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► **To cite this version:**

Alice Monnier-Corbel, Anne-Christine Monnet, Léo Bacon, Blas Benito, Alexandre Robert, et al..
Density-dependence of reproductive success in a Houbara bustard population. *Global Ecology and
Conservation*, 2022, 35, pp.e02071. 10.1016/j.gecco.2022.e02071 . mnhn-03766599

HAL Id: mnhn-03766599

<https://mnhn.hal.science/mnhn-03766599v1>

Submitted on 22 Jul 2024

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Density-dependence of reproductive success in a Houbara bustard population

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1 **Density-dependence of reproductive success in a Houbara bustard** 2 **population**

3 **Abstract**

4 Although density-dependent processes and their impacts on population dynamics are key issues
5 in ecology and conservation biology, empirical evidence of density-dependence remains scarce
6 for species or populations with low densities, scattered distributions, and especially for
7 managed populations where densities may vary as a result of extrinsic factors (such as
8 harvesting or releases). Here, we explore the presence of density-dependent processes in a
9 reinforced population of North African Houbara bustard (*Chlamydotis undulata undulata*). We
10 investigated the relationship between reproductive success and local density, and the possible
11 variation of this relationship according to habitat suitability using three independent datasets.
12 Based on eight years of nests monitoring (more than 7,000 nests), we modelled the Daily Nest
13 Survival Rate (DNSR) as a proxy of reproductive success. Our results indicate that DNSR was
14 negatively impacted by local densities and that this relationship was approximately constant in
15 space and time: (1) although DNSR strongly decreased over the breeding season, the negative
16 relationship between DNSR and density remained constant over the breeding season; (2) this
17 density-dependent relationship did not vary with the quality of the habitat associated with the
18 nest location. Previous studies have shown that the demographic parameters and population
19 dynamics of the reinforced North African Houbara bustard are strongly influenced by extrinsic
20 environmental and management parameters. Our study further indicates the existence of
21 density-dependent regulation in a low-density, managed population.

22

23 **Keywords**

24 Density-dependence; breeding success; density; habitat suitability; nest; reinforcement

25 **1. Introduction**

26 The spatial and temporal distribution of species and population abundances is shaped by various
27 processes that can have opposing effects. Habitat, social interactions, interspecific interactions,
28 but also human impact influence population abundance through processes that can be density-
29 dependent or density-independent, and that can interact with each other (Reed et al., 2013). In
30 the context of a particular plant or animal population, density-dependence occurs when one or
31 more demographic parameters vary with population density or population size. Whereas
32 density-dependent processes influence abundance variation in space and time, the intensity of
33 these processes themselves can vary with the environment to modulate carrying capacity (i.e.,
34 i.e. the maximum population size of a particular species that can be sustained by a specific
35 environment, given the resources available for the species, Chapman et al., 2018; Fowler et al.,
36 2010; Hui, 2006; Iijima et al., 2016). Habitat quality is a key component of carrying capacity
37 (Downs et al., 2008) that varies over space and time. This spatial heterogeneity can be
38 approximated by spatial projections such as the habitat suitability index coming from models
39 relating the local occurrences of a species to different environmental characteristics to reflect
40 niche parameters that are most suitable for an individual (Araújo et al., 2002). It is expected
41 that local abundance, and local growth rate would be positively correlated with habitat
42 suitability, based on the idea that densities should be higher where environmental conditions
43 are optimal for a species compared to less favorable habitats (Acevedo et al., 2017; Weber et
44 al., 2017). However, empirical studies show contrasting results on the type of relationship
45 between habitat suitability index and population abundance (or demographic rates; Acevedo et
46 al., 2017; Dallas et al., 2017; Lunghi et al., 2018). On one hand, in highly favorable habitats,
47 higher carrying capacities and higher (and potentially more stable) growth rates are expected,
48 compared to less favorable habitats. On the other hand, in these highly suitable sites,
49 demographic parameters are expected to be impacted by density-dependence.

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

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

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

79 **2. Methods**

80 **2.1. Study species and study area**

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

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

98 **2.2. Nest Survival**

99 In the Eastern region of Morocco, nests were located every year through the collaboration of
100 local populations (mainly shepherds) and the tracking of females equipped with transmitters
101 (see Bacon, 2017c). Nests were regularly visited (every 5.2 ± 4.4 days) by observers to evaluate
102 their status: unhatched eggs, hatched or failed (see Bacon, 2017c for detailed protocol). Nests
103 were considered as failed after egg disappeared between visits without any evidence of
104 hatching, or if the nest was abandoned. Egg predation is the main cause of houbara nest failure
105 (at least 74% of nest failures caused by predation, mainly by Red Fox (*Vulpes vulpes*), Bacon,
106 2017c), followed by abandonment, destruction by trampling and failure due to unidentifiable
107 causes. In addition, since 2013, some nests are monitored with camera traps providing accurate
108 estimation of their fate. From 2012 to 2019, 7,050 nests were monitored in the Eastern region.

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

118 **2.3. Density**

119 A standardized counting protocol using the point-count method was carried out yearly, between
120 September and December, in the Eastern region of Morocco (see Monnier-Corbel et al., 2021
121 for details on counting points protocol). Monnier-Corbel et al., (2021) used a Density Surface
122 Modelling (hereafter, “DSM”) approach using 2011 to 2018 count data to estimate houbara

123 abundance. First, the count data were used to model a detection function using the distance
124 sampling method (Buckland et al., 1993). The fundamental concept of this method is that the
125 probability of detecting an object decreases as its distance from the observer increases. Then,
126 DSM was used to spatialize abundance estimates from distance sampling data (Miller et al.,
127 2013). The prediction grid, restricted to areas favorable to the presence of houbara in the region
128 (excluding mountainous areas, areas where the slope is greater than 5% and urban areas), with
129 pixels of 73.27 km² (grid of 5 minutes of arc), represented a total of 38,575 km² (77% of the
130 50,170 km² of the Eastern region). Using a Generalized Additive Model (GAM), Monnier-
131 Corbel et al., (2021) modeled the annual estimate of houbara abundance as a function of
132 geographic coordinates, using a Tweedie response distribution to tune model flexibility (Miller
133 et al., 2013). This step resulted in abundance maps for each year between 2011 and 2018 (see
134 Monnier-Corbel et al., 2021 for details on the analyses).

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

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

148 **2.4. Habitat Suitability Index**

149 *2.4.1. Presence data*

150 To model the suitable habitat of the reinforced population (wild-born and captive-born houbara)
151 in Morocco, we used presence records collected by the ECWP conservation programme. We
152 used different types of houbara geolocalized data: nest positions, display observations and
153 positions of wild-born and captive-born individuals (from individuals equipped with satellite-
154 transmitter, VHF transmitters or occasional observations; see details on occurrences data in
155 Appendix A4). We discarded all positions of young captive-born individuals (< 1 years old) to
156 favor settled individuals. We grouped the presence data in ~1km² grid cells (resolution of the
157 environmental predictors, see section Environmental data). For each grid cell we computed the
158 number of weeks of observed data, to be used as relative sampling probabilities of training cases
159 in random forest models. The number of weeks of the presences had a range of values from
160 0.142 (one day) to 262.5 weeks. However, to avoid inflating the weight of grid cells where the
161 observation programme has been running for a longer time, we ran a sensitivity analysis
162 (Appendix C) to find a meaningful threshold for the maximum training weight, and set it to the
163 quantile 0.25 of the total number of weeks (5.28 weeks). We then thinned the occurrences by
164 imposing a minimum separation of two grid cells between nearby records and selecting the
165 pixels with higher weights preferentially. In the end, we accumulated a total of 7,205 weighted
166 presence grid cells.

167 *2.4.2. Background data*

168 Due to a lack of absence data we used background data instead to model use *versus* availability
169 rather than presence *versus* absence (Boyce and McDonald 1999; Gianpasquale, 2017). When
170 modeling use *versus* availability, the presence data represents habitat use, while the background
171 data represents availability. To generate an ecologically meaningful background dataset we first
172 computed a convex hull around the presence records, calculated the maximum possible distance

173 between two presence records (~1,540 km), and used such distance as radius to define a buffer
174 around the convex hull enclosing the presence data. The region inside the buffer represents all
175 the areas and ecological conditions the species has potential access via dispersal. We then
176 selected randomly 10,000 background points within this area. The case weight for each
177 background record was set to 0.14, the sum of weights of all the presences divides by 10,000
178 (see section “Preparing background data” in Appendix B).

179 2.4.3. *Environmental data*

180 We prepared 51 environmental predictors from diverse sources at a 1 km resolution (see
181 complete list of variables in Appendix B). To select a subset of non-collinear predictors we first
182 fitted 30 Random Forest models using the presence and background data as response variable
183 against the 51 predictors with the function *rf_repeat()* in the R package *spatialRF* (Benito,
184 2021), and ranked the predictors by median permutation importance. We then removed
185 variables sequentially when their variance inflation factor was higher than 5 (O’Brien, 2007),
186 their maximum Pearson correlation with any other variable was higher than 0.75, and their
187 median importance ranking was the lower. We thus obtained a set of variables with the
188 maximum explanatory power that were not correlated among themselves.

189 2.4.4. *Modelling*

190 We fitted and analyzed a Random Forest model with the R package *ranger* (Wright and Ziegler,
191 2017) via the R package *spatialRF* (Benito, 2021). The model was trained using the “presence”
192 column (with 1 representing presences and 0 representing background records) as response
193 variable, the selected environmental variables as predictors, and the number of weeks of data
194 for the presences and 0.14 for the background records as case weights. The model comprised
195 1000 regression trees, with a minimum node size set to 20 observations. To analyze the model
196 results we first assessed variable permutation importance which represents accuracy loss when
197 a variable is permuted across all the forest trees (Breiman, 2001). As a complement to the

198 variable importance analysis, we also assessed partial dependence curves for every predictor,
199 and interaction surfaces for the most important predictors. Finally, we evaluated the predictive
200 performance of the models on independent data by computing the area under the receiver
201 operating characteristics curve (AUC, Fielding and Bell, 1997) via spatial cross-validation on
202 100 independent spatial folds. Each training fold was geographically contiguous and included
203 75% of the total training records. We then fitted a model on each training fold, predicted over
204 the remaining data on each iteration, and computed the median AUC across spatial folds. The
205 complete reproducible workflow is available in Appendix B.

206 **2.5. Statistical analyses**

207 *2.5.1. Model covariates*

208 In our main statistical model, we explored the link between the DNSR (response variable) and
209 demographic and environmental conditions, based on a generalized linear mixed-effects models
210 with a logistic exposure link function (Herzog et al., 2009). In addition to houbara density and
211 HS index, we considered a set of other explaining covariates not used to build the HS index
212 known to be related to variation in DNSR of female houbara. Meteorological conditions of
213 previous seasons have a major influence on seasonal productivity of habitats in semi-desert
214 environments (Reichmann et al. 2013), and potentially on reproductive performance of bustards
215 (Bacon et al., 2017b; Morales et al., 2002). For each nest location, and for each year, we
216 extracted the mean temperature (**Temp**, in °C) and the mean precipitation amount (**Precp**, in
217 mm/month) of the previous winter (December to February), from the Global Land Data
218 Assimilation System (GLDAS V2.1, Beaudoin and Rodell, 2020; Rodell et al., 2004). In
219 species with extended breeding season as the houbara (up to five months), environmental
220 conditions and intra- and inter-species interactions are also susceptible to show temporal
221 variation and trend within the breeding season, as show in Bacon et al., (2017a) for the houbara.
222 The monitoring **Date** (in Julian day) was thus included as a quantitative covariate. The year

223 was included as a random factor (Year) and spatial coordinates (Latitude LAT and longitude
224 LON) were included as fixed quantitative covariates. We tested for spatial autocorrelation of
225 the DNSR, using a Moran.I test (Gittleman et al., 1990) on the residuals of models with or
226 without LAT and LON. For the analyses, all covariates were rescaled (centered and
227 standardized).

