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Density-dependence of reproductive success in a Houbara bustard population

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ABSTRACT

Although density-dependent processes and their impacts on population dynamics are key issues in ecology and conservation biology, empirical evidence of density-dependence remains scarce for species or populations with low densities, scattered distributions, and especially for managed populations where densities may vary as a result of extrinsic factors (such as harvesting or releases). Here, we explore the presence of density-dependent processes in a reinforced population of North African Houbara bustard (*Chlamydotis undulata undulata*). We investigated the relationship between reproductive success and local density, and the possible variation of this relationship according to habitat suitability using three independent datasets. Based on eight years of nests monitoring (more than 7000 nests), we modeled the Daily Nest Survival Rate (DNSR) as a proxy of reproductive success. Our results indicate that DNSR was negatively impacted by local densities and that this relationship was approximately constant in space and time: (1) although DNSR strongly decreased over the breeding season, the negative relationship between DNSR and density remained constant over the breeding season; (2) this density-dependent relationship did not vary with the quality of the habitat associated with the nest location. Previous studies have shown that the demographic parameters and population dynamics of the reinforced North African Houbara bustard are strongly influenced by extrinsic environmental and management parameters. Our study further indicates the existence of density-dependent regulation in a low-density, managed population.

Abbreviations: HS, Habitat Suitability; DNSR, Daily Nest Survival Rate.

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1. Introduction

The spatial and temporal distribution of species and population abundances is shaped by various processes that can have opposing effects. Habitat, social interactions, interspecific interactions, but also human impact influence population abundance through processes that can be density-dependent or density-independent, and that can interact with each other (Reed et al., 2013). In the context of a particular plant or animal population, density-dependence occurs when one or more demographic parameters vary with population density or population size. Whereas density-dependent processes influence abundance variation in space and time, the intensity of these processes themselves can vary with the environment to modulate carrying capacity (i.e., i.e. the maximum population size of a particular species that can be sustained by a specific environment, given the resources available for the species, Chapman and Byron, 2018; Fowler, 1987; Hui, 2006; Iijima et al., 2016). Habitat quality is a key component of carrying capacity (Downs et al., 2008) that varies over space and time. This spatial heterogeneity can be approximated by spatial projections such as the habitat suitability index coming from models relating the local occurrences of a species to different environmental characteristics to reflect niche parameters that are most suitable for an individual (Araújo et al., 2002). It is expected that local abundance, and local growth rate would be positively correlated with habitat suitability, based on the idea that densities should be higher where environmental conditions are optimal for a species compared to less favorable habitats (Acevedo et al., 2017; Weber et al., 2017). However, empirical studies show contrasting results on the type of relationship between habitat suitability index and population abundance (or demographic rates; Acevedo et al., 2017; Dallas and Hastings, 2018; Lunghi et al., 2018). On one hand, in highly favorable habitats, higher carrying capacities and higher (and potentially more stable) growth rates are expected, compared to less favorable habitats. On the other hand, in these highly suitable sites, demographic parameters are expected to be impacted by density-dependence.

In this study, we explore the relationship between the density, the habitat suitability and an index of breeding success in a steppe bird to understand how this relationship varies between and within years as a function of the environment. Our analysis is based on an eight years' dataset of a reinforced population of the North African Houbara bustard (*Chlamydotis undulata undulata*, hereafter "houbara") in Morocco. In general, density-dependence processes are expected in populations with aggregative patterns and with high local densities (Hixon and Webster, 2002; White and Warner, 2007; Zhu et al., 2010). In contrast, the houbara is a species characterized with a scattered distribution, presenting low densities of individuals, even for populations under restoration or protection program (0.44 ± 0.05 houbara/km² in Eastern Morocco, Monnier-Corbel et al., 2021; 1.08 houbara/km² in the Lanzarote island, in the Canary archipelago, Alonso et al., 2019). However, the species is living in arid environments with low resource availability, and even for such population density values, recent studies have suggested the presence of density-dependent processes: (1) in post-release dispersal depending on release group size (Hardouin et al., 2014) as well as (2) in terms of survival during their dispersal to the most favorable habitats (Monnet et al., 2015a). In a closely related species, the Asian Houbara bustard (*Chlamydotis macqueenii*), Azar et al. (2016) also demonstrated density-dependent processes, where long-term survival of individuals in fenced and managed reserves was negatively affected by local increases in density related to the population reinforcement strategy.

