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# Patterns of abundance reveal evidence of translocation and climate effects on Houbara bustard population recovery

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3

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## 22 **Abstract:**

23 Population reinforcement, through translocations of individuals, aims to restore populations of  
24 threatened species. The increase in population size or geographic distribution is often used as positive  
25 facts when assessing the recovery of a species, making abundance monitoring a major criterion. Based  
26 on 8-year monitoring of a reinforced population of North African Houbara bustard (*Chlamydotis*  
27 *undulata undulata*), over an area of 50,170 km<sup>2</sup> in the eastern region of Morocco, we assessed the  
28 success of management actions by assessing spatial and temporal variation in abundance as well as the  
29 factors driving this variation. We used count data to estimate and spatialize population abundance. We  
30 then assessed environmental (climate) and management covariates (release effort and hunting  
31 management) associated with temporal and spatial variation in abundance. The overall estimate of  
32 abundance in the study area was 16,918 individuals (95% CI = 13,629 to 21,027) over our study period,  
33 with strong variation between years (range = 10,409 - 32,401). Our results highlighted strong spatial  
34 heterogeneity over the study area, linked to spatial variation in local climate and management conditions.  
35 Local abundances were negatively associated with local temperature, were higher in hunting than in  
36 non-hunting areas, and were positively influenced by the number of birds released around the focal  
37 point. In addition to describing the spatio-temporal variation in the abundance of the species on a large  
38 scale, we estimated two major proxies of its conservation status: population size and population trend.  
39 The determination of these proxies and the comparison with the counterfactual state of the species  
40 confirms the beneficial impact of the restoration and protection programme on the dynamics of the North  
41 African Houbara bustard, while underlining the dependence of these dynamics on ongoing management.

## 42 **Keywords**

43 Population abundance; release; hunting; management; distribution; temperature

44

## 45 **Introduction**

46 Population size, i.e. the absolute number of individuals in a population, is a key demographic property  
47 of populations. It is linked to their evolutionary resilience (Sgrò, Lowe, & Hoffmann, 2011), their  
48 dynamics and viability, as well as the functioning of ecosystems (Conner, 1988; Reed & McCoy, 2014).  
49 This makes population size one critical factor to define conservation statuses in various classification  
50 systems (e.g. living planet index, IUCN Red List Criteria C and D, etc.; IUCN, 2001 and 2012; WWF,  
51 2018). In this context, population size is both a diagnosis (to detect a previous decline, a problem related  
52 to habitat, the over exploitation of a species, etc.) and a demographic property associated with factors  
53 limiting viability (Caughley, 1994), such as Allee effects, demographic stochasticity, genetic  
54 deterioration or reduction of evolutionary potential (Courchamp, Clutton-Brock, & Grenfell, 1999;  
55 Lande, Engen, & Sæther, 2003; Robert, 2011). The measure of the population size strongly relies on a  
56 good definition and use of the concept of population. The term “population” can be defined as a group  
57 of individuals of the same species that live in a particular geographic area at the same time, with the  
58 capability of interbreeding. Although the boundaries of a population can be technically and conceptually  
59 complex to define, from an ecological and genetic point of view, individuals belonging to the same  
60 population are more similar and interact more with each other than with individuals from other  
61 populations. Population density is a measurement of population size per unit area, i.e. population size  
62 divided by total land area. Abundance refers to the representation of a species within a particular area,  
63 which may be expressed in absolute or relative terms (e.g. in relation to the abundance of the same  
64 species at different points in space or time, or in relation to the abundance of other species). Abundance  
65 is linked to the number of individuals of the focal species, but (1) can be either relative or absolute, (2)  
66 is not necessarily linked to the concept of population (for example, the abundance of a species in a  
67 particular geographical area may be the sum of several independent and isolated populations).

68 Abundance is generally the most convenient measure in practice. However, the relationship between  
69 abundance measured at a given spatial and temporal scale and population size is not necessarily trivial,  
70 particularly for species with large variation in population size, ecologically structured populations,  
71 diffuse habitats, or population boundaries that are impossible to assess (Holt *et al.*, 1997; Freckleton *et*

72 *al.*, 2005). Further, beyond the average abundance, the assessment of the spatial and temporal variation  
73 in abundance and the understanding of their drivers are critical for population conservation. First, the  
74 temporal variation in abundance may reveal population trends (increasing or decreasing), which are  
75 critically related to the risk of extinction (e.g. IUCN Red List Criteria A and C; IUCN, 2012). Second,  
76 the temporal stochastic variation in abundance is another major component of the extinction risk (Engen,  
77 Sæther, & Møller, 2001; Lande *et al.*, 2003; Melbourne & Hastings, 2008). Finally, assessing the factors  
78 behind the variation in abundance (and more generally any demographic number, property or parameter)  
79 is necessary to understand the link between demography and any form of environmental variation. In  
80 particular, for spatial variation, some recent studies have uncovered complex relationships between  
81 habitat quality and abundance in a range of taxa (VanDerWal *et al.*, 2009; Acevedo *et al.*, 2017). With  
82 respect to temporal variation, the scenarios of future changes in the anthropogenic and non-  
83 anthropogenic environments, either trend, cyclical or stochastic, provide a necessary basis for projecting  
84 population dynamics (Beissinger, 1995; Keith *et al.*, 2008).

