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Meteorological conditions influence short-term survival and dispersal in a reinforced bird population

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Summary

1. A high immediate mortality rate of released animals is an important cause of translocation failure ('release cost'). Post-release dispersal (i.e. the movements from the release site to the first breeding site) has recently been identified as another source of local translocation failure. In spite of their potential effects on conservation program outcomes, little is known about the quantitative effects of these two sources of translocation failure and their interactions with environmental factors and management designs.

2. Based on long-term monitoring data of captive-bred North African houbara bustards *Chlamydotis undulata undulata* (hereafter, houbara) over large spatial scales, we investigated the relative effects of release (e.g. release group size, period of release), individual (e.g. sex and body condition) and meteorological (e.g. temperature and rainfall) conditions on post-release survival ($n = 957$ individuals) and dispersal ($n = 436$ individuals).

3. We found that (i) rainfall and ambient air temperature had, respectively, a negative and a positive effect on houbara post-release dispersal distance; (ii) in interaction with the release period, harsh meteorological conditions had negative impact on the survival of houbara; (iii) density-dependent processes influenced the pattern of departure from the release site; and (iv) post-release dispersal distance was male-biased, as natal dispersal of wild birds (although the dispersal patterns and movements may be influenced by different processes in captive-bred and in wild birds).

4. *Synthesis and applications*. Our results demonstrate that post-release dispersal and mortality costs in translocated species may be mediated by meteorological factors, which in turn can be buffered by the release method. As the consequences of translocation programs on population dynamics depend primarily upon release costs and colonization process, we suggest that their potential interactions with meteorological conditions must be carefully addressed in future programs (i) through monitoring of short-term post-release mortality to understand its link with environmental conditions, (ii) by carefully choosing the season of release to minimize exposition of inexperienced individuals to harsh conditions and (iii) by generalizing the use of long-term weather forecast to adapt release effort and staggering releases over several years to buffer meteorological effects.

Key-words: bustard, captive-breeding, ESURGE, lek mating, natal dispersal, reinforcement, translocation, trap dependence

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Introduction

Although high immediate mortality of released animals is an important cause of translocation failure ('release cost', Tavecchia *et al.* 2009), post-release dispersal was identified as another source of local failure (Le Gouar *et al.* 2008). At the population scale, translocation may serve to improve population viability (Seddon, Strauss & Innes 2012). At the metapopulation scale, translocation may promote the connectivity of local populations and/or extend the species' range (Seddon, Strauss & Innes 2012). Although dispersal is a key component of metapopulation dynamics, it is also associated with local failure (Mihoub *et al.* 2011). Furthermore, if dispersal entails survival costs (Bonte *et al.* 2012), it may contribute to mortality patterns associated with restoration projects (Tweed *et al.* 2003). Hereafter, we will refer to the three stages of dispersal following Bonte *et al.* (2012) general definitions and nomenclature for wild populations (i.e. departure from natal area, transfer – the movement *per se* and settlement at the reproduction site), although adapted to the case of translocations (i.e. considering departure from the release site, see Le Gouar, Mihoub & Sarrazin 2012). Overall, the factors affecting mortality and dispersal following release events can strongly influence the success of conservation strategies (Le Gouar *et al.* 2008; Oro *et al.* 2011).

Despite adequate post-release monitoring (Seddon, Armstrong & Maloney 2007), temporal and spatial replicates of release events are still uncommon (Le Gouar *et al.* 2008). Conservationists rely primarily on short-term survival and dispersal data to assess release effects on population dynamics and inform management strategies. However, the short-term survival of a released population might poorly reflect its long-term persistence (Armstrong *et al.* 1999). Since individual phenotype and environmental conditions shape dispersal patterns, they may differ in captive-bred and wild individuals, having in turn an impact on translocation success (Clobert *et al.* 2009).

Post-release survival and dispersal of individuals may be influenced by two main types of factors: (i) those relating to the release management (for instance and non-exhaustively: release group size, period of release; hereafter, release factors) and (ii) those relating to individual characteristics (hereafter, individual factors), such as sex, age and body condition. Additionally, although it is likely that local meteorological factors can also greatly influence the survival and dispersal of translocated animals, they have, to our knowledge, never been investigated. Here, we aimed at providing a comprehensive framework for future and current translocation programs by contrasting different release conditions and their subsequent effects on demographic components. We quantify short- and long-term processes and the relative effects of release, individual and local meteorological factors on survival and dispersal in a captive-bred population of North African houbara bustards *Chlamydotis undulata undulata* (family Otididae; hereafter, houbara). Our analysis relies on intensive post-release and large spatial scale monitoring data collected as part of a reinforcement (i.e. an addition of individuals to an existing population, IUCN 2012) program in Morocco.