Our study is based on three datasets on a reinforced houbara population in Morocco: (1) abundance monitoring estimated from count data via distance sampling (from 2011 to 2018), (2) nests monitoring (from 2012 to 2019), and (3) HS index built on houbara occurrences and tracking data, excluding count data. By relating these three datasets, we investigated the relationship between nest survival and local density, as well as the possible variation of this relationship with habitat suitability and along the breeding season. We predict:

- a negative relationship between local density and daily nest survival, showing negative density-dependence effects.
- a moderation of the effect of local density on daily nest survival by the habitat suitability, with a lower effect in habitats of higher suitability.

2. Methods

2.1. Study species and study area

The North African Houbara bustard (*Chlamydotis undulata undulata*) is a medium-sized bird living in semi-arid areas with open and sparse vegetation (Hingrat et al., 2007), formerly distributed from North Mauritania to Egypt. In the Eastern region of Morocco, the breeding period extends from January to June. Males display from January to May, and females nest from February to June. Females generally lay 2–3 eggs per clutch, incubating for about 23 days (Bacon et al., 2017b; Gaucher, 1995).

Our study focuses on the Eastern region of Morocco, the main area of intervention (50,170 km²) of the Emirates Center for Wildlife Propagation (hereafter, "ECWP"). In the last decades, the houbara has declined dramatically throughout the species' range due to habitat degradation, poaching and unregulated-hunting (Lacroix et al., 2003), and the species is classified as vulnerable (BirdLife International, 2016). Since 1996, ECWP has ensured the reinforcement of the houbara population in the Eastern region through releases of individuals bred in captivity (Rabier et al., 2020). The ECWP intervention area (hereafter, "the Eastern region") was divided into two management types of area: hunting areas (hunting permitted from October to mid-January) and non-hunting areas (hunting totally prohibited the whole year). Individuals bred in captivity are released during the whole year, and every year, in both types of areas. From 1998–2019, 108,915 individuals were released.

2.2. Nest survival

In the Eastern region of Morocco, nests were located every year through the collaboration of local populations (mainly shepherds) and the tracking of females equipped with transmitters (see Bacon, 2017c). Nests were regularly visited (every 5.2 ± 4.4 days) by observers to evaluate their status: unhatched eggs, hatched or failed (see Bacon, 2017c for detailed protocol). Nests were considered as failed after egg disappeared between visits without any evidence of hatching, or if the nest was abandoned. Egg predation is the main cause of houbara nest failure (at least 74% of nest failures caused by predation, mainly by Red Fox (*Vulpes vulpes*), Bacon, 2017c), followed by abandonment, destruction by trampling and failure due to unidentifiable causes. In addition, since 2013, some nests are monitored with camera traps providing accurate estimation of their fate. From 2012–2019, 7050 nests were monitored in the Eastern region.

Nest survival is the probability that a nest will survive until at least one chick hatches (Rotella et al., 2004). To calculate the daily nest survival rate (hereafter, “DNSR”), we used the logistic exposure approach of Shaffer (2004) employed by Bacon et al. (2017a, 2017b) in their work on the reproductive success of houbaras. We used generalized linear mixed-effects models (GLMM) with a binomial probability distribution and a customized logit link function that considered the differences in exposure periods between nest visits. The nest exposure period ended when the first egg hatched. If the hatching date was not known, the mean date between the last visit with intact eggs and the first visit with at least one hatching egg was used as the hatching date and thus the end of the nest exposure period.

2.3. Density

A standardized counting protocol using the point-count method was carried out yearly, between September and December, in the Eastern region of Morocco (see Monnier-Corbel et al., 2021 for details on counting points protocol). Monnier-Corbel et al. (2021) used a Density Surface Modelling (hereafter, “DSM”) approach using 2011–2018 count data to estimate houbara abundance. First, the count data were used to model a detection function using the distance sampling method (Buckland et al., 1993). The fundamental concept of this method is that the probability of detecting an object decreases as its distance from the observer increases. Then, DSM was used to spatialize abundance estimates from distance sampling data (Miller et al., 2013). The prediction grid, restricted to areas favorable to the presence of houbara in the region (excluding mountainous areas, areas where the slope is greater than 5% and urban areas), with pixels of 73.27 km² (grid of 5 arc-min), represented a total of 38,575 km² (77% of the 50,170 km² of the Eastern region). Using a Generalized Additive Model (GAM), Monnier-Corbel et al. (2021) modeled the annual estimate of houbara abundance as a function of geographic coordinates, using a Tweedie response distribution to tune model flexibility (Miller et al., 2013). This step resulted in abundance maps for each year between 2011 and 2018 (see Monnier-Corbel et al., 2021 for details on the analyses).