85 In conservation science, population size (and the associated notions of abundance and density) is  
86 particularly crucial information in the field of conservation translocations, i.e. the deliberate movement  
87 of organisms from one site to another where the primary objective is a conservation benefit (IUCN/SSC,  
88 2013). These operations often rely on very small initial population sizes (as in the case of  
89 reintroductions) or on initially declining populations (as in the majority of population reinforcements),  
90 and the monitoring of the abundance of translocated populations is a major tool in the diagnosis of these  
91 operations. Assessing the success of translocation programmes requires an understanding of the  
92 demographic functioning of translocated populations, which in turn requires an examination of survival  
93 and reproduction parameters and their consequences in terms of overall dynamics and risk of extinction  
94 (Robert *et al.*, 2015). However, in the absence of detailed parameters, in large populations, or when the  
95 parameters are likely to vary greatly in space and time, population size (or abundance) assessment offers  
96 a direct measure of population trends and remains an important indicator of success before estimating  
97 viability (Traill, Bradshaw, & Brooks, 2007).

98 In this study, we focused on understanding the variation in abundance of a reinforced population of the  
99 North African Houbara bustard (*Chlamydotis undulata undulata*; hereafter, houbara). The houbara is a  
100 steppe bird listed as "Vulnerable" on the IUCN Red List considering the large decline of its populations  
101 in the last decades, mainly due to unregulated hunting, habitat loss and degradation (Birdlife  
102 International/IUCN, 2016). For the past 25 years, the Moroccan population of houbara has been the  
103 subject of a restoration and conservation programme conducted by the Emirate Center for Wildlife  
104 Propagation (ECWP) through reinforcement in the wild with captive-bred individuals, in situ protection  
105 and management measures (Lacroix *et al.*, 2003). The present study on the abundance of the reinforced  
106 population of houbara aims to provide diagnostic elements on the current conservation status of the  
107 species and the potential contribution of the protection and reinforcement programme put in place. The  
108 three main elements of diagnosis are (1) the assessment of population size and population trend, which  
109 are two major proxies used to define conservation status, (2) the assessment of the role of the programme  
110 in the currently observed conservation status compared to the likely conservation status in the absence  
111 of the programme (Akçakaya *et al.*, 2018) and (3) the influence of the continuation of the current  
112 restoration program on the dynamics of the houbara population. Based on more than 10,000  
113 observations, covering nine years (2010-2018) in a study area of 50,170 square kilometers, we aimed  
114 to: 1) estimate the average density of the houbara population in the area; 2) estimate the size of the total  
115 population in the study area by year; 3) investigate the drivers of temporal and geographical variation  
116 in abundances.

117 Given the numbers of individuals released over the study period ( $N = 89\ 881$ ), we expect these releases  
118 to significantly influence houbara abundance. However, the impact of such release effort might greatly  
119 vary in space and time, as pointed out in previous studies on the reinforced houbara population showing  
120 large variation in demographic rates (survival, dispersal and reproduction parameters) in relation with  
121 three main types of drivers: (1) habitat heterogeneity of the ECWP intervention area, particularly in  
122 terms of habitat suitability for the species (Monnet *et al.*, 2015a; Bacon *et al.*, 2017a); (2) spatial  
123 variation in the management of the intervention area, which is divided into protected and hunting areas

124 (Hardouin *et al.*, 2015); (3) weather conditions (temperature and precipitation, Hardouin *et al.*, 2014 ;  
125 Bacon *et al.*, 2017a).

126 Based on the aforementioned studies, we predict (1) strong spatial variation in density in relation to  
127 habitat heterogeneity; (2) the stability or at least consistency of the densest areas from one year to the  
128 next (i.e. the fact that areas that are denser than others in a given year tend to remain denser in following  
129 years); (3) temporal variation in houbara abundances, in particular linked to the variation in  
130 meteorological conditions: high temperature and low precipitation should be associated with low  
131 abundances; (4) greater abundances where release effort has been more important. Beyond its  
132 fundamental interest, one major objective of our study was to diagnose the current success of the houbara  
133 reinforcement programme in Morocco.

## 134 **Methods**

### 135 **Species**

136 The North African houbara bustard (*Chlamydotis undulata undulata*) is a medium-sized bird inhabiting  
137 semi desert steppes with open and sparse vegetation (Hingrat *et al.*, 2007). At the landscape scale,  
138 permanent ergs, mountains and rivers are natural factors limiting the distribution of the species (Hingrat  
139 *et al.*, 2008); in addition, the houbara bustard avoids environments disturbed by humans (*Le Cuziat et*  
140 *al.*, 2005). Formerly distributed from North Mauritania to Egypt, the growