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**Evidence of a link between demographic rates and species habitat
suitability from post release movements in a reinforced bird population**

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Abstract

Despite the increasing use of Species Distribution Models for predicting current or future animal distribution, only a few studies have linked the gradient of habitat suitability (HS) to demographic parameters. While such approaches can improve the reliability of models, they can help to better predict the response of species to changes in HS over space and time, as induced by ongoing global change. Here, we tested whether the spatial variation in HS along the individual movement path is related to survival, using extensive tracking data collected from captive-born individuals translocated to reinforce the wild populations of Houbara bustard. We first modelled and mapped the HS from presence data of wild individuals using niche models in a consensus framework. We further analysed survival of released individuals using capture-recapture modelling and its links to HS, as the trend in suitability from the release sites along movements. We found that the survival of released individuals was related to changes in HS along their movements. For instance, individuals which moved to sites of lower HS than their release sites have lower survival probabilities than the others, independently of the HS of the release sites and daily movement rate. Our results provide an empirical support of the relationship between HS and survival, a major fitness component.

Keywords:

niche modelling

survival

translocation

1. INTRODUCTION

Species Distribution Models (SDM) have rapidly become widely used to model habitat suitability and predict current or potential future species distributions, with enhanced computing platform and presence data increasingly easy to access and use. SDM are a niche modelling framework based on a statistical approach linking spatial data on the presence/absence of species to predictive environmental variables. Because they do not account for species' life-history traits that constrain demographic responses to environmental factors, the projections of SDM cannot be used directly to predict the associated extinction risk (Araújo and Peterson 2012, Fordham et al. 2013). In this context, approaches accounting for mechanistic processes directly linked with extinction, such as demographic rates (e.g. survival, reproduction), movements (e.g. either exploratory or related to dispersal) or the evolutionary potential (i.e. the ability of a species to evolutionarily respond to environmental change) across distribution ranges are considered as promising steps to better understand and predict the response of species to environmental change (Thuiller et al. 2008, Brook et al. 2009).

Spatial variation in demographic processes was mostly studied to explore the nature of species range limits (Gaston 2009). Nevertheless, this approach provided little evidence of a difference in abundance or fitness along the spatial gradient from the core to the edges of species ranges, partly because suitable habitat can be randomly distributed along this range (Gaston 2009, Sexton et al. 2009, but see Purves 2009). One way to address this issue is to explicitly link the demographic response along a gradient of habitat suitability by assessing the movement, survival and reproduction success of individuals. Yet little empirical evidence exists in animals for a relationship between habitat suitability, and demographic or ecological

processes (Gallien et al. 2010, Jiguet et al. 2013). Previous studies showed a relationship between the spatial variation in the abundance of species and the habitat suitability predicted from presence-only models (VanDerWal et al. 2009, Kulhanek et al. 2011, Oliver et al. 2012) or addressed whether the spatial variation in habitat suitability predicts species performance, e.g. in terms of reproductive fitness (Moore and Elmendorf 2006) or functional traits (Thuiller et al. 2010). However, previous investigations of spatial variation in demographic or ecological processes across habitat suitability focused on inter-individual comparisons but not on variation along an individual's life (such as environmental and intrinsic variation associated with movements across different habitats).

Understanding the relation between demographic parameters, population dynamics and the environment is a crucial element to refine species conservation efforts. The use of SDM has been advocated at different stages of conservation translocation programs (i.e. the intentional movements and releases of a living organism for conservation purposes (IUCN 2012): to prioritize release areas according to the species ecological requirements (e.g. Pearce and Lindenmayer 1998, Olsson and Rogers 2009) or to assess the potential impacts of future environmental change on the distribution of remnant or translocated populations (Martínez-Meyer et al. 2007, Willis et al. 2009, Carroll et al. 2009). Yet, the application of SDM is still sparse in the context of conservation translocation (Guisan et al. 2013) and we have little evidence about the benefit of SDM to improve translocation success (Osborne and Seddon 2012, but see Moorhouse et al. 2009). The link between habitat suitability and demographic processes is therefore a key factor to assess the efficiency of SDM in the establishment of translocation actions (Chauvenet et al. 2013). Here we provide an original analysis linking survival and movement estimates to habitat suitability (as predicted by SDM) using data from a reinforced population (i.e. a population supplemented by the intentional release of

conspecific individuals (IUCN 2012) of a bird species (the North African Houbara bustard, *Chlamydotis undulata*, hereafter Houbara). This translocation program provides an ideal study framework including information on the spatial distribution of wild-born individuals and intensive individual-based monitoring of captive-bred released individuals.

Using a niche modelling framework, we first modelled and mapped the habitat suitability of the species breeding range using occurrence data of wild individuals. In the reinforcement program, release events occurred at different sites and released individuals could move to habitats of higher, lower or equivalent suitability. We investigated whether the survival of released individuals differed according to the predicted suitability of habitat they came across. We first tested whether individual post-release movements through more suitable habitats led to higher survival probabilities, and conversely, whether movements through less suitable habitats led to lower survival probabilities. We also tested whether the habitat suitability of the release site had an effect on individual survival probability. Finally, as the distance travelled by an individual can have direct survival-related costs (Bonte et al. 2012, Hardouin et al. 2012), we contrasted the relative influence of habitat suitability and daily movement rates on survival.