228 2.5.2. *Model averaging*

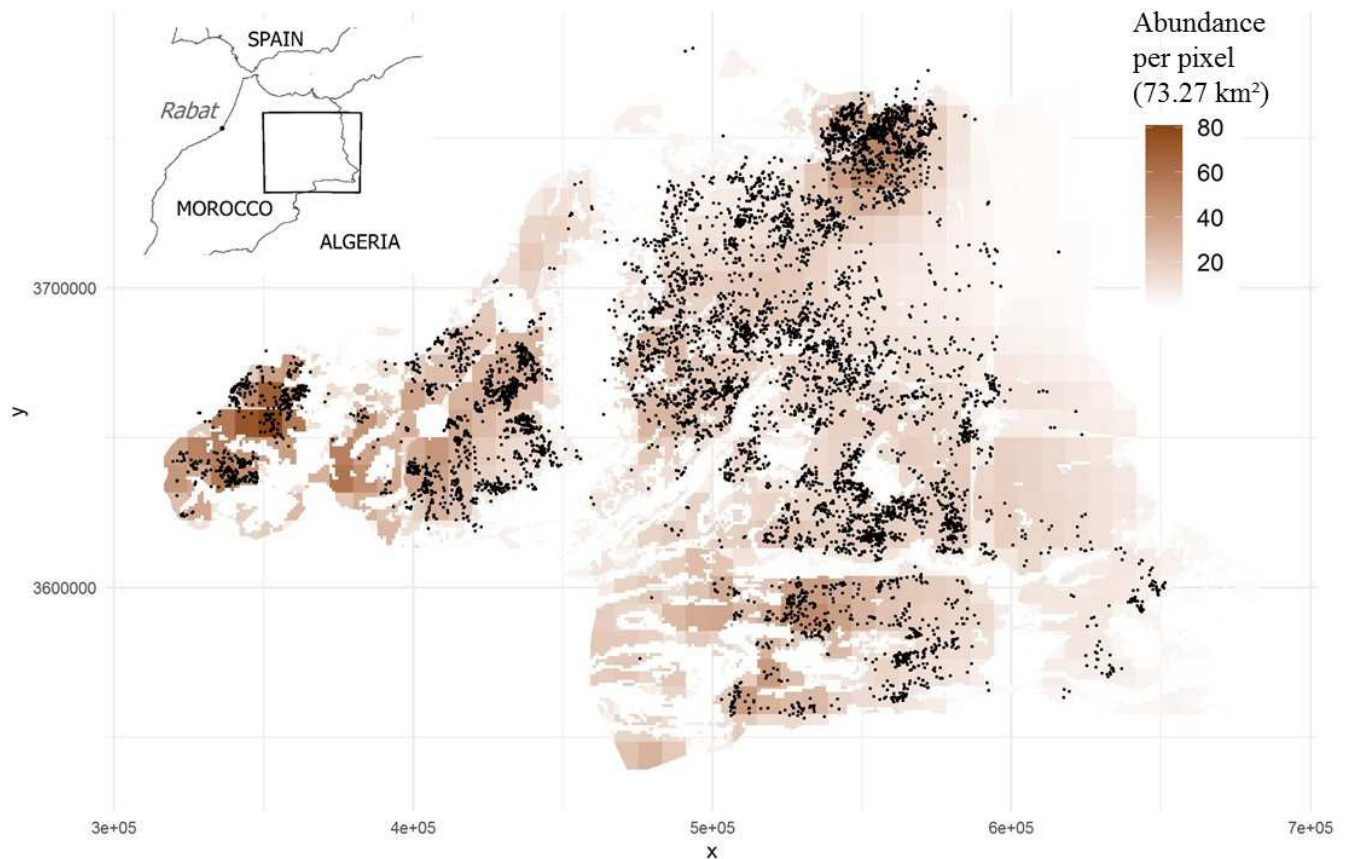
229 We tested all combinations of additive effects as well as some interaction terms and polynomial
230 effects of Density. We investigated the (1) variation in the effect of density on the DNSR, with
231 covariates accounting polynomial effects of Density (quadratic effect, *Density2* and cubic
232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

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

248 calculated the weighted average (and relative 95% confidence interval) of parameter estimates
249 through model averaging (Burnham and Anderson, 2002). We assumed significance of model-
250 averaged coefficients for the covariates if their 95% unconditional confidence intervals (CIs)
251 did not include zero.

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

255 3. Results



256
257 Fig. 1: Abundance distribution map of houbara in the Eastern region of Morocco (i.e. average abundance over the
258 study period, from 2011 to 2018). Abundance is given in terms of absolute density per pixel of 73.27 km² (length
259 side of the pixel: 8.56 km), projected in an area of 38,268 km² excluding some areas identified as unsuitable for

260 the houbara (see section “Density” in Methods). To illustrate the distribution of nests across the abundance map,
261 locations of the 7,050 nests located during the study period are shown (from 2012 to 2019; black dots).