Around each nest, within a spatial buffer, we calculated a mean houbara density (number of individuals per km²). Density was calculated by considering mean abundance estimates (on the previous autumn) from the prediction grid (DSM), divided by the spatial buffer area around the nest. Different spatial buffers were tested around each nest: 10 km, 30 km, 50 km and 100 km (Appendix A3).

Despite the time lag between the count period (autumn) and nest location (breeding season, spring), the spatial relationship between abundance and nest distribution was tested and showed a positive and significant relationship (Appendix A2). In addition, previous studies suggest that the distribution of autumn abundance estimates can be a good proxy of the distribution of the displaying males and nesting females during the breeding season. Hingrat et al. (2008) showed, by modeling the lek formation, that males settle at sites where they experienced the highest density of females during the non-breeding season and that nesting females tented to aggregate around leks.

2.4. Habitat suitability index

2.4.1. Presence data

To model the suitable habitat of the reinforced population (wild-born and captive-born houbara) in Morocco, we used presence records collected by the ECWP conservation program. We used different types of houbara geolocated data: nest positions, display observations and positions of wild-born and captive-born individuals (from individuals equipped with satellite-transmitter, VHF transmitters or occasional observations; see details on occurrences data in Appendix A4). We discarded all positions of young captive-born individuals (< 1 years old) to favor settled individuals. We grouped the presence data in ~ 1 km² grid cells (resolution of the environmental predictors, see section Environmental data). For each grid cell we computed the number of weeks of observed data, to be used as relative sampling probabilities of training cases in random forest models. The number of weeks of the presences had a range of values from 0.142 (one day) to 262.5 weeks. However, to avoid inflating the weight of grid cells where the observation program has been running for a longer time, we ran a sensitivity analysis (Appendix C) to find a meaningful threshold for the maximum training weight, and set it to the quantile 0.25 of the total number of weeks (5.28 weeks). We then thinned the occurrences by imposing a minimum separation of two grid cells between nearby records and selecting the pixels with higher weights preferentially. In the end, we accumulated a total of 7205 weighted presence grid cells.

2.4.2. Background data

Due to a lack of absence data we used background data instead to model use versus availability rather than presence versus absence (Boyce and McDonald, 1999; Gianpasquale, 2017). When modeling use versus availability, the presence data represents habitat use, while the background data represents availability. To generate an ecologically meaningful background dataset we first computed a

convex hull around the presence records, calculated the maximum possible distance between two presence records (~1540 km), and used such distance as radius to define a buffer around the convex hull enclosing the presence data. The region inside the buffer represents all the areas and ecological conditions the species has potential access via dispersal. We then selected randomly 10,000 background points within this area. The case weight for each background record was set to 0.14, the sum of weights of all the presences divides by 10,000 (see section “Preparing background data” in Appendix B).

2.4.3. Environmental data

We prepared 51 environmental predictors from diverse sources at a 1 km resolution (see complete list of variables in Appendix B). To select a subset of non-collinear predictors we first fitted 30 Random Forest models using the presence and background data as response variable against the 51 predictors with the function *rf_repeat()* in the R package *spatialRF* (Benito, 2021), and ranked the predictors by median permutation importance. We then removed variables sequentially when their variance inflation factor was higher than 5 (O’Brien, 2007), their maximum Pearson correlation with any other variable was higher than 0.75, and their median importance ranking was the lower. We thus obtained a set of variables with the maximum explanatory power that were not correlated among themselves.

2.4.4. Modeling

We fitted and analyzed a Random Forest model with the R package *ranger* (Wright and Ziegler, 2015) via the R package *spatialRF* (Benito, 2021). The model was trained using the “presence” column (with 1 representing presences and 0 representing background records) as response variable, the selected environmental variables as predictors, and the number of weeks of data for the presences and 0.14 for the background records as case weights. The model comprised 1000 regression trees, with a minimum node size set to 20 observations. To analyze the model results we first assessed variable permutation importance which represents accuracy loss when a variable is permuted across all the forest trees (Breiman, 2001). As a complement to the variable importance analysis, we also assessed partial dependence curves for every predictor, and interaction surfaces for the most important predictors. Finally, we evaluated the predictive performance of the models on independent data by computing the area under the receiver operating characteristics curve (AUC, Fielding and Bell, 1997) via spatial cross-validation on 100 independent spatial folds. Each training fold was geographically contiguous and included 75% of the total training records. We then fitted a model on each training fold, predicted over the remaining data on each iteration, and computed the median AUC across spatial folds. The complete reproducible workflow is available in Appendix B.