2. MATERIAL AND METHODS

a) Presence data

We modelled the habitat suitability of the breeding range of wild Houbara population. We used occurrence data with precise geographical coordinates primarily from monitoring of wild individuals equipped with satellite and VHF transmitters (for details see Supplementary material Appendix 1 Table A1). We only kept locations recorded during the breeding period (from February to May; $N = 83,560$). We summarized presence data and environmental variables according to the 2.5 arc-minutes (approximately $4.5\text{km} \times 4.5\text{km}$) grid of Worldclim database. To limit the sampling bias, we removed the duplicated locations within each grid cell, resulting in 992 cells where Houbara were recorded. We then completed presence data from a random sampling of an equivalent number of coordinates in the digitized and georeferenced map of the historic distribution of the breeding range of the species (Goriup 1997).

b) Environmental data

We characterized the ecological niche of Houbara through a comprehensive set of eleven environmental predictors. From four sources of data, we extracted climate variables, assumed to be the main drivers to bird species niche delimitations at large scale (Luoto et al. 2007, Pigot et al. 2010), and habitat variables, used to characterize the semi-desertic habitats of Houbara. (i) We kept the three first axes of the principal components analysis calibrated on eight bioclimatic variables from the Worldclim database (Hijmans et al. 2005; see Supplementary material Appendix 2 Table A2). (ii) We calculated the standard deviation of elevation from the CIGAR-CSI SRTM 250m database within each grid cell (Jarvis et al. 2008). (iii) We calculated a mean annual soil water stress from CGIAR-CSI Global Soil-

Water Balance Database provided at a resolution of 30 arc-seconds (Trabucco and Zomer 2010). (iv) We aggregated Global Land Cover classes provided at a 1km² pixel resolution (Mayaux et al. 2004) in seven land cover variables according to ecological requirements of Houbara: open shrubland, sparse grassland, cropland, bare rock, stony desert, sandy desert and unfavourable habitat (for details see Supplementary material Appendix 2 Table A3). Then we calculated the percentage covered by these seven land cover classes within each cell of the environmental grid.

c) Habitat suitability modelling

We performed seven modelling techniques using BIOMOD computer platform (Thuiller et al. 2009): (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) generalized boosted models (GBM), (4) classification tree analysis (CTA), (5) artificial neural networks (ANN), (6) random forests (RF) and (7) multivariate adaptive regression splines (MARS). All of these modelling techniques require both presence and absences data. Because our datasets do not provide true absences, we generated 10,000 artificial absence records (pseudo-absences) by randomly sampling from the grid cells of the whole study area. Random sampling was recently advocated in preference to the exclusion of pseudo-absences from spatial or environmental extents where presence occurrences were recorded (Stokland et al. 2011, Barbet-Massin et al. 2012). Because different pseudo-absence samples can provide different results, we ran models for two pseudo-absence samples.

Each model was calibrated on a random subset of 70% of the data and evaluated against the remaining 30% by cross-validation. We replicated twice this data-splitting into “evaluation” and “calibration” subsets. We used a graphical method, the area under the receiver operating characteristics (ROC) curve (AUC) (Fielding and Bell 1997) to evaluate the predictive

performance of each modelling technique. A good model performance (generally AUC values over 0.8, Araujo et al. 2005) is characterized by a ROC curve which maximizes true positive fraction (sensitivity) for low values of the false positive fraction (1-specificity). The final calibration of each model used 100% of the available data for making projections. Among the niche modelling techniques available and the high inter-model variability in predictive performance, consensus methods (or ‘ensemble forecasting’) which retain the central tendency given by different models were preferred to single-model approaches, because they provide the best predictive performance (Araújo and New 2007, Marmion et al. 2009). We followed one of the most robust methods identified by Marmion et al. (2009) to provide ensemble predictions: we averaged the predictions of models across pseudo-absences and data-splitting runs from the seven modelling techniques. We calculated the average values of AUC as evaluation of the ensemble-model. The AUC criteria has been subject of some criticism concerning potential bias in accuracy because it varies with parameters such as the prevalence, the number of pseudo-absences and the total extent to which models are carried out (Lobo et al. 2008), which does not occur here because we use AUC to compare different models obtained for one species, using the same presences and pseudo-absences data, across the same geographical area. All models were calibrated using the BIOMOD package (Thuiller et al. 2009) in R v2.15.0 (R Development Core Team 2012).

d) Survival analysis

Here, we combined information from live telemetry locations and dead recoveries to estimate the survival, recapture and recovery rates of 957 radio-tagged captive-bred Houbaras. A detailed description of breeding program can be found in Chargé et al. (2014) and the sample and release conditions was previously detailed in Hardouin et al. (2014). Releases occur at an average age of 7 ± 2 months old (mean $\pm$ SD) during two periods: from August to December

(hereafter, ‘autumn’) and from February to June (hereafter, ‘spring’). Captive-bred Houbaras were searched (by terrestrial or aerial telemetry) at least once a week from their release from March 2001 to February 2010 for an average of 306 ± 343 days (mean $\pm$ SD, max = 2,870 days; see Supplementary material Appendix 3 for a detailed description of the standardised monitoring protocols). The average lifespan of transmitters is 98 ± 51 weeks and most of them (72.5%) were equipped with a movement or mortality signal (see details in Supplementary material Appendix 3 Table A4). 11 individuals were recaptured (within the lifespan of transmitters) and equipped with a new transmitter. 44% of the birds ($n = 422$) were lost during monitoring after an average of 462 ± 370 days of monitoring.

We gathered observations into three-month time steps from the release and used two time-classes to distinguish short-term post-release survival (first interval, from release to three months) from long-term survival (subsequent intervals, three months onward) and thus account for the high survival-related costs of release in the first three months post-release (see Tavecchia et al. 2009, Hardouin et al. 2014). From this two time-classes model, we focused in this study on long-term survival where the cost-benefit of changes in habitat suitability along movements is expected to be more effective. Estimates produced by the model are thus survival probabilities over a three-month interval. For each interval, we considered four states to code the individual states: two ‘alive’ states (to account for the positive trap dependence found in our dataset, i.e. higher capture probability at $j+1$ when individuals are captured at occasion j , see Supplementary material Appendix 4), ‘freshly’ dead and dead. We considered three events to code for the observed fate of an individual at each occasion (0: not observed, 1: individual observed alive, 2: individual recovered dead).

Following previous knowledge on the data set (Hardouin et al. 2014), we then started model selection using the best structure of recovery [R], capture [P] and survival [S] probabilities (see Genovart et al. 2013 for similar procedure). Hardouin et al. (2014) previously showed that the release period (autumn or spring) has an effect on short-term survival but no effect on long-term survival. Thus, the starting model $[S_{shortT*autumn*t+shortT*spring+longT*t}]$ assumed short- *versus* long-term-, time- and release period-dependent survival for each year. The goodness-of-fit, tested with UCARE (Choquet et al. 2009b), and the model structure are fully detailed in Supplementary material Appendix 4).