262 Around each nest, in a spatial buffer, we calculated an average density of houbara. The selected
263 spatial buffer around nests was *density10* which represented the density within a 10 km radius
264 around a nest. The mean number of houbaras within the spatial buffer was 25.4 (SD =19)
265 individuals and ranged from 0.18 to 248 individuals, i.e. corresponding to densities between
266 5×10^{-4} and 0.8 individual per km². Moran test revealed spatial autocorrelation on DNSR, but no
267 longer when we included nests coordinates (LAT and LON) in tested models (see details in
268 Appendix A6).

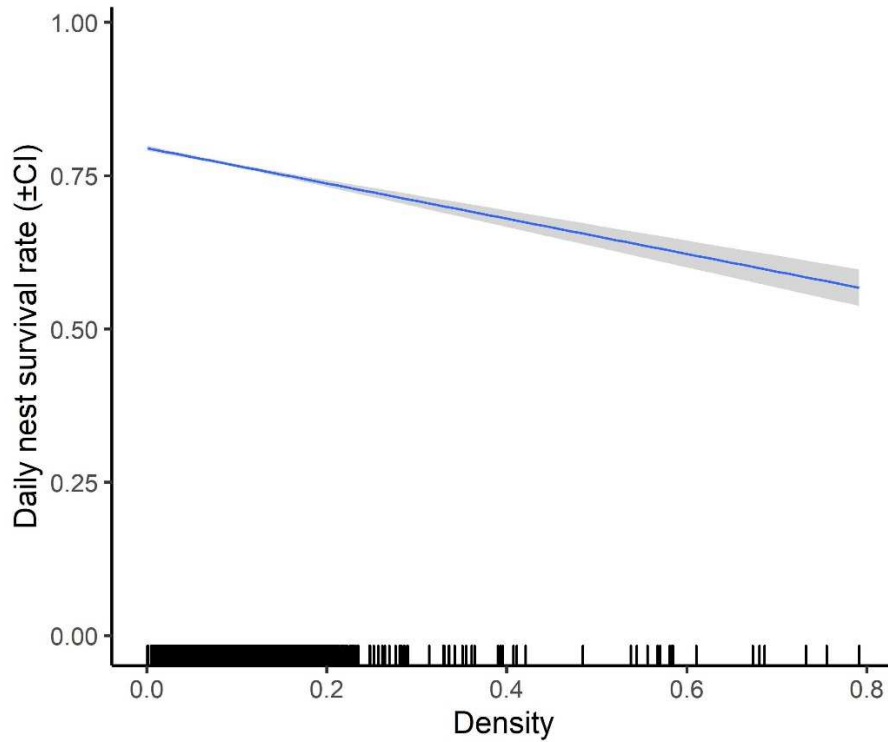
269 We modelled the habitat suitability (HS) index from a set of 11 non-collinear environmental
270 variables selected from a pool of 50 candidate predictors. The selected predictors were climate
271 variables: temperature seasonality (bio4), precipitation of the warmest quarter (bio18), climate
272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

279 The median of AUC values across the tested spatial folds was 0.942 (median absolute deviation
280 = 0.049), with values ranging from 0.319 to 0.983 over 100 iterations. Mean HS values over
281 the study area was 0.82 ± 0.23 and ranged from 0.029 to 1. We extracted the values of the HS
282 at the nest locations (Fig. 1). Mean HS at nest locations in the Eastern region was 0.97 ± 0.04
283 and ranged from 0.41 to 1.

284 The first set of models, using additive effects only, revealed that the DNSR was negatively
285 related to density around the nest (Fig.2). For nests located in highest density area of 0.8
286 ind/km², DNSR was reduces by more than 25% as compared with nests located in lowest density
287 areas (Fig.2). DNSR was also influenced by the Date, i.e. the progression of the breeding
288 season, with nests having higher daily survival probabilities at the beginning of the breeding
289 season (Table 1). The DNSR was also negatively related with the longitude and positively
290 related with the amount of precipitation received in the winter pre-breeding season.

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

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



302

303 Table 1: Model-averaged coefficients and 95% confidence intervals (CIs) from the set of best models ($\Delta AICc <$
 304 2) for the first set of models. The first set of models focuses on the additive effects of covariates selected on the
 305 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

306

307 Table 2: Model-averaged coefficients and 95% confidence intervals (CIs) from the set of best models ($\Delta AICc <$
 308 2) for the second set of models. The second set of models focuses on the additive, interactions and polynomial
 309 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

310

311

312 **4. Discussion**

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

319 Density-dependent reproduction or survival are important mechanisms in the regulation and
320 dynamics of populations (Cubaynes et al., 2014). A negative relationship between increased
321 density and reproductive success has been found in several bird species (Both, 1998;
322 Bretagnolle et al., 2008; Fasce et al., 2011; Paradis et al., 2002) and has been explained by
323 densities affecting brood provisioning rate, competition for food, behavioral interference

324 (frequency of interactions with conspecifics; Alatalo et al., 1984), or nest predation (increased
325 detectability; Gunnarsson and Elmberg, 2008). However, the presence of density-dependent
326 mechanisms is not systematic, and many studies failed to uncover such processes (Krebs, 1995).
327 Methods that attempt to relate a trait, such as fecundity, to density, tend to underestimate the
328 strength of density-dependence processes (Lebreton and Gimenez, 2013). The detection of
329 density-dependence depends on the species density itself (Hubbell et al., 1990) and the spatial
330 scale considered. The density relationships may be obscured by averaging over areas of
331 heterogeneous population densities (Ray and Hasting, 1996). In our analysis, such constraints
332 were avoided: (1) the scale of the pixel from which density was estimated locally, is rather small
333 (pixel of 73.27 km²), as compared with the home range of the species (6,100,000 km², BirdLife,
334 2021) or the average dispersal distance of females (9.1 ± 6.6 km, Hardouin et al., 2012); (2) at
335 the nest scale, we selected a biologically meaningful radius around each nest in which to extract
336 the mean density (10 km radius around each nest selected after different radius were tested,
337 Appendix A3). Considering such fine spatial scales, our data allowed us to uncover a negative
338 relationship between density and demography of strong biological significance, as DNSR drops
339 from 0.8 to 0.6 (i.e. a reduction of 25%) along the increasing density gradient in which nests
340 are located.

341 In houbara, the DNSR is an important component of nesting success which fate is directly
342 related to the behavior of the female in response to her immediate environment (Bacon, 2017c).
343 Nesting females are looking for optimal nest location, providing concealment and visibility of
344 the surrounding for predator detection (Hingrat et al., 2008). During their 23 days of incubation,
345 female will stay nights and days on their eggs and will leave the nest for short feeding trips in
346 the immediate vicinity of the nest (Gaucher et al., 1995). Such optimal sites are limited and
347 competition between breeding females for best habitats is expected as illustrated by our results
348 (Table A5 and Fig. A5.2 in Appendix A), leading to an aggregative distribution of nests

349 (Hingrat et al., 2008). In addition, the socio-sexual system of the species is promoting
350 individuals' spatial aggregation leading to density-dependent processes. The houbara is a
351 polygynous species with an exploded-lek mating system (Hingrat et al., 2004). During the
352 breeding season, males aggregate for courtship, and female nests are spatially associated with
353 the occurrence of leks in habitats of highest suitability (Hingrat et al., 2004; Hingrat et al.,
354 2008). Higher density of conspecifics in the vicinity of houbara nests will increase intra and
355 inter-species interactions. In terms of intra-species interactions, behaviors like nest parasitism
356 (Lesobre et al., 2010), male harassment, and competition for food, will increase disturbance,
357 alter foraging (duration of feeding trips / food depletion), and incubation behaviors (egg turning
358 and temperature regulation). All of these perturbations of nesting females will in turn influence
359 interspecific interactions by decreasing concealment and favoring nest predation (Gunnarson
360 and Elmenberg, 2008).

361 Intraspecific interactions and environmental conditions are expected to change along the
362 breeding season. However, although nest survival was decreasing over the breeding season (as
363 previously demonstrated on different houbara reproductive parameters: DNSR, clutch size, egg
364 volume. Bacon et al., 2017b), our results suggest that the density-dependence pattern did not
365 vary over time (no significant interaction between date and density) despite the observation of
366 different slopes of the DNSR-density relationship between the beginning and the end of the
367 breeding season (Table A9.1 in Appendix A). This may suggest that density over the season
368 and thus the density-dependent relationship may vary but that our density proxy does not
369 account for this variation. Furthermore, the effect of date on reproductive success reflects an
370 interaction between individual and environmental characteristics at a certain time of the season.
371 In houbara, more experienced and older females tend to breed earlier in the breeding season
372 (Bacon et al., 2017b), a demographic heterogeneity that could drive seasonal variation in nest
373 survival. Furthermore, environmental conditions are expected to change along the breeding

374 season. Previous studies have highlighted the effects of weather variations on different
375 demographic parameters, such as survival (Hardouin et al., 2014), dispersal distance (Hardouin
376 et al., 2014), abundances (Monnier-Corbel et al., 2021), and reproductive parameters (clutch
377 size, Bacon et al., 2017b), suggesting that changes in weather conditions may also impact nest
378 survival along the breeding season. Beyond the direct impact of weather factors on houbara
379 demographic parameters, meteorological variation could interact with density-dependence
380 processes and affect population dynamics and size, where weather factors would tend to
381 increase population variability, while negative density-dependence tends to decrease this
382 variability (Hambäck, 2021).

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

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

399 Jalme, 2005). In this study, we used the HS index as a proxy of spatial heterogeneity, reflecting
400 the environmental conditions encountered by the houbara. Density dependence was not
401 moderated by the HS index associated with the nest, i.e. the interaction between the HS index
402 and density did not show significant effect on nest survival. This absence of effect may be due
403 to too slight variation in HS index: all houbara nests located in habitats of high suitability (Table
404 A5 and Fig. A5.2 in Appendix A). It is a common issue when studying breeding locations that
405 are often the result of a strong selection process (Latif et al., 2012). Alternatively, this absence
406 of effect may be due to the existence of a non-linear effect between the HS index and density
407 not tested here. Indeed, HS index is not systematically linearly correlated with demographic
408 parameters and/or abundances. In houbara population for instance, it has been showed that the
409 most suitable habitats were not always associated with best demographic performances
410 (Monnet et al., 2015a), suggesting complex demographic-environment relationships in the most
411 suitable habitats. Complex, non-linear relationships between habitat suitability and abundance
412 have previously been identified in a range of taxa (Acevedo et al., 2017; VanDer Wal et al.,
413 2009; Weber et al., 2017).

414 In Eastern Morocco, several studies have documented the effectiveness of the reinforcement
415 programme initiated in 1998 on the progressive recovery of the houbara population. It has
416 notably been shown that the regular release of suitable captive-bred individuals (Rabier et al.,
417 2020), had positively impacted local abundances (Monnier-Corbel et al., 2021). The survival
418 of captive-bred released birds (Hardouin et al., 2014), their settlement across the ecological
419 space of the species (Bourass and Hingrat, 2015; Monnet et al., 2015b), and their effective
420 contribution to the annual productivity (Bacon et al., 2019), all contributed to the gradual
421 restoration of the population. However, recent findings also highlighted that after a growing
422 phase (first decade of the programme), observed densities in the last years (second decade)
423 stagnated around 0.38 individuals per km² (from 2016 to 2018, Monnier-Corbel et al., 2021),

424 suggesting some population growth regulation mechanisms, as hypothesized in previous studies
425 (Bacon et al., 2017a; Hardouin et al., 2015; Monnet et al., 2015a). In a growing population, the
426 progressive colonization of the available ecological space and the increase in population size
427 can have positive effects (Courchamp et al., 1999). However, such growth might be limited by
428 the habitat carrying capacity (Shaffer, 1981), and the increase in population size can then have
429 some negative effects on one or more demographic parameters, contributing to the regulation
430 of the population growth rate.

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

442

443 **Acknowledgments**

444 We are grateful to HH Sheikh Mohamed bin Zayed Al Nahyan, Crown Prince of Abu Dhabi
445 and Founder of the IFHC, HH Sheikh Theyab Bin Mohamed Al Nahyan, Chairman of the IFHC,
446 and HE Mohammed Ahmed Al Bowardi, Deputy Chairman, for their support. This study was
447 conducted under the guidance of RENECO International Wildlife Consultants LLC., a

448 consulting company managing ECWP. The authors also thank Dr. F. Lacroix, managing
449 director, and G. Leveque, project director, for their guidance. Additionally, the authors thank
450 ECWP staff from the Ecology division who participated in data collection and Thibault
451 Dieuleveut, Christelle Lucas, Cedric Ferlat, and Eric le Nuz, for their advice on the database.

452 **Funding:**

453 The study was funded by Emirates Center for Wildlife Propagation (ECWP), a project of the
454 International Fund for Houbara Conservation (IFHC).

455 **Declaration of Competing Interest**

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

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