In numerous species, empirical findings suggest that (i) meteorological factors strongly influence individual survival (Nevoux, Barbraud & Barbraud 2008), particularly in fragile, weak or inexperienced individuals (Robert *et al.* 2012), and (ii) released individuals suffer high immediate mortality after release (Tavecchia *et al.* 2009). We predict that survival of released houbara will be negatively affected by harsh or extreme meteorological conditions (in terms of rainfall and temperature) and that meteorological effects will be strongest shortly after release due to the inexperience of birds in their release habitat.

Although theoretical predictions deal with dispersal rate in patchy habitat, most hypotheses were generalized to movement patterns and can be applied to non-colonial species and continuous habitat (e.g. Débarre & Gandon 2010). Accordingly, we predict that time to departure will be negatively correlated with release group size, a surrogate of the local density at the time of release, as (i) intra-specific competition has been identified as an important ultimate cause of dispersal in both theoretical works and empirical studies of many species (Perrin & Mazalov 2000), including houbara bustards (Hardouin *et al.* 2012), and (ii) the release protocol involves very large groups. In addition, recent evidence suggests that natal dispersal distance is male-biased in this species (Hardouin *et al.* 2012). Therefore, we predict that post-release dispersal distance should be male-biased if dispersal behaviour is not altered by the translocation protocol.

Materials and methods

GENERAL METHODS

Study sites and biological model

The North African houbara bustard is a non-migratory, sexually dimorphic species, with males being larger and heavier than females and presenting an exploded-lek mating system (Hingrat *et al.* 2008). This vulnerable species (BirdLife International 2012) has suffered severe declines in wild populations over the last 40 years, leading to the establishment of the Emirates Centre for Wildlife Propagation (ECWP) in Morocco in 1995 (Lacroix 2003). A comprehensive strategy combining ecological research, reinforcement using captive-bred houbara individuals and hunting management was established over an area of 74 400 km² (Fig. 1) in order to restore houbara populations and allow regulated traditional Arab falconry. The study area represents 13% of the species distribution range in North Africa (Species Distribution Modelling, presence threshold = 0·5, A.-C. Monnet, unpublished data). Hunting was banned between 2000 and spring 2005 and then restricted to the wintering period (October–January) in 60% of the managed area. The present study was conducted from March 2001 to February 2010.

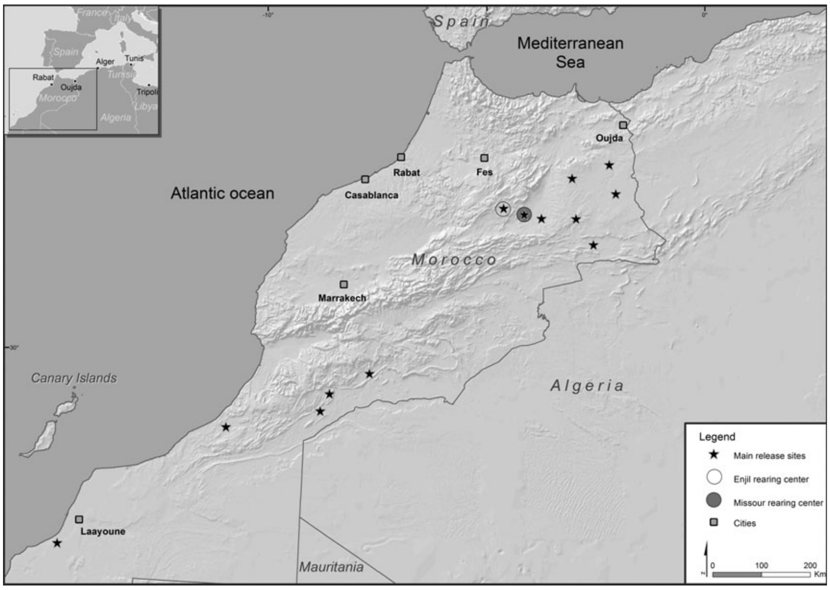

Fig. 1. Locations of main release sites in Morocco. Houbara individuals were bred at two breeding stations: Missour (grey circle) and Enjil (white circle).

Breeding stations, release and radiotracking procedure

The ECWP has released 20 652 houbara in Morocco over the study period (see Lesobre 2008 for detailed protocols). Individuals were released in spring (March–May) and in autumn (September–November). The autumn releases are managed to avoid direct mortality and disturbance due to hunting. Release sites (Fig. 1) and group size (10–292 individuals) varied over time. Before release, each individual was weighed (±1 g), blood-sampled for molecular sexing and tagged with a metal ring or subcutaneous electronic microchip (TROVAN LID100, DorsetID).

One thousand and four hundred individuals were fitted with necklace battery-powered transmitters with mortality signals (11 g model RI-2B-M, 20 g model RI-2D-M, Holohil System Ltd.). Sixty-five birds were recaptured before their batteries died and fitted with new 20 g transmitters. They were monitored from the ground and by aerial telemetry (details of the monitoring procedure in Appendix S1 in supporting information). For 90 days (±10 days) post-release, they were searched for twice a week over the entire study area in Morocco (Fig. 1). Beyond 90 days, they were searched for once a week in north-eastern Morocco. The first period was primarily used to get accurate measures of movement to analyse the short-term post-release dispersal (see below). Both periods were used to determine the distance from the release site to the first breeding site (i.e. settlement distance) and to build capture histories for survival analyses. For survival analysis, we considered only individuals released in north-eastern Morocco ($n = 957$ individuals, Fig. 1) because of the longer monitoring period in that area.

POST-RELEASE DISPERSAL

Movement and transfer phase

Short-term post-release dispersal behaviour was defined as departure and transfer within 3 months of release. The linear distance between an individual's release site and any of its successive locations measured the propensity to disperse away from the release site (Hardouin *et al.* 2012). Repeated measures of this metric over the whole monitoring period characterized the net dispersal distance (NDD). From the distance between two successive locations, we calculated cumulative distance (CD), as the full-path distances covered by an individual from the release site to the last location (Hardouin *et al.* 2012). Distances were measured using ArcGIS 9.2 (Environmental Systems Research Institute) and Hawth's Analysis Tools (Beyer 2004). Only birds located at least 10 times and at least once per 30 days were considered for analysis (Hardouin *et al.* 2012). Therefore, 436 individuals and 8679 localizations were considered in this analysis, yielding 20 ± 8 (Mean ± SD) localizations, 92 ± 8 days of monitoring per individual and 4·7 ± 4·3 days between localizations.

Departure phase

Departure date was defined as the date at which CD begins to increase with time, inducing a break on the regression line between CD and time (detailed procedure in Appendix S2).

Settlement distance

We continuously monitored 69 females and 17 males out of the 436 individuals until their first breeding attempt. Released females initiated reproduction at the age of 1·6 ± 0·5 years, whereas released males started displaying at the age of 2·1 ± 0·8 years (data from our study sample), making them difficult to monitor over the long term. Settlement distance was described as the linear distance from the release site to the first nest (for females) or display site (for males).

Meteorological data

In the north-eastern region of the study area, a network of 10 weather stations close to the primary release sites (Fig. S1, Supporting information) recorded daily ambient air temperature (°C) and sum rainfall (mm). For each bird's location, we considered temperature and rainfall for the ±3 days surrounding the localization event, using data from the nearest weather station. High temperature was significantly correlated with dryness ($r = -0{\cdot}13$, $P < 0{\cdot}001$). We assessed the effects of local meteorological factors on houbara during transfer using only individuals for which release site and subsequent localizations were near the weather stations to properly assess the effects of the meteorological variables ($n = 223$ out of 436 individuals). The mean distance to weather stations was 17·8 ± 12·7 km ($n = 3628$ localizations) and did not exceed 65 km.

Released bird body condition and age

The 436 individuals were released at an average age of 234 ± 89 days, weighing 1092 ± 140 g (females) and 1482 ± 235 g (males) (see Table S1, Supporting information for the sample details). An index of body condition was extracted for each individual using the residuals of the regression of the body weight and release age (as body weight linearly increased with age at the time of the release; inflexion point of the growth curve = 44 ± 8 days for males and 38 ± 6 days for females) with sex as a covariate ($F_{2,433} = 322{\cdot}7$, Adj. $R^2 = 0{\cdot}6$, $P < 0{\cdot}001$, Hardouin *et al.* 2012).

Statistical analysis

We first investigated the effects of release and individual factors on departure date using linear mixed-effect models. The model tested for effects of body condition (BC and its quadratic term), sex, release age (Ra), release group size (RGr) and first-order interactions on departure date. 'Year', 'release site' and 'period' were added as random terms. We then tested the effect of BC (and its quadratic term), sex, Ra, RGr, time after release (i.e. based on the dates of the localization events) and first-order interactions on NDD to analyse the pattern of movement along the short-term post-release dispersal. We considered 'individual ID' (nested into 'release site', $n = 22$), 'year' and 'period of release' as random terms. Thirdly, we tested for effects of rainfall and temperature, sex, BC and their first-order interactions on NDD for individuals with available meteorological data ($n = 223$ individuals, see above). The random slope terms were added as in the previous model, and 'time after release' was considered as a random intercept to account for the repeated measures over time. Finally, we investigated whether settlement distance was explained by BC at the time of the release, sex or age at first reproduction (as longer-distance dispersers might reproduce later). 'Year of reproduction' was added as a random slope term. For all models, we started from the global model (all explanatory variables and first-order interactions) and compared its performance with submodels from which non-significant terms were deleted one at a time. We used Markov chain Monte Carlo sampling to calculate the coefficients and highest posterior densities of the models, which were reported in the result section as MCMCmean; HPD95 (lowerHPD95; higherHPD95) (see details in Appendix S3). NDDs and departure dates were log-transformed, and the cumulative distances were square-root-transformed to meet normality and homoscedasticity assumptions. The freeware R 2.10.1 (R Development Core Team 2009) and the libraries lme4 (Bates & Maechler 2010), languageR (Baayen 2009) and segmented (Muggeo 2008) were used for analyses.

SURVIVAL ANALYSIS

We used multi-event capture–recapture modelling (Pradel 2005) using a mixture of alive recaptures and dead recoveries to estimate the effect of sex and release period on survival of radio-marked individuals. Each bird was monitored for an average of 306 ± 343 days (max = 2721 days). We gathered observations into 3-month time steps from the release occasion ($k = 36$ occasions). Survival over the first interval (k_0–k_1) described short-term post-release effect, while survival for subsequent intervals (k_1–k_{35}) described long-term effects. Estimates produced by the model are trimestral survival probabilities (e.g. survival probability over a 3-month interval). The time-dependent model was coded to possibly estimate (when relevant): (i) short-term survival for each release cohort (i.e. autumn and spring release), sex and year and (ii) long-term survival for each release cohort, sex and year. We also assessed the influence of individual and temporal covariates on survivorship. Details of the sample and the models are given in Table S2 and Appendix S4.

Briefly, we considered two states to code whether an individual is alive or dead and three events to code for the observed fate of an individual at each occasion (0: not observed, 1: alive individual, 2: recovery of a dead individual). We verified the fit of the general, time-dependent model with program U-CARE version 2.3.2 (Choquet *et al.* 2009a; Appendix S4). A step-down model selection was performed using program E-SURGE version 1.7.1 (Choquet, Rouan & Pradel 2009b) based on the Akaike information criterion corrected for sample size and overdispersion (QAICc, c-hat = 2·07, Appendix S4). When ΔQAICc was smaller than 2, we selected the model with the smallest number of parameters, following the parsimony principle (Lebreton *et al.* 1992). Starting from the time-dependent model (Appendix S5), we thus proceeded of three successive steps of model selection: (i) we performed model selection for recovery probabilities (models E1–E10 in Table S3); (ii) recapture probabilities (models C1–C4 in Table S4); (iii) and survival probabilities (models S1–S16 in Table S5). Unless indicated otherwise, estimates of survival, recapture and recovery probabilities are presented as the value ±standard error (SE).

Selection of individual and meteorological covariates and modelling

To test whether variation in meteorological conditions explains a significant part of the temporal variation in survival rate, we integrated meteorological information as temporal covariates into models. We used the daily temperature and rainfall data from the 10 weather stations (Fig. S1) to create annual meteorological indices. We then calculated the annual mean daily temperature (ADT) and rainfall amount (ADR) over the ten stations. After 6 years of reinforcement, regulated hunting on houbara occurred from 2005 to 2009 in the winter (non-breeding) season. Although hunting was not our focus and autumn releases mainly occurred in non-hunted areas, we accounted for hunting in our analyses by integrating a temporal covariate describing the presence (1) or absence (0) of hunting in a given year.

We first assessed the effects of meteorological indices on the selected time-dependent model to estimate which one (ADT, ADR or their interaction) had the greatest effect on temporal variation in survival (Models T1–T11 in Table S6). The contribution of temporal covariates to the model was assessed using an analysis of deviance (ANODEV), and the amount of temporal variation in the focal rate explained by the covariate was evaluated by R^2dev (Skalski, Hoffmann & Smith 1993).

We also examined the relationship of BC, Ra and RGr (and their interactions) with survival probabilities, resulting in 16 candidate models with individual covariates (models 1–16 in Table S7). A covariate has an effect when the associated 95% confidence interval of the corresponding slope does not include zero.

Results

DISPERSAL

Departure date

Departure dates were calculated for 396 individuals occurred on average 29·7 ± 20·2 days after release (median = 24·7, range = 2–90 days). From the selected model ($R^2 = 0·13$, $\chi^2_{\text{null}} = 8·2$, d.f. = 3, $P = 0·04$), departure date was significantly explained by a positive interaction between BC and RGr (MCMCmean = 1·04, HPD95 (1·001–1·08), $P = 0·04$): individuals with low BC released in a large group tended to leave the release site first.