From this model, we tested the effect on the long-term survival of two different groupings of individuals from discretization of the gradient of habitat suitability. (i) We separated released Houbaras in four groups (quartile cut) according to the value of habitat suitability of their release sites (hereafter, ‘hs’, for details see Supplementary material Appendix 5 Table A5). To test whether there is a significant difference of survival among these groups, we then built the model $[S_{longT*hs*t}]$, assuming no effect of these groups on recovery and recapture rates. (ii) We created five different groups (hereafter, ‘g’) according to the temporal changes in habitat suitability across each successive location ($N = 26,053$; mean per individuals $\pm$ SD = 27.2 ± 30.6), describing whether individuals gain or loss in habitat suitability along movements. First, we excluded from the group formation the individuals with less than 5 locations ($N = 186$) for correctly estimating the gain or loss in habitat suitability. These individuals were incorporated in the model to refine the recovery, capture and survival probabilities, but were not considered *per se* to test the link between changes in habitat suitability values during movement and long-term survival. For each of the remaining 771 individuals, we tested the relationship between the successive habitat suitability values and time (i.e. from the release location to their last location) using linear regression and then extracted the slope estimates

and p-values. We distinguished individuals with significant ($N = 308$) and non-significant slopes (called ‘null’ group; $N = 463$). We separated individuals with significant slopes in four distinct groups using the median of the estimates to split positive and negative slopes into lower and upper values: 1) high loss (HighL), 2) low Loss (LowL), 3) low gain (LowG) and 4) high gain (HighG) of suitability. Since we had no prediction on the effect of these groups on recovery and recapture rates and that monitoring effort is constant over the whole study area (see Supplementary Material Appendix 3), we assumed no effect of the groups on [P] and [R]. We therefore built the following starting model $[S_{longT*g*t}]$, assuming that long-term survival can be related to the change in habitat suitability during movement (i.e. among the five groups defined above). Step-down model selection was performed using the program E-SURGE version 1.7.1 (Choquet et al. 2009a) based on the Akaike Information Criterion corrected for sample size and overdispersion (QAICc). When $\Delta QAICc$ was smaller than 2, we selected the model with the smallest number of parameters (Lebreton et al. 1992). Estimates of survival probabilities are presented as the value $\pm$ standard error (SE).

On the selected model, we also tested the effects of the individual daily movement rate and of the initial habitat suitability (i.e. habitat suitability of release site) on survival probabilities. The metric used to calculate the individual daily movement rate corresponds to the distances between two successive locations. From this metric, we extracted the full cumulative distance (overall path distance covered by the individual between release site to last location, Hardouin et al. 2012) and we divided it by the time of the monitoring. The daily movement rate and the habitat suitability of release site were modelled as individual covariates to specifically test their effect within each group. Their relationships with model parameters were examined on the final model resulting from the step-down model selection protocol described above. The contributions of covariates on each parameter were assessed using model coefficients (Betas).

A coefficient is deemed significantly different from zero when the associated 95% confidence interval (CI) does not include zero.

e) Statistical analysis

Our main prediction is that the survival of released Houbaras should differ according to the slope of temporal changes in suitability they came across (hereafter, ‘HS slope’), reflecting a link between HS slope and survival at the inter-individual level. However, because temporal changes in habitat suitability and survival were computed on the same data, spurious relationship between survival and HS slope may arise if the slope changes along an individual’s life. Thus, in order to ensure that results are linked to differences between individuals rather than intra-individual variation in HS slope, we checked whether there were systematic changes in HS slope along monitoring by regressing the changes between two successive values of habitat suitability on time using linear mixed-effects model for the 952 individuals with at least two locations. We performed statistical analyses using the lme4 package (Bates et al. 2014) in R v2.15.0 (R Development Core Team 2012).

We performed alternative modeling to ensure that there is no strong consistent curvilinear pattern and that linear regression is the most appropriate for subsequent comparison between all individuals in survival analyses. We performed quadratic and cubic regressions between habitat suitability and time for each of the 771 individual with at least 5 locations and compared the results to linear regression results. For quadratic regression, we then described the convex or concave shape of the curve of significant polynomial regressions.

3. RESULTS

a) Predicted habitat suitability

The average area under the curve (AUC) of the seven modelling techniques was high (mean = 0.904 ± 0.0122 , range [0.878-0.927]). The ensemble forecasting of seven niche modelling techniques provides the likelihood of species presence, or habitat suitability (hereafter called ‘p’ for ‘probability of presence’; Fig. 1). The higher predicted probabilities of presence define the more suitable habitats for Houbara and delimit its potential current distribution from North Mauritania to Sinai in North East Africa (Fig. 1).

b) Linking the loss or gain in habitat suitability with long-term survival

Over the study period, captive-bred Houbaras were released in Eastern Morocco into highly suitable areas ($p = 0.85 \pm 0.05$, mean $\pm$ SD, Table 1 and Fig. 2). The model with individuals grouped according to the habitat suitability of the release sites was not selected according to its higher QAICc value (Supplementary material Appendix 6 Table A6).

Figure 2 illustrated the habitat suitability of locations from release sites of all individuals during their monitoring. From release, about 60% of individuals ($N = 463$) stayed in habitats of the same suitability value as their release habitat (‘null’ group, non-significant slopes between successive habitat suitability values and time; see graphs for ten randomly sampled individuals in Supplementary Material Appendix 7. Among individuals with significant slopes, 38% ($N = 117$) moved towards more suitable habitats and 62% ($N = 191$) towards less suitable habitats (see ten examples in Supplementary Material Appendix 8).