2.5. Statistical analyses

2.5.1. Model covariates

In our main statistical model, we explored the link between the DNSR (response variable) and demographic and environmental conditions, based on a generalized linear mixed-effects models with a logistic exposure link function (Herzog et al., 2009). In addition to houbara density and HS index, we considered a set of other explaining covariates not used to build the HS index known to be related to variation in DNSR of female houbara. Meteorological conditions of previous seasons have a major influence on seasonal productivity of habitats in semi-desert environments (Reichmann et al., 2013), and potentially on reproductive performance of bustards (Bacon et al., 2017b; Morales et al., 2002). For each nest location, and for each year, we extracted the mean temperature (**Temp**, in °C) and the mean precipitation amount (**Precp**, in mm/month) of the previous winter (December to February), from the Global Land Data Assimilation System (GLDAS V2.1, Beaudoin and Rodell, 2020; Rodell et al., 2004). In species with extended breeding season as the houbara (up to five months), environmental conditions and intra- and inter-species interactions are also susceptible to show temporal variation and trend within the breeding season, as show in Bacon et al. (2017a) for the houbara. The monitoring **Date** (in Julian day) was thus included as a quantitative covariate. The year was included as a random factor (Year) and spatial coordinates (Latitude LAT and longitude LON) were included as fixed quantitative covariates. We tested for spatial autocorrelation of the DNSR, using a Moran.I test (Gittleman et al., 1990) on the residuals of models with or without LAT and LON. For the analyses, all covariates were rescaled (centered and standardized).

2.5.2. Model averaging

We tested all combinations of additive effects as well as some interaction terms and polynomial effects of Density. We investigated the (1) variation in the effect of density on the DNSR, with covariates accounting polynomial effects of Density (quadratic effect, *Density2* and cubic effect, *Density3*); and (2) different interactions: (i) between Date and Density to study the potential variation in the effect of density on the daily survival rate of the nest during the breeding season (**Date: Density**); (ii) between HS index and density to study the potential variation in the effect of density on the daily survival rate of the nest depending on site suitability (**HS: Density**); (iii) between Date and HS index following the hypothesis that the relationship between the daily nest survival probability and the HS index changes progressively during the breeding season (**Date: HS**; previously tested in Bacon et al., 2017a).

Because in model averaging techniques, the interpretation of model-averaged regression coefficients are not relevant with the presence of interaction terms in models (Cade, 2015), we divided our analysis into two separate steps: (1) starting model including additive effects only and (2) starting model including additive plus interaction and polynomial effects. For each step, we used multi-model inference analysis (Burnham and Anderson, 2002) by considering a set of all simplified model combinations of fixed effect terms in the starting model (we kept the Year as random effects in all models of each set). We ranked models based on AICc criterion (i. e. the small sample size correction of Akaike’s Information Criteria, AIC; Burnham and Anderson, 2002). For each set of models, we

selected the best models ($\Delta AICc < 2$) and calculated the weighted average (and relative 95% confidence interval) of parameter estimates through model averaging (Burnham and Anderson, 2002). We assumed significance of model-averaged coefficients for the covariates if their 95% unconditional confidence intervals (CIs) did not include zero.

For the analyses, all covariates were rescaled: centralized and standardized. We performed all analyses with R version 4.0.2 (R Development Core Team, 2020) using the *lme4* 1.1–23 (Bates et al., 2015) and *MuMIn* 1.43.17 (Barton, 2020).

3. Results

Around each nest, in a spatial buffer, we calculated an average density of houbara. The selected spatial buffer around nests was *density10* which represented the density within a 10 km radius around a nest. The mean number of houbaras within the spatial buffer was 25.4 (SD =19) individuals and ranged from 0.18 to 248 individuals, i.e. corresponding to densities between 5×10^{-4} and 0.8 individual per km^2 . Moran test revealed spatial autocorrelation on DNSR, but no longer when we included nests coordinates (LAT and LON) in tested models (see details in Appendix A6).

We modeled the habitat suitability (HS) index from a set of 11 non-collinear environmental variables selected from a pool of 50 candidate predictors. The selected predictors were climate variables: temperature seasonality (bio4), precipitation of the warmest quarter (bio18), climate aridity index; the annual range of the Normalized Difference Vegetation Index; topographic variables: maximum topographic sun radiation, topographic roughness, wetness, position, and diversity; variables representing human presence and impact: human footprint and human accessibility (see details in Appendix B). According to the permutation importance analysis and the partial dependence curves, aridity, solar radiation, and temperature and precipitation seasonality were the most important predictors, followed by human accessibility and footprint, and the NDVI range.

The median of AUC values across the tested spatial folds was 0.942 (median absolute deviation = 0.049), with values ranging from 0.319 to 0.983 over 100 iterations. Mean HS values over the study area was 0.82 ± 0.23 and ranged from 0.029 to 1. We extracted the values of the HS at the nest locations (Fig. 1). Mean HS at nest locations in the Eastern region was 0.97 ± 0.04 and ranged from 0.41 to 1.

The first set of models, using additive effects only, revealed that the DNSR was negatively related to density around the nest (Fig. 2). For nests located in highest density area of 0.8 ind/ km^2 , DNSR was reduced by more than 25% as compared with nests located in lowest density areas (Fig. 2). DNSR was also influenced by the Date, i.e. the progression of the breeding season, with nests having higher daily

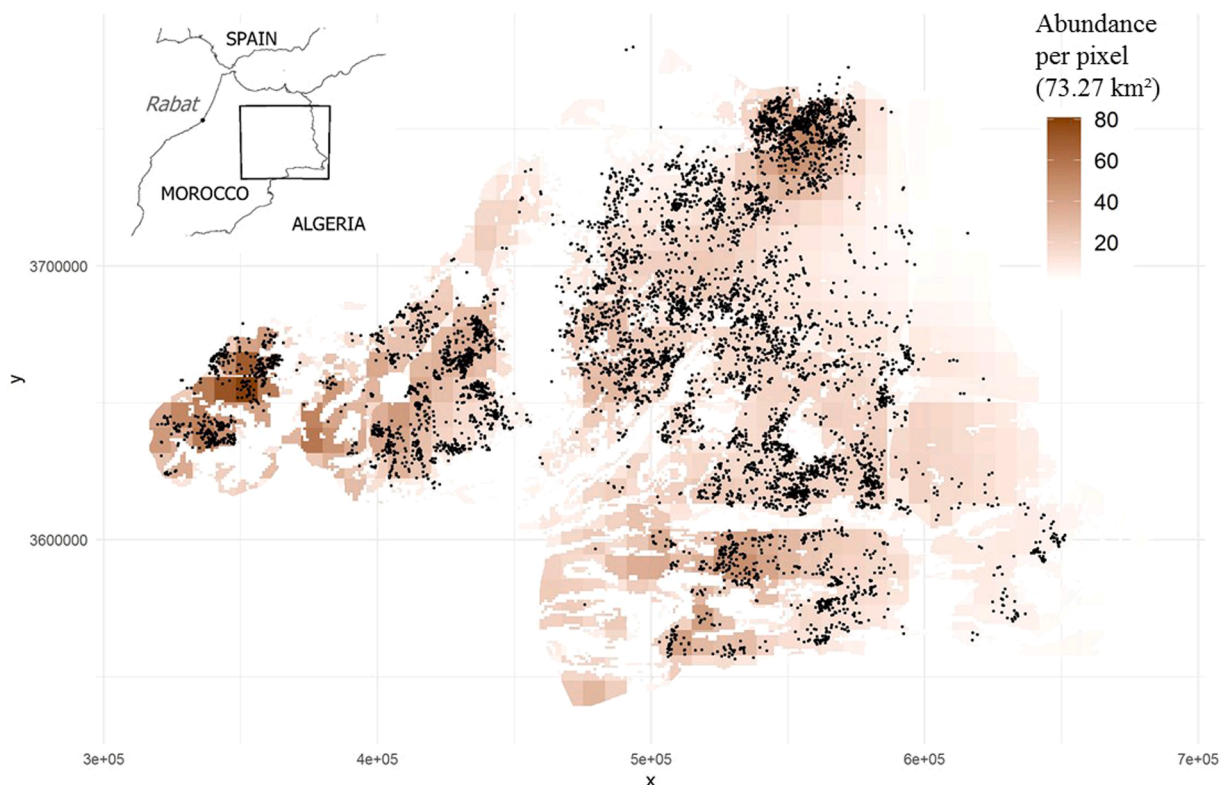


Fig. 1. Abundance distribution map of houbara in the Eastern region of Morocco (i.e. average abundance over the study period, from 2011 to 2018). Abundance is given in terms of absolute density per pixel of 73.27 km^2 (length side of the pixel: 8.56 km), projected in an area of $38,268 \text{ km}^2$ excluding some areas identified as unsuitable for the houbara (see section “Density” in Methods). To illustrate the distribution of nests across the abundance map, locations of the 7050 nests located during the study period are shown (from 2012 to 2019; black dots).