Transfer

The most parsimonious model of NDD ($R^2 = 0·65$, $\chi^2_{\text{null}} = 2387·8$, d.f. = 7, $P < 0·001$) revealed significant effects of BC, Ra, time after release and first-order interactions of time after release with BC, Ra and sex (Table 1). Individuals in good BC moved farther than those in poor BC (Fig. 2). Older released birds travelled farther shortly after release, but not later (Table 1, Fig. S2). Sex-specific movement differed over time (Table 1). Males moved shorter distances than females shortly after release, but over time, the pattern reversed. This interaction suggests an increase of NDD in males or a decrease of NDD in females. RGr did not affect NDD (MCMCmean = 0·0007, HPD95 (−0·0006; 0·002), $P = 0·4$).

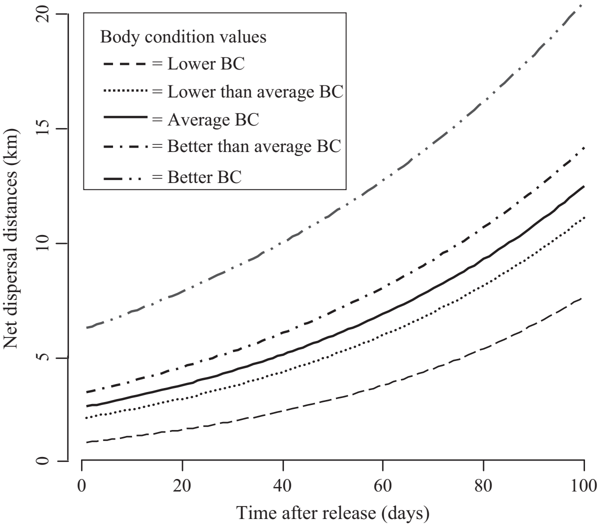

Fig. 2. Partial plot representing the interaction between time and body condition (BC, given as quantiles) according to the net dispersal distance (in km) of houbara (log-transformed data were back-transformed).

When including meteorological factors as explanatory variables ($R^2 = 0·76$, $\chi^2_{\text{null}} = 16·1$, d.f. = 3, $P = 0·001$), BC remained positively associated with movements (0·0012 ± 0·0004, *t*-value = 3·1). Individuals covered greater distance when facing high ambient air temperature (0·0133 ± 0·0045, *t*-value = 2·9) and low rainfall (−0·0226 ± 0·0067, *t*-value = −3·3) conditions.

Settlement distance

The selected model ($R^2 = 0·21$, d.f. = 1, $\chi^2_{\text{null}} = 7·15$, $P = 0·007$) revealed that settlement distance was sex-biased,

Table 1. Effects of release and individual factors on net dispersal distance (NDD) in houbara. The results of the selected linear mixed-effects model are given, with NDD as the response variable and body condition, sex, release age, time after release and their interactions as explanatory variables. Parameter estimates (i.e. fixed-effects estimates), highest posterior density (HPD) intervals, Markov chain Monte Carlo means (MCMCmeans) and *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. 'Time' refers to 'time after release'

Fixed terms	Estimate	MCMCmean	HPD95lower	HPD95upper	pMCMC
Intercept	1980·24	1923·25	391·00	10627·22	<0·001
Body condition	1·17	1·17	1·13	1·22	<0·001
Sex	0·93	0·92	0·82	1·04	0·19
Release age	1·18	1·20	1·06	1·35	0·002
Time	5·83	5·84	4·85	6·94	<0·001
Body condition × Time	0·9994	0·9994	0·9991	0·9998	0·001
Sex × time	1·1339	1·1385	1·0167	1·2798	0·008
Release age × time	0·9986	0·9986	0·9979	0·9992	<0·001

Random terms	SD	MCMCmean	HPD95lower	HPD95upper
Individual: release site	0·69	0·49	0·46	0·52
Release site	0·36	0·33	0·23	0·45
Year	0·26	0·29	0·15	0·44
Period of release	0·15	0·76	0·01	1·57
Residual	0·75	0·77	0·76	0·78

with males settling farther from the release site than females (MCMCmean = 0·61, HPD95 (0·15; 1·05), $P = 0{\cdot}008$). Neither BC nor age at first reproduction significantly affected settlement distance.

SURVIVAL

Model selection procedures are detailed in Appendix S5, Tables S3 & S4 for encounter probabilities and Table S5 for survival.

The selected model [$S_{\mathrm{shortT*period1*t+shortT*period2+longT*t}}$] highlighted an influence of short- vs. long-term, time and release period on survival (Model S1 in Table S5). In particular, short-term survival differed according to time for autumn releases ([$S_{\mathrm{shortT*period1*t}}$] range between 0·19 ± 0·07 in 2009 and 0·92 ± 0·06 in 2006, Fig. 3a), while being constant for releases occurring in spring ([$S_{\mathrm{shortT*period2}}$] = 0·86 ± 0·02). Long-term trimestral survival varied according to year ([$S_{\mathrm{longT*t}}$], Fig. 3b), with a relatively low survival rate in 2008 (0·72 ± 0·03).

Meteorological covariates

Meteorological covariates (Fig. 3c) were incorporated into the selected time-dependent model S1 (Table S6). The interaction between ADT and ADR explained a significant part of the short-term survival for autumn releases (model T1 in Table S6, Fig. 3a), and an additive effect of ADT and ADR explained a significant part of the long-term survival (Fig. 3b, Model T1 in Table S6). The selected meteorological indices explained 83% of the deviance in the temporal variation of survival probabilities (F-Anodev$_{1,9}$ = 44·6, $P < 0{\cdot}001$). It is important to note that when hunting is removed from the previous model, 76% of the deviance was still explained by meteorological covariates (F-Anodev$_{1,11}$ = 35·7, $P < 0{\cdot}001$).

Individual covariates

Individual covariates were incorporated into the selected time-dependent model (Table S7). The models with 'Ra' as covariate (Models 1, 2 and 3 in Table S7) on long-term survival were preferred, with Ra being negatively related to long-term survival probabilities [Model 1 in Table S7: slope = −0·20 ± 0·07; CI (−0·05; −0·35)]. This constitutes an average loss of 3% ± 1% in survival every 100 days of age at release.

Discussion

We found that (i) meteorological factors had critical effects on houbara survival, although these effects can be mitigated by appropriate timing/method of release; (ii) density-dependent processes (e.g. intraspecific competition) partly shaped the pattern of (early) post-release dispersal, as suggested by the interaction between release group size and body condition; and (iii) post-release

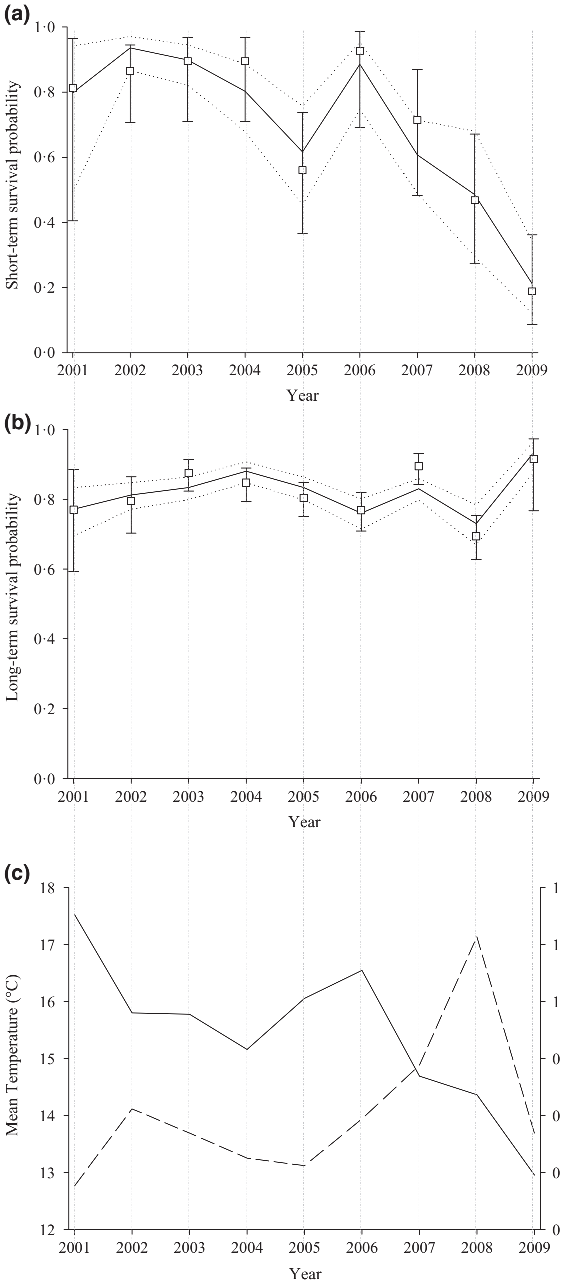

Fig. 3. Annual variation in trimestral houbara survival probabilities: a) Short-term survival probabilities estimated for autumn release, b) Long-term survival probabilities. For both, we present survival probabilities estimated from the selected time-dependent model and the 95% confidence intervals (white squares). Survival probabilities (black lines) and 95% confident intervals (dotted lines) are estimated from the temporal covariates for a) with the interaction between ADT and ADR. [$S_{\mathrm{shortT*period1*t*(ADT*ADR)}}$] and for b) survival probabilities and 95% confident interval estimated with additive effect of ADT and ADR [$S_{\mathrm{LongT*t*(ADT+ADR)}}$]. c) Annual variation of the ambient air temperature (ADT, straight black line) and the daily rainfall (ADR, straight dashed line). Note that hunting stopped from winter 2001–2004 and started from winter 2005. The presence/absence of hunting was integrated in all the models as temporal covariate. Note that [$S_{\mathrm{ShortT*period2}}$] is constant = 0·86 ± 0·02 and not shown.

dispersal was male-biased, as in natal dispersal of wild houbara (Hardouin *et al.* 2012).