The comparison between linear and curvilinear regressions revealed no strong consistent curvilinear pattern and provided support for the use of results from the linear model to conduct a comparison between all individuals in survival analysis: (1) among the subsample of individuals with significant linear regression, model fit was not significantly improved by adding a higher order component in 58.1% of the cases (Supplementary Material Appendix 9 Table A7 and Figure A1); (2) among the subsample of individuals non-significant for linear regressions, polynomial regression was not significant in 72.4% of the cases (Supplementary Material Appendix 9 Table A7). Most importantly, significant polynomial (quadratic) regressions did not show strong consistent pattern (n=140 exhibited convex patterns vs. n=117 concave patterns; Supplementary material Appendix 9 Table A8).

Ultimately, the model assuming different temporal survival trends according to the gain or loss of habitat suitability groups was selected (Supplementary material Appendix 6 Table A6). Specifically, we found that the group with high loss of habitat suitability had overall lower survival probabilities than the other groups ($[S_{HighL}]$ ranges between 0.50 ± 0.07 and 0.86 ± 0.07 , Fig. 3). The highest survival probabilities were observed for the group with low gain in suitability ($[S_{LowG}]$ ranges between 0.83 ± 0.03 and 0.96 ± 0.02 , Fig. 3). In between, we found similar rates of survival for the remaining groups ($[S_{LowL HighG Null}]$ ranges between 0.69 ± 0.03 and 0.93 ± 0.04 , Fig. 3). Finally, neither the ‘daily movement rate’ nor the ‘release habitat suitability’ individual covariates did improve the fit of the aforementioned model ($\Delta QAICc = -2.7$ and -5.7 respectively; Supplementary material Appendix 10 Table A9).

We found no significant change in the slope of temporal changes in suitability along an individual’s life (estimate $\pm$ SE = $2.9 \times 10^{-7} \pm 2.4 \times 10^{-7}$, t-value = 1.19), indicating that the

329 relationship between changes in habitat suitability and survival is due to inter-individual
330 differences and not to intra-individual change in suitability slope with time.
331

4. DISCUSSION

In a rapidly changing world, the need to understand species response to environmental change has triggered a large body of research on species range distribution, but few have linked them to demographic processes (Gallien et al. 2010). Yet, change in environmental conditions has direct effect on quality and distribution of suitable habitats, which ultimately affects species persistence along their distribution range (Thuiller et al. 2008). Here, in a reinforced population of Houbara bustard, from empirical investigations, we show a relationship between survival of released individuals and changes in habitat suitability along the individual movement path, independently of the daily movement rates and habitat suitability of release sites. Interestingly, this relationship was not straightforward and the most positive changes in habitat suitability were not characterized by highest survival probabilities. These results illustrate the relevance of linking demographic processes with Species Distribution models (SDM), but also underline the importance of other mechanisms acting on demographic parameters and possibly mitigating such relationship (social organisation, density dependence).

The post-release movements of captive-bred animals determine the environmental conditions experienced by released individuals that can directly affect survival. For this reason, it is important to examine how variation in habitat suitability of sites visited after release relates to post-release survival. In this context, translocation programs provide a useful study system to assess the relationship between population dynamics and habitat suitability, to better model and disentangle ecological processes that affect demographic parameters (e.g. Nicoll et al. 2003, Martín et al. 2012). Movement of individuals to highly suitable habitat is expected to reflect higher individual performance in habitat selection and/or higher competitive ability, which may in turn be positively correlated with survival. It is also expected to affect directly

and positively demographic parameters and to increase survival probability in released populations (Osborne and Seddon 2012). We thus expected that the most positive increases in habitat suitability result in the most benefits in terms of survival and that conversely, birds moving towards sites of lower suitability would survive less.

Using long-term monitoring, we identified a link between survival and changes in habitat suitability along individual movement path. As predicted, we showed that Houbaras moving to sites of lower habitat suitability have reduced survival probabilities and those moving to sites of greater habitat suitability have increased survival probabilities. However, and counterintuitively, the group of Houbaras with the largest gain in habitat suitability along movements was not characterized by the highest survival probability. Indeed, the direct benefit of moving to more suitable habitats can be masked by other factors that interact with a search for optimal habitat (Bowler and Benton 2005). Indeed, the lack of a notable gain in survival probability might be explained, at least partly, by enhanced intra-specific competition in most suitable sites as the number of both released and wild-born conspecifics is expected to be highest at those sites. Increased density has been reported in the Great bustard where the abundance was primarily explained by the presence of neighbouring conspecifics settled in suitable habitats (Martín et al. 2012). Yet, arrival and settlement of new individuals can involve negative density-dependent processes (Stamps and Krishnan 2005). Such processes can favour movements towards less suitable habitats as a result of intra-specific exploitation or interference competition (Bowler and Benton 2005). While it is crucial to understand how evolutionary pressures of intrinsic habitat quality affect movements in the context of ongoing environmental change (Bowler and Benton 2005), equivocal results found in the literature call for further studies on the effect of density-dependence processes in population dynamics.

Although survival and movement are thus closely linked through density-dependent processes, we were unable to rigorously test here the effect of density. In the beginning of the release program, the estimations of autumn densities in three distinct zones showed that the densities varied and increased over time. The initial density, estimated in 2001, ranged between 0.05 and 0.1 individuals per km² in the zone with the largest remnant population core (ECWP, unpublished data). In 2009, the density averaged 0.45 ± 0.08 individuals per km² in the three zones. The maximum density reached 0.76 individuals per km² in 2010, a value consistent with the maximum densities observed in other Houbara populations (e.g., *Chlamydotis undulata fuerteventura*: Carrascal et al. 2006). Importantly, these counts were conducting at large scale producing a mean density estimate for each sampled region in a particular year. Consequently while in our data set habitat suitability may greatly vary between bird locations within a region, the corresponding density is stable. This prevented us from using density estimates in the quantitative analysis of survival and movement.

