males to 8.6 ± 6.5 km ($n=6$, median = 7.3 km) for females (ECWP, unpubl.), which are consistent with the male-biased dispersal pattern observed during the onset of dispersal.

Another result of interest is the negative relationship found between body condition and net dispersal distances in juvenile houbara males. Males in lower body condition moved further than males in better condition. These effects of sex and body conditions suggest that strong selective pressures act on juvenile males to disperse, which seems likely to arise from the need to avoid inbreeding and/or intraspecific competition (Perrin and Goudet 2001). Under the inbreeding avoidance hypothesis, immature males could be evicted due to male–male competition for mates (Dobson 1982) and/or females could refuse to mate with males born in the same area (Liberg and von Schantz 1985). In addition, father–son competition for mating access might also occur and favour male-biased dispersal (Perrin and Goudet 2001). Under the intraspecific competition for resources hypothesis, males in good condition might be better able to compete and so remain in their natal area, while those in poorer body condition could be more easily expelled by competitors from natal area, forcing them to disperse (Pyke 1984). They could also increase their activity levels, i.e. larger cumulative distance, to avoid starvation (Astheimer et al. 1992). Cumulative distances tend to decrease with increasing body condition, supporting this idea. In contrast to the net dispersal distances, the cumulative distances varied independently of sex, suggesting that the ‘exploratory’ component of this metric (and thus its underlying causes) is not sex dependent. This interpretation was confirmed by the absence of sex effect on the straightness index.

For both metrics, we did not detect any effect of the timing of reproduction of parents on offspring dispersal movement, in accordance with several other avian studies (Verhulst et al. 1997). Finally, the straightness index was not influenced by the proximate factors tested here:

neither body condition index, sex nor hatching date seemed to affect individual’s exploratory behaviour. It is possible that this index may depend on other factors that we have not examined here, such as individual differences in dispersal strategy (Selonen and Hanski 2006), habitat quality (Doerr and Doerr 2005), hormonal states (Dufty and Belthoff 2001) or genetic component (Dingemanse et al. 2003).

Survival cost of dispersal

The onset of dispersal is a short but crucial period that has important consequences on individual life history traits (Lumma and Clutton-Brock 2002), drives population growth rate (Baker 1993) and contributes significantly to local recruitment (Naef-Daenzer et al. 2001). We found that young houbara females had lower survival rates than males, but only in the first age class. At older ages, we did not detect any sex differences in survival.

Dispersal costs were demonstrated in several taxa, including plants and micro-organisms (Bonte et al. 2011). These costs can have strong influence on individual investment in dispersal, dispersal distance range and then on metapopulation processes (Baguette and Schtickzelle 2006, Clobert et al. 2009). Our model revealed that cumulative distances are negatively related with survival. While this relationship may be due to some heterogeneity in individual quality (i.e. because low quality individuals tend to both survive less and to disperse more than high quality individuals), the absence of a relationship between survival and body condition suggests that movement itself carries a mortality cost. Recent review on dispersal costs suggests that direct mortality risk during transfer is a prominent cost in birds (Bonte et al. 2011). In line with these results, we suggest that the distance-dependent survival cost of dispersal observed in the houbaras is related to a lack of familiarity with novel environments, and that greater dispersal distances correspond to habitats that are increasingly divergent from natal areas (Yoder et al. 2004). We also suggest that greater exploratory movements increased the risk of encountering predators, starving due to low foraging efficiency or both (Johnson and Gaines 1990, McNamara and Houston 1990, Clarke et al. 1993).

Here, the costs of dispersal could be greater in one sex and might partly explain sex-biased dispersal patterns (Pusey 1987). The cost of movement may also shift the balance between natural and sexual selection; it can for instance lead to a decrease in male secondary sexual trait investment (Kinnison et al. 2003). In houbaras, we found that cumulative distance affected the survival rates of males and females similarly, meaning that the cost of dispersal did not differ between sexes. Therefore, the male-biased dispersal found in the houbara could not be explained by differential cost of movement between male and female.

Our study relied on a two-step protocol designed to circumvent potential biases. First, the analysis of movement was conducted on a subset of individuals that survived over the third months after the start of dispersal, which may be biased due to differential survival, but allowed us to investigate the precise determinants of movement patterns. Second, the survival analysis was conducted on all tagged individuals to understand the consequences of dispersal

on survivorship. The joint interpretations of these two components provide us with a clear picture of how patterns of movements are shaped by proximate factors, individual strategies and differential mortality during the onset of dispersal. Results illustrate sex differences in houbara behaviour at a very early stage of life, with respect to two key components of demography: dispersal and survival. Our results confirmed the existence of distinct dispersal strategies between sexes. Further work should be conducted to uncover potential costs and benefits of early natal dispersal occurring later in life (Doligez and Pärt 2008) and to further determine the basis of differences in dispersal patterns within sexes.

Dispersal is generally considered a means to reduce kin competition and inbreeding (these two explanations not being mutually exclusive, Ronce 2007). While our study does not allow us to uncover the ultimate causes of observed dispersal patterns, our results are consistent with general predictions related to both hypotheses. Sex-biased dispersal is often interpreted as a mechanism for reducing inbreeding and intra-sex competition (Perrin and Mazalov 1999, 2000); whereas kin competition may also theoretically result in positive or negative relationship between body condition and dispersal propensity (Bonte and de la Peña 2009). Our results illustrate the shortcomings associated with the classical disperser versus non disperser dichotomy and the need of quantitative approaches to dispersal and its associated cost, since 1) in most non colonial species, individuals never exactly stay in the natal area, and 2) the distributions of dispersal distances and costs have major implications to the genetic and dynamics of metapopulations (Johst et al. 2002, Murrell et al. 2002, Baguette and Schtickzelle 2006).

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Supplementary material (available online as Appendix O20313 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A7.