EFFECTS OF THE METEOROLOGICAL, RELEASE AND INDIVIDUAL FACTORS ON POST-RELEASE DISPERSAL PHASES

Our results highlight the influence of meteorological conditions during the transfer phase (see also Walls, Kenward & Holloway 2005) of post-release dispersal and their potential impact on the colonization processes of translocated populations. We found that rainfall and ambient air temperature had a negative and a positive effect, respectively, on net dispersal distance, independently of the release period. Recent findings showed that the houbara plant diet is dominated by young green leaves of annual plants, whereas ants dominate the animal diet of the species (Bourass *et al.* 2012). The availability of these food resources is driven by ambient air temperature and rainfall (e.g. López, Acosta & Serrano 1993), suggesting an indirect effect of meteorological conditions through food availability that may force individuals to disperse.

The release group size interacted with body condition (BC) and affected departure from the release site. This finding suggests that individuals with poor BC leave the vicinity of the release site sooner in larger release groups. Birds in good BC may be less affected by density-dependent processes (such as intraspecific competition, Matthyssen 2005) and may remain at the release site for longer to gain sufficient reserve and/or experience in their novel environment.

Previous results on wild juvenile houbara indicate that males in poor BC move farther than those in good BC during natal dispersal, distance being independent of BC in wild females (Hardouin *et al.* 2012). Here, captive-bred houbara show the opposite pattern suggesting that selective pressures exerted by captivity (Robert 2009) and/or the release protocol (Le Gouar, Mihoub & Sarrazin 2012) may interact with the ultimate factors shaping individual dispersal strategies (e.g. inbreeding avoidance and intraspecific competition). In contrast to wild juveniles that already occupy favourable breeding habitats, released individuals may have to search more extensively for lekking or nest sites. Thus, only individuals in good condition may afford the distance-dependent cost of dispersal (Bonte *et al.* 2012). Hence, older released birds had longer net dispersal distances than younger ones just after release, but not later. Presumably, the longer distances initially covered by older individuals reflect age differences in muscular development or hormonal activity (Dufty & Belthoff 2001).

Finally, we detected male-biased dispersal, consistent with studies of natal dispersal in wild houbara (Hardouin *et al.* 2012). Sex-biased dispersal is generally interpreted in the theoretical context of the inbreeding avoidance hypothesis (Szulkin *et al.* 2013). Recent findings in Morocco demonstrated a lack of kin association within and between leks in male houbara but a higher genetic relatedness in males than in females (Lesobre 2008). Genetic study suggests greater philopatry in males (Lesobre 2008), in contrast to our demographic results. However, breeding dispersal is female-biased in houbara (L.A. Hardouin, unpublished data), as rare long-dispersal events (three females dispersed more than 100 km in our study) suggest that they may be vectors of gene flow at the metapopulation level (Ibrahim, Nichols & Hewitt 1996).

EFFECTS OF THE METEOROLOGICAL, RELEASE AND INDIVIDUAL FACTORS ON SHORT- AND LONG-TERM SURVIVAL

Meteorological conditions have been demonstrated to strongly influence individual survival in many taxa (e.g. Grosbois *et al.* 2008; Nevoux, Barbraud & Barbraud 2008) and, consequently, population dynamics and viability (e.g. little bustards *Tetrax tetrax*, Morales, Bretagnolle & Arroyo 2005). While several studies have reported substantial short-term mortality costs in translocated populations (Tavecchia *et al.* 2009), these costs have primarily been attributed to release methods, individual characteristics and habitat requirements. Here, we report a strong interaction between release strategy (autumn vs. spring releases) and meteorological conditions on short-term survival, which suggests that release costs are likely to be modulated by environmental stochasticity (Nicoll, Jones & Norris 2003). Although low temperatures in association with extreme precipitation conditions (flooding or aridity) negatively affected short-term survival in autumn, survival of individuals released in spring, when the meteorological conditions are generally milder, was high and constant over years. In contrast, we did not observe any difference in long-term survival between release cohorts, but an effect of annual rainfall and temperature (note a severe flooding in 2008). Although environmental stochasticity is in essence unpredictable, knowledge of its magnitude and its complex effect on the life history of released individuals should greatly improve the accuracy of demographic projection models designed to examine the feasibility of translocation protocols. We thus advocate that environmental fluctuations be considered in future release strategies in houbara and other translocation efforts (Robert, Couvet & Sarrazin 2007; Sæther *et al.* 2007).

Our results also showed that, when they have survived, younger released individuals are more tolerant later in life to meteorological variation. The choice of the release age in translocation program is particularly important, and conservationists are often divided on favouring either age or habitat-related advantages in captive-bred individuals (Sarrazin & Legendre 2000). In our context, all individuals might pay a cost of release, as no learning relevant to survival in the wild environment (e.g. identification of resource locations, antipredator behaviour) can occur in pre-release aviaries. However, older released individuals might benefit short-term advantages (e.g. in terms of competitive ability) that fade outside of the captive environment. Therefore, selection on older individuals might be expressed later, potentially explaining their higher mortality over the long term. Time spent in captivity can alter the behaviour and/or physiology (e.g. Pedersen & Jeppesen 1990) in ways that negatively affect survival once released (Bremmer-Harrison, Prodohl & Elwood 2004). Interestingly, short- and long-term survival probabilities of captive-bred houbara appear to approach or even exceed those estimated from 2006 to 2009 in wild houbara (Hardouin *et al.* 2012).

CONSERVATION IMPLICATIONS AND CONCLUSIONS

In conservation translocations, post-release dispersal rate can be particularly high after release (Le Gouar *et al.* 2008). Thus, understanding the factors influencing post-release dispersal is crucial in managing the trade-off between site fidelity and adaptive dispersal (Le Gouar, Mihoub & Sarrazin 2012). Whereas high post-release dispersal rates can be associated with project failures (e.g. dispersal of released individuals outside the focal populations, Le Gouar *et al.* 2008), the absence of dispersal can limit habitat selection or be detrimental for metapopulation dynamics, for example, in terms of gene flow (Trakhtenbrot *et al.* 2005). Our results suggest that timing and local release conditions can affect short-term post-release dispersal patterns and lead to different responses between wild and captive-bred houbara. However, the release protocol results in the same male-biased pattern of dispersal as for wild-born individuals and similar dispersal distances (natal dispersal distance: wild male $19{\cdot}4 \pm 12{\cdot}8$ km, wild female = $8{\cdot}6 \pm 6{\cdot}5$ km; Hardouin *et al.* 2012). From a management perspective, both the release group size and the period of release have to be carefully chosen to limit both premature departures of weak individuals and long-distance dispersal that may result from harsh meteorological conditions. Further investigations on the effect of the local density (Le Gouar *et al.* 2008) will be helpful in refining release strategies and accounting for post-release dispersal in population projections (Armstrong & Reynolds 2012), independently of mortality (Tweed *et al.* 2003).

Although release cost has previously been identified as an important cause of translocation failure in several species (Griffith *et al.* 1989; Tavecchia *et al.* 2009), our empirical study highlights the temporal scale of this cost (in the third months following releases) and the underlying mechanisms (mortality mediated by meteorological conditions) and provide support for a general framework to mitigate this cost.

One potential approach to address the release cost is to conduct intensive monitoring to assess the short-term post-release mortality and to examine how variation in this component is related with meteorological conditions. Finally, once relationships between mortality and meteorological conditions have been quantified, systematic use of long-term weather forecast should be implemented to adapt release effort (McCarthy, Armstrong & Runge 2012). If conditions are unpredictable and highly variable among years, staggering releases over several years is the best strategy to buffer meteorological effects (Haccou & Iwasa 1996; Robert, Couvet & Sarrazin 2004). Given that observed variations in survival appear to be related to general processes (meteorological effects, interseasonal differences, role of experience to the release environment), it is likely that these results can be generalized to a large proportion of managed animal populations facing similar constraints, which make them useful to the discipline of reintroduction biology (Seddon, Armstrong & Maloney 2007) in providing stakeholders with information for reducing uncertainty associated with different release strategies and facilitating discrimination among competing models of post-release performance (Nichols & Armstrong 2012).

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Data accessibility

Data available from DRYAD Digital Repository: http://doi.org/10.5061/dryad.3523q (Hardouin *et al.* 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed monitoring procedure.

Appendix S2. Details of the breakpoint procedure.

Appendix S3. Model selection procedure of the linear mixed effect models.

Appendix S4. Goodness-of-fit and structure of the capture–recapture models.

Appendix S5. Modelling variation in recovery and recapture probabilities.

Fig. S1. Map with the locations of the weather stations in the study area in Morocco.

Fig. S2. Plot of the interaction between time and release age according to the NDDs of houbara.

Table S1. Details of the dispersal analysis sample of houbara.

Table S2. Details of the survival sample of houbara.

Table S3. Model selection for recovery probabilities.

Table S4. Model selection for detection probabilities.

Table S5. Model selection for survival probabilities.

Table S6. Model selection with temporal covariates.

Table S7. Model selection with individual covariates.