The observed relationship between survival and habitat suitability of moving individuals was independent of the total amount of their daily movement. Although the overall distance covered during post-release movements has been shown to be costly (e.g. in wild Houbara, Hardouin et al. 2012), we expected that change in habitat suitability along movements would have more consequences in the long-term. Our results support this hypothesis as the amount of exploratory movements, a proxy of both the propensity to disperse and the exploratory behaviour, did not explain changes in survival within groups based on gain or loss in habitat suitability. Mitigating the cost of exploratory movement on survival can have important implications for translocation programs as post-release movements can allow individuals to escape from unsuitable conditions and competitive pressure. Sound understanding of the

demographic impacts of post-release is particularly relevant for conservation strategies in the context of projected increased frequency and severity of weather extreme events (IPCC 2013).

In contrast with our initial expectations, we found no relationship between survival probability and habitat suitability of the release sites. This might be related to usual post-release movements engaged in that species (Hardouin et al. 2014), but also to the relatively low variance in habitat suitability across release sites selected in the translocation program in Eastern Morocco. Indeed, the selection of release sites of Houbara was based on field surveys (occurrence of remnant wild populations) and habitat use studies (Hingrat et al. 2006, 2007), all targeting locations identified as highly suitable from expert knowledge. This was also confirmed by predictions of our SDM which show that selected release sites are generally characterized by a high level of suitability (i.e. high predicted probabilities of presence, $p = 0.85 \pm 0.05$, mean $\pm$ SD). This result should be therefore interpreted with caution as our data (release site locations) did not cover a complete gradient of habitat suitability, from low to high.

Despite this, the absence of relationship between survival probability (on the long term) and habitat suitability of the release sites raises the issue of the relative importance of the suitability of *release site*, (where actual releases occur), with regard to the suitability of *release area*, (habitats in which released organisms are expected to disperse) (Seddon 2013). In other words, our results emphasize the importance of carefully measure dispersal behaviour of released individuals according to individual characteristics (sex, age, body condition, personality, etc.) and surrounding environmental factors (habitat, climate, density dependence process), as these factors may overwhelm the importance of the local release site quality to predict whether individuals disperse to surrounding areas. As a consequence, and in line with

the apparent relationship between habitat suitability and survival along individual movement, the habitat suitability of surrounding habitats seems critical in the choice of the release site. Until now studies that link the habitat suitability of release sites with survival in translocation programs have often measured the habitat suitability from expert knowledge (Moorhouse et al. 2009, White et al. 2012). An experimental framework designed to formally test the relationship between habitat suitability, as predicted by SDM, and translocation success is currently being tested with Houbaras in Morocco. The aim is to test whether the information provided by SDM on the ecological requirements of the species at a wide scale, in addition to the selection of suitable habitats by experts, can optimize the translocation success.

Ecological processes involved in species-environment relationship are complex and the SDM, based on a correlative approach, does not integrate demographic and ecological processes that may constrain responses to environmental factors at a population level, suggesting that there are fundamental limits to the accurate prediction of habitat suitability (Pearson and Dawson 2003). We may thus not expect a strong agreement between changes in habitat suitability predicted by SDM and survival probability. Yet, although most positive increases in habitat suitability do not result in the largest benefit in survival, as discussed above, we found a significant relationship between changes in habitat suitability and survival probability. We thus provide a substantial support for the consistency and relevance of distribution models to inform on demographic rates and possible species persistence. Our results highlight the usefulness of relating SDM with demographic parameters to further develop our understanding of processes underlying distribution patterns and potentially develop better SDM that could integrate factors driving species distribution and persistence (Boulangeat et al. 2012). A recent generation of models that explicitly integrate spatial population or community processes – such as dispersal or biotic interactions – to niche modelling (Gallien

et al. 2010) can help to improve the reliability of SDM and thereby increase their predictive power. By linking species distribution patterns with the processes driving their response to environmental change, empirical works such as this study are essential to develop and calibrate ecologically sound models. Research on recruitment and density-dependence within species' ecological niche can be particularly useful as the general assumption of species performing better in highly suitable habitats has not been widely explored (Moore and Elmendorf 2006, Thuiller et al. 2010, Brambilla and Ficetola 2012). In this context, translocation experiments combined with SDM provide a great opportunity to test the relationship between demographic processes and habitat suitability.

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Table and figure captions

Table 1: Temporal changes in habitat suitability (HS) on the long-term, size, sex-ratio, mean HS of the release sites and mean daily movement rate of five groups of captive-bred released Houbara: high loss (HighL), low loss (LowL), low gain (LowG), high gain (HighG) in HS, and ‘null’ group.

Figure 1: Predicted distribution range of the North African Houbara bustard (*Chlamydotis undulata undulata*) obtained with seven niche modelling techniques within the ensemble forecast framework BIOMOD (Thuiller et al. 2009) (a) at the scale of whole distribution range and (b) focused on the study area in Morocco. White triangles correspond to release sites.

Figure 2: Habitat suitability of locations from release sites (black lines) of 957 individuals during monitoring (in days since release)

Figure 3: Annual variation in survival probabilities of groups of individuals according to the gain or loss of habitat suitability (HS) along movement. We present survival probabilities and the standard errors estimated from the selected model $[S_{longT.g(HighL,Null LowL HighG,LowG)+t}]$. Blank circles and straight lines correspond to the group *HighL*, i.e. individuals with high loss in HS.

Blank squares and dotted lines symbolize three groups of similar survival probabilities over time: *LowL*, *HighG* and *Null* individuals with, respectively, low loss, high gain and no significant gain/loss in HS.

Blank diamond and dashed lines represent the group *LowG* of individuals with low gain in HS.

Table and figures

Table 1

		slope HS~time			group size				HS release site	movement rate
group name		sign	value	p-value	total	male	female	sex ratio	mean $\pm$ SD	mean $\pm$ SD
high loss	HighL	-	-0.01999 to -0.00017	<0.05	92	46	46	1.00	0.87 $\pm$ 0.04	0.53 $\pm$ 0.3
low loss	LowL	-	-0.00017 to 0		99	47	52	0.90	0.87 $\pm$ 0.03	0.3 $\pm$ 0.15
low gain	LowG	+	0 to 0.00016		59	30	29	1.03	0.84 $\pm$ 0.06	0.34 $\pm$ 0.19
high gain	HighG	+	0.00016 to 0.00494		58	35	23	1.52	0.79 $\pm$ 0.06	0.31 $\pm$ 0.18
null	null	null	null	NS	463	245	218	1.12	0.85 $\pm$ 0.05	0.42 $\pm$ 0.6
TOTAL:					771	403	368	1.049	0.85 $\pm$ 0.05	0.46 $\pm$ 0.56

Figure 1

Figure 2

Figure 3

Supplementary material Appendix for

‘Evidence of a link between demographic rates and species habitat suitability from post release movements in a reinforced bird population’

Monnet A.-C., Hardouin L. A., Robert A., Hingrat Y., Jiguet F.