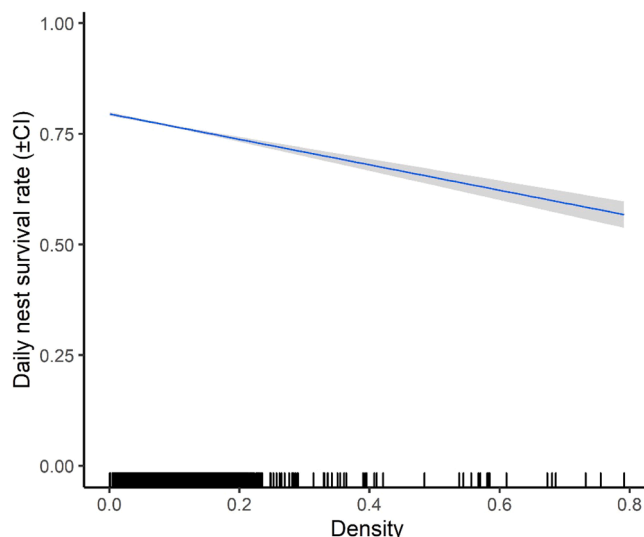


Fig. 2. Relationship between the daily nest survival rate predictions (with \pm 95% CIs) and density in a 10 km radius around the nests, for the second set of models. Rug lines are added on the X axis to illustrate the distribution of points.

survival probabilities at the beginning of the breeding season (Table 1). The DNSR was also negatively related with the longitude and positively related with the amount of precipitation received in the winter pre-breeding season.

The analysis of the second set of models (with additive effects, polynomial effects and interactions), indicated that the DNSR decreased with the density around the nest, the Date and the longitude (Table 2). No global effect of HS on the DNSR was observed. Polynomial effects of density were retained in the best models (Δ AICc < 2; see details in Table A8.2 in Appendix A8) but model coefficients indicated no significant non-linear effects of density on the DNSR. No significant interaction between Date and local density was found. The *HS x Density* and *Date x HS* interactions were not retained in the best models (Δ AICc < 2; see details in Table A8.2 in Appendix A8).

4. Discussion

Our study establishes a clear negative link between the daily nest survival rate (DNSR), a key parameter of breeding success, and the density of houbara estimated around nests, highlighting the occurrence of density-dependent processes in the reinforced houbara population in Eastern Morocco. Our results suggest that this negative effect of density on reproduction is stable in space and time, i.e. it does not vary during the breeding season, nor with the habitat suitability associated with the nest location.

Density-dependent reproduction or survival are important mechanisms in the regulation and dynamics of populations (Cubaynes et al., 2014). A negative relationship between increased density and reproductive success has been found in several bird species (Both, 1998; Bretagnolle et al., 2008; Fasce et al., 2011; Paradis et al., 2002) and has been explained by densities affecting brood provisioning rate, competition for food, behavioral interference (frequency of interactions with conspecifics; Alatalo and Lundberg, 1984), or nest predation (increased detectability; Gunnarsson and Elmgren, 2008). However, the presence of density-dependent mechanisms is not systematic, and many studies failed to uncover such processes (Krebs, 1995). Methods that attempt to relate a trait, such as fecundity, to density, tend to underestimate the strength of density-dependence processes (Lebreton and Gimenez, 2013). The detection of density-dependence depends on the species density itself (Hubbell et al., 1990) and the spatial scale considered. The density relationships may be obscured by averaging over areas of heterogeneous population densities (Ray and Hastings, 1996). In our analysis, such constraints were avoided: (1) the scale of the pixel from which density was estimated locally, is rather small (pixel of 73.27 km²), as compared with the home range of the species (6,100,000 km², BirdLife International, 2021) or the average dispersal distance of

Table 1

Model-averaged coefficients and 95% confidence intervals (CIs) from the set of best models (Δ AICc < 2) for the first set of models. The first set of models focuses on the additive effects of covariates selected on the daily nest survival rate.

Covariate	Coefficients	Lower CI	Upper CI	Relative importance
Date	-0.20	-0.23	-0.16	1
Density	-0.07	-0.10	-0.03	1
LON	-0.06	-0.09	-0.02	1
Precp	0.07	0.00	0.14	0.89
Temp	-0.03	-0.09	0.02	0.47
HS	-0.02	-0.06	0.01	0.46

Table 2

Model-averaged coefficients and 95% confidence intervals (CIs) from the set of best models ($\Delta\text{AICc} < 2$) for the second set of models. The second set of models focuses on the additive, interactions and polynomial effects of covariates selected on the daily nest survival rate.

Covariate	Coefficients	Lower CI	Upper CI	Relative importance
Date	-0.19	-0.23	-0.16	1
Density	-0.13	-0.19	-0.07	1
Density2	-0.03	-0.01	0.06	1
LON	-0.06	-0.09	-0.02	1
Precp	0.06	0.00	0.13	0.86
Density3	0.00	0.00	0.00	0.75
HS	-0.03	-0.06	0.01	0.58
Density:HS	-0.03	-0.07	0.01	0.42
Temp	-0.02	-0.07	0.03	0.14
LAT	0.01	-0.03	0.05	0.13
Date:Density	0.01	-0.02	0.04	0.05
Date:HS	-0.01	-0.03	0.02	0.04

females (9.1 ± 6.6 km, [Hardouin et al., 2012](#)); (2) at the nest scale, we selected a biologically meaningful radius around each nest in which to extract the mean density (10 km radius around each nest selected after different radius were tested, Appendix A3). Considering such fine spatial scales, our data allowed us to uncover a negative relationship between density and demography of strong biological significance, as DNSR drops from 0.8 to 0.6 (i.e. a reduction of 25%) along the increasing density gradient in which nests are located.

In houbara, the DNSR is an important component of nesting success which fate is directly related to the behavior of the female in response to her immediate environment ([Bacon, 2017c](#)). Nesting females are looking for optimal nest location, providing concealment and visibility of the surrounding for predator detection ([Hingrat et al., 2008](#)). During their 23 days of incubation, female will stay nights and days on their eggs and will leave the nest for short feeding trips in the immediate vicinity of the nest ([Gaucher et al., 1995](#)). Such optimal sites are limited and competition between breeding females for best habitats is expected as illustrated by our results (Table A5 and Fig. A5.2 in Appendix A), leading to an aggregative distribution of nests ([Hingrat et al., 2008](#)). In addition, the socio-sexual system of the species is promoting individuals' spatial aggregation leading to density-dependent processes. The houbara is a polygynous species with an exploded-lek mating system ([Hingrat et al., 2004](#)). During the breeding season, males aggregate for courtship, and female nests are spatially associated with the occurrence of leks in habitats of highest suitability ([Hingrat et al., 2004, 2008](#)). Higher density of conspecifics in the vicinity of houbara nests will increase intra and inter-species interactions. In terms of intra-species interactions, behaviors like nest parasitism ([Lesobre et al., 2010](#)), male harassment, and competition for food, will increase disturbance, alter foraging (duration of feeding trips / food depletion), and incubation behaviors (egg turning and temperature regulation). All of these perturbations of nesting females will in turn influence interspecific interactions by decreasing concealment and favoring nest predation ([Gunnarsson and Elmenberg, 2008](#)).

Intraspecific interactions and environmental conditions are expected to change along the breeding season. However, although nest survival was decreasing over the breeding season (as previously demonstrated on different houbara reproductive parameters: DNSR, clutch size, egg volume. [Bacon et al., 2017b](#)), our results suggest that the density-dependence pattern did not vary over time (no significant interaction between date and density) despite the observation of different slopes of the DNSR-density relationship between the beginning and the end of the breeding season (Table A9.1 in Appendix A). This may suggest that density over the season and thus the density-dependent relationship may vary but that our density proxy does not account for this variation. Furthermore, the effect of date on reproductive success reflects an interaction between individual and environmental characteristics at a certain time of the season. In houbara, more experienced and older females tend to breed earlier in the breeding season ([Bacon et al., 2017b](#)), a demographic heterogeneity that could drive seasonal variation in nest survival. Furthermore, environmental conditions are expected to change along the breeding season. Previous studies have highlighted the effects of weather variations on different demographic parameters, such as survival ([Hardouin et al., 2014](#)), dispersal distance ([Hardouin et al., 2014](#)), abundances ([Monnier-Corbel et al., 2021](#)), and reproductive parameters (clutch size, [Bacon et al., 2017b](#)), suggesting that changes in weather conditions may also impact nest survival along the breeding season. Beyond the direct impact of weather factors on houbara demographic parameters, meteorological variation could interact with density-dependence processes and affect population dynamics and size, where weather factors would tend to increase population variability, while negative density-dependence tends to decrease this variability ([Hambäck, 2021](#)).

In the current study, we did not observe any variation in the relationship between nest survival and habitat suitability (HS) over the breeding season, as shown by [Bacon et al. \(2017a\)](#) on the same species. These contrasting results could be explained by the different spatial extents used to model the HS: our study focuses on the Eastern region of Morocco ([Fig. 1](#)) with an overall high HS at nesting sites (mean: 0.97 ± 0.04); while the study of [Bacon et al. \(2017a\)](#) included an additional region in the South of Morocco, with lower quality environments and thus a larger range of HS values. While the HS index has no effect on nest survival, nest survival may be influenced by other environmental factors that are not always included in environmental indices such as the HS index, such as biotic interactions (i.e. predation, presence of conspecifics) or dispersal limitations.

Spatial heterogeneity may influence density-dependence processes through its impact on abundances. In houbara, spatial variation of abundances is partly explained by spatial heterogeneity of weather conditions ([Monnier-Corbel et al., 2021](#)). Nests were also non-randomly distributed in the Eastern region of Morocco: we found presence of spatial autocorrelation in nest survival and, a positive spatial relationship between nest distribution and houbara abundances, in agreement with studies on the species mating

system (Hingrat and Saint Jalme, 2005). In this study, we used the HS index as a proxy of spatial heterogeneity, reflecting the environmental conditions encountered by the houbara. Density dependence was not moderated by the HS index associated with the nest, i.e. the interaction between the HS index and density did not show significant effect on nest survival. This absence of effect may be due to too slight variation in HS index: all houbara nests located in habitats of high suitability (Table A5 and Fig. A5.2 in Appendix A). It is a common issue when studying breeding locations that are often the result of a strong selection process (Latif et al., 2012). Alternatively, this absence of effect may be due to the existence of a non-linear effect between the HS index and density not tested here. Indeed, HS index is not systematically linearly correlated with demographic parameters and/or abundances. In houbara population for instance, it has been showed that the most suitable habitats were not always associated with best demographic performances (Monnet et al., 2015a), suggesting complex demographic-environment relationships in the most suitable habitats. Complex, non-linear relationships between habitat suitability and abundance have previously been identified in a range of taxa (Acevedo et al., 2017; VanDerWal et al., 2009; Weber et al., 2017).

In Eastern Morocco, several studies have documented the effectiveness of the reinforcement program initiated in 1998 on the progressive recovery of the houbara population. It has notably been shown that the regular release of suitable captive-bred individuals (Rabier et al., 2020), had positively impacted local abundances (Monnier-Corbel et al., 2021). The survival of captive-bred released birds (Hardouin et al., 2014), their settlement across the ecological space of the species (Bourass and Hingrat, 2015; Monnet et al., 2015b), and their effective contribution to the annual productivity (Bacon et al., 2019), all contributed to the gradual restoration of the population. However, recent findings also highlighted that after a growing phase (first decade of the program), observed densities in the last years (second decade) stagnated around 0.38 individuals per km² (from 2016 to 2018, Monnier-Corbel et al., 2021), suggesting some population growth regulation mechanisms, as hypothesized in previous studies (Bacon et al., 2017a; Hardouin et al., 2015; Monnet et al., 2015a). In a growing population, the progressive colonization of the available ecological space and the increase in population size can have positive effects (Courchamp et al., 1999). However, such growth might be limited by the habitat carrying capacity (Shaffer, 1981), and the increase in population size can then have some negative effects on one or more demographic parameters, contributing to the regulation of the population growth rate.

Because mechanisms shaping population dynamics are complex and depend on the trait considered, Nevoux et al. (2011) advised studying all vital rates that are likely to significantly impact population growth before concluding on how a population is regulated. For example, previous studies have documented non-random movements of houbaras according to habitat quality (Monnet, 2014) and management practices (Hardouin et al., 2014), suggesting a heterogeneity in terms of site attractiveness, possibly leading to an increase of local abundance. Furthermore, local abundances are also influenced by releases (Monnier-Corbel et al., 2021). These results suggest that knowledge of the intrinsic population dynamics is necessary but not sufficient to fully understand the mechanisms driving local abundances and determine optimal release strategy minimizing negative density-dependence. Further research on dispersal and habitat selection patterns is needed to assess the attractiveness of sites of different qualities.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02071](https://doi.org/10.1016/j.gecco.2022.e02071).

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