Appendix 1 – Presence data of wild Houbara

We modelled the habitat suitability of the breeding range of wild Houbara population from two types of presence data:

1) We used occurrence data with precise geographical coordinates mainly from monitoring of wild individuals captured from 1997 to 2010 and equipped with satellite-transmitters (backpack solar-powered transmitters, PTT-100 30/45g Solar GPS PTT, Microwave Telemetry, Inc., Maryland, USA) or VHF-transmitters (necklace battery-powered transmitters with mortality signals, 11g model RI-2B-M and 20g model RI-2D-M, Holohil System Ltd., Ontario, Canada).

Table A1: Presence data of wild Houbara used for Species Distribution Models

Type	Individuals number	Occurrences number	Year	Country	Source
VHF monitoring	249	13391	1997-2012	Morocco, Algeria, Tunisia	ECWP's data
satellite monitoring	31	70169	2002-2012	Morocco, Algeria, Tunisia	ECWP's data
occurrences & fresh tracks	-	10	2007	Algeria	de Smet <i>et al.</i> 2009
occurrences & fresh tracks	-	15	2008-2010	Algeria	Fellous A., in prep.
fresh tracks	-	2	2006	Tunisia	Wacher T., in prep.
captures and nest	-	14	1986-2006	Morocco, Algeria, Tunisia	Lesobre <i>et al.</i> 2009

2) We completed presence data from a random sampling of an equivalent number of coordinates in the digitized and georeferenced map of the historic distribution of the breeding range of the species (Goriup 1997).

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Appendix 2 – Environmental data for Species Distribution Modelling

Table A2: Bioclimatic variables from the Worldclim database (Hijmans et al. 2005)

code	variables
BIO1	mean annual temperature
BIO6	minimum temperature of the coldest month
BIO5	maximum temperature of the warmest month
BIO4	temperature seasonality (standard deviations of mean monthly temperatures)
BIO12	annual precipitation
BIO14	precipitation of the driest month
BIO13	precipitation of the wettest month
BIO15	precipitation seasonality (coefficient of variation of monthly precipitations)

Table A3: Summarized land cover variables from Global Land Cover classes

Global Land-Cover classes	Summarized land cover variables
Open deciduous shrub land	open shrubland
Sparse grassland	sparse grassland
Croplands (>50%)	
Irrigated croplands	cropland
Tree crops	
Bare rock	bare rock
Stony desert	stony desert
Sandy desert and dunes	sandy desert
Closed evergreen lowland forest	
Degraded evergreen lowland forest	
Montane evergreen forest (> 1500 m)	
Sub-montane forest (>900 m)	
Mangrove	
Mosaic Forest / Croplands	unfavorable
Closed deciduous forest (Miombo)	
Deciduous woodland	
Salt hardpans	
Waterbodies	
Cities	

Table A3 shows 19 land cover classes which occur in the study area (North Africa) within the 27 Global Land Cover classes of Africa at a 1km² pixel resolution (Mayaux et al. 2004).

Appendix 3 – Release and monitoring of captive-bred Houbara

Houbara is a lekking bird which inhabits semi-desert steppes. It was red-listed as Vulnerable to extinction by the IUCN primarily because of overhunting and overgrazing which have caused a severe population decline (BirdLife International 2012)⁴. A restoration program, the Emirates Center for Wildlife Propagation (ECWP, <http://www.ecwp.org/>), started in Morocco in 1995 to reinforce wild populations with captive-born individuals (Lacroix 2003). Two ECWP breeding stations were established in Morocco for captive-breeding (in Missour in 1995 and Enjil in 2005). A detailed description of the breeding program can be found in Lesobre *et al.* (2008), Chargé *et al.* (2010, 2014).

Equipment and monitoring of VHF-equipped individuals

Every captive-bred Houbara was tagged with a unique metal leg band or a subcutaneous microchip (TROVAN RIFD 100, DorsetID).

Before release, each individual was weighed (± 1 g), blood-sampled (for molecular sexing) and (Trovan ID100 Implantable Transponder, Dorset Group, Aalten, Netherlands) in the right tibia (injected via a single-use sterilized needle). Trovan ID100 chips are bio-compatible, pre-sterilized and specifically designed for animal identification. Their use is endorsed by the Captive Breeding Specialist Group (CBSG) of the IUCN. Microchips were implanted one month before release to control for any adverse effects such as infection, migration in the body or rejection.

Table A4: Number and technical characteristics of VHF-transmitters

transmitters model	number of transmitters	attachment type	mortality signal	weight (g)	manufacturer lifespan (week)	manufacturer's name and location
RI-2B-M	412	necklace	Y	11, 16, 19	52, 104, 156	
RI-2D-M	247	necklace	Y	19	156	Holohil System Ltd., Ontario, Canada
RI-2D	143	necklace	N	19	156	
RI-2B	120	necklace	N	11	52	
MortFast backpack-solar +-7P	26	backpack	Y	35	52	Advanced Telemetry System, The Lowell Mallory Group Pty Ltd., Gold Coast, Queensland, Australia
MOD-080	11	backpack	movement signal	43	60	Telonics, Mesa, Arizona, USA
D-Cycle MortFast necklace 3v-1/2f	6	necklace	Y	20	76	
Backpack Solar Merlin	2	backpack	N	22	(solar-powered)	Merlin Systems, Boise, Idaho, USA
PD-2, 2.93g, Tailmnt	1	backpack	N	3	21	Holohil System Ltd., Ontario, Canada

Two standard protocols are defined for the individual-based monitoring of VHF-equipped individuals. (i) For 90 days (± 10 days) post-release, Houbara were searched for twice a week over the entire study area in Morocco. (ii) After 90 days, Houbara were searched for once a week in Eastern Morocco.

The first protocol was primarily used to get accurate measures of post-release movement. Both protocols were used in combination to determine the movement from the release site and to build capture histories for survival analyses. We doubled the frequency of surveying in the first three months after release to better estimate movement and survival, as Houbara movements and mortality events are known to be greater during this period (based on ECWP surveys conducted from 1998 to 2001).

Houbara were primarily ground-based monitored at their last location within a radius buffer of 5km. Ground radio-tracking was undertaken by direct observation with 4-wheel drive vehicles using a portable scanner-receiver and a 3-element yagi antenna (AF Antronics, Inc., Urbana, Illinois).

When not detected, Houbara were searched for using aerial telemetry (detection up to 80km) for 6 months following an approximate radius of 40km from its last location. Aerial locations were taken from a Maule-7 B-235 aircraft using one 2-element yagi antennas fixed to each wing strut. Houbara were systematically searched for during other aerial telemetry procedures (i.e. when searching for other 'lost' birds). After 6 months without any location, an individual is considered as 'lost' and searching is ceased. Because of the large-spatial scale and intense searching for 'lost' individuals (303 ± 138 flying hours per year), we believe we have a representative sample of the different movement patterns (e.g. long-distance movements), that are usually problematic in studies of open populations (Doligez & Pärt 2008).

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Appendix 4 – Goodness-of-fit and structure of the multi-event capture-recapture models

We verified the fit of the general, time-dependent model with program U-CARE version 2.3.2 (Choquet *et al.* 2009a). Because there is no test available to assess goodness-of-fit (GOF) of the general model when combining live telemetry locations and dead recoveries, we performed GOF tests separately on recaptures and recoveries (Duriez *et al.* 2009).

For dead recoveries, GOF tests indicated that recoveries is higher in the first occasion after release than later (M.ITEC test: $\chi^2 = 241.5$, $df = 66$, $P < 0.001$) and detect no excess of recoveries concentrated in some later occasions (M.LTEC test: $\chi^2 = 77.2$, $df = 86$, $P = 0.7$). For live recaptures, the GOF test was highly significant ($\chi^2 = 6458$, $df = 168$, $P < 0.001$), primarily due to a positive trap-dependence effect on live recaptures (i.e. higher capture probability at $j+1$ when individuals are captured at occasion j ; $P < 0.001$) that was accounted for following Pradel & Sanz-Aguilar (2011).

We calculated an approximate over-dispersion coefficient using tests M.ITEC and M.LTEC based on recoveries ($\Sigma\chi^2 / \Sigma df = 318.7 / 154 = 2.07 = \hat{c}$) for model selection. Therefore, we considered a modified version of the standard Cormack-Jolly-Seber model incorporating trap-dependence effect to account for this lack of fit (Pradel & Sanz-Aguilar, 2011). We considered 4 states: alive individuals captured at $t-1$ [AC] or not captured at $t-1$ [$\overline{AC}$], just dead [JD] or dead [D] and 3 events to code for the observed fate of an individual at each occasion (event 0: not observed, event 1: observed as alive individual, event 2: observed as dead individual). The tracking data used for this analysis represent a particular (i.e. continuous) situation violating the general assumptions of a short period in which individuals are recaptured required by capture-recapture models (Lebreton *et al.* 1992). However, this assumption can be violated without biasing survival if recapture rate is >0.2 (O'Brien *et al.* 2005). We defined an occasion as a time step of three months, but as only one event can be coded per occasion, the situation was problematic when two different events occurred within a single occasion (e.g. recaptured then recovered dead at t). Thus, in that case, we postpone the recovery to the next occasion ($t+1$) to take into account that the individual was known to have survived from $t-1$ to t . To illustrate this, if a male is released at the first occasion, missed at the second, recaptured at the third occasion and found dead in the same occasion, the history would be coded '1012'.

First, the initial state probability matrix reported the probability of being in a given state when first encounter. In our case, individuals are alive when released.

$$\begin{array}{c} \text{States} \end{array} \begin{array}{ccc} \text{AC} & \overline{\text{AC}} & \text{D} \\ [1 & 0 & 0] \end{array}$$

The transition matrix estimated individual (ϕ_t) survival. By convention, ‘from states’ are in columns and ‘to states’ are in rows.

$$\begin{array}{c} \begin{bmatrix} & \text{AC} & \overline{\text{AC}} & \text{JD} & \text{D} \\ \text{AC} & \Phi & 0 & 1 - \Phi & 0 \\ \overline{\text{AC}} & 0 & \Phi & 1 - \Phi & 0 \\ \text{JD} & 0 & 0 & 0 & 1 \\ \text{D} & 0 & 0 & 0 & 1 \end{bmatrix} \end{array}$$

The transition matrix estimated detection probabilities, we considered two detection probabilities at time t ‘P*’ and ‘P’ depending on whether an individual was previously captured or not at the previous occasion t-1.

$$\begin{array}{c} \begin{bmatrix} & \text{AC} & \overline{\text{AC}} & \text{JD} & \text{D} \\ \text{AC} & p^* & 1 - p^* & 0 & 0 \\ \overline{\text{AC}} & p & 1 - p & 0 & 0 \\ \text{JD} & 0 & 0 & 1 & 0 \\ \text{D} & 0 & 0 & 0 & 1 \end{bmatrix} \end{array}$$

Finally, the matrix of event probabilities reported the encounter probabilities.

$$\begin{array}{c} \begin{bmatrix} & 0 & 1 & 2 \\ \text{AC} & 0 & 1 & 0 \\ \overline{\text{AC}} & 1 & 0 & 0 \\ \text{JD} & 1 - r & 0 & r \\ \text{D} & 1 & 0 & 0 \end{bmatrix} \end{array}$$

Event matrix described: r : recovery rate of dead individuals.

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Appendix 5 – Survival analysis: groups

We created four balanced groups of individuals (following interquartile range) according to predicted values of habitat suitability in release site.

Table A5: Size of groups of released Houbara based on habitat suitability of release sites (HS release site)

interquartile	group name	HS release site	group size			
			total	male	female	sex ratio
0.75 - 1	Q4	0.8881 to 0.9028	269	139	130	1.07
0.5 - 0.75	Q3	0.8589 to 0.8881	214	108	106	1.02
0.25 - 0.5	Q2	0.8398 to 0.8589	236	126	110	1.15
0 - 0.25	Q1	0.6649 to 0.8398	238	117	121	0.97
total:			957	490	467	1.05

Appendix 6 – Survival analysis: model selection

Table A6: Model selection for long-term survival probabilities $[S_{longT}]$ with recovery and detection probabilities $[P_{+t}^* + P_{+t} + R_{longT}]$. See Hardouin *et al.* (2014) for the detailed model selection on detection, recovery, and short-term survival.

Model N°	Long-term survival	Np	Deviance	QAICc	$\Delta QAICc_i$	w_i
S1	$S_{longT.g(1,2\ 4\ 5,3)+t}$	35	6432.7	3178.1	0	0.49
S2	$S_{longT.g(1,2\ 4,3,5)+t}$	36	6431.4	3179.5	1.4	0.24
S3	$S_{longT.g(1,2\ 5,3\ 4)+t}$	36	6432.7	3180.2	2.1	0.17
S4	$S_{longT.g+t}$	37	6431.0	3181.4	3.3	0.09
S5	$S_{longT.g(1,2\ 3\ 4\ 5)+t}$	34	6472.9	3195.5	17.4	0
S6	$S_{longT.g(1,2\ 3\ 5,4)+t}$	35	6472.3	3197.3	19.2	0
S7	$S_{longT.g(1\ 2\ 3\ 4,5)+t}$	34	6487.5	3202.6	24.5	0
S8	$S_{longT.g}$	29	6516.9	3206.6	28.5	0
S9	$S_{longT.hs(Q1,Q2,Q3,Q4)+t}$	34	6533.7	3224.9	46.8	0
S10	$S_{longT.t}$	32	6550.8	3229.1	51	0
S11	$S_{longT.g.t}$	76	6387.4	3240.3	62.2	0

We show here a limited number of relevant models for clarity, ranked by increasing value of QAICc (with $\hat{c} = 2.07$), with the best model in bold.

Model deviances, number of estimable parameters (Np), QAICc, $\Delta QAICc_i$ values and QAIC weights (w_i) are given.

Notation:

t time-dependent on a yearly basis.

longT	long-term time-classe
hs	groups of individuals according to the habitat suitability of release site following interquartile range, respectively hs(Q1,Q2,Q3,Q4)
g	groups of individuals according to the gain or loss of habitat suitability along movement (HighL, LowL, LowG, HighG, Null), respectively g(1,2,3,4,5)
‘ ,	lumped groups
,	distinct groups
.	interaction effect
+	additive effect

Appendix 7 – Examples of linear regression ($P > 0.05$) between habitat suitability and time for ten randomly sampled individuals

Appendix 8 – Examples of linear regression ($P < 0.05$) between habitat suitability and time for ten randomly sampled individuals

Appendix 9 – Comparisons linear *versus* curvilinear regressions between habitat suitability and time

Table A7: Comparisons of results from linear regressions and curvilinear (quadratic and cubic) regressions between habitat suitability and time

CURVILINEAR LINEAR			quadratic regression				cubic regression			
			number of individuals		percentage of individuals		number of individuals		percentage of individuals	
			P < 0.05	NS	P < 0.05	NS	P < 0.05	NS	P < 0.05	NS
linear regression	P < 0.05	(N = 308)	129	179	41.9	58.1	133	175	43.2	56.8
	NS	(N = 463)	128	335	27.6	72.4	106	357	22.9	77.1
			257	514			239	532

Figure A1: Linear ($P < 0.05$; in black), quadratic ($P < 0.05$; in red) and cubic ($P < 0.05$; in blue) regressions between habitat suitability and time from release for the individual U05M01150.

Table A8: Number and percentage of individuals with convex (upwards) and concave (downwards) curves within the significant quadratic regressions between habitat suitability and time

CURVILINEAR LINEAR			quadratic regression - $p < 0.05$			
			number of individuals		percentage of individuals	
			upwards	downwards	upwards	downwards
linear regression	P < 0.05	(N = 129)	57	72	44.2	55.8
	NS	(N = 128)	83	45	64.8	35.2
			140	117		

Appendix 10 – Survival analysis: individual covariates

Table A9: Tests of the effect of the daily movement rate [cov_{MR}] and the habitat suitability of release site [cov_{HSR}] from the best model [$S_{longT.g(1,2\ 4\ 5,3)+t}$].

Model	Best model or - Difference from the best model	Np	Deviance	QAICc
$S_{longT.g(1,2\ 4\ 5,3)+t}$	Best Model	35	6432.7	3178.1
$S_{longT.g(1,2\ 4\ 5,3).cov_{MR}+t}$	- Effect of the daily movement rate on survival assessed separately for each remaining group	38	6425.6	3180.8
$S_{longT.g(1,2\ 4\ 5,3).cov_{HSR}+t}$	- Effect of the release habitat suitability on survival assessed separately for each remaining group	38	6431.7	3183.8

Model deviances, number of estimable parameters (Np), QAICc values and biological interpretations are given.

Notation:

t	time-dependent on a yearly basis.
longT	long-term time-classe
cov_{MR}	daily movement rates as individual covariate
cov_{HSR}	daily movement rates as individual covariate
g	groups of individuals according to the gain or loss of habitat suitability along movement (HighL, LowL, LowG, HighG, Null), respectively g(1,2,3,4,5)
‘ , ’	lump groups
,	distinct groups
.	interaction effect
+	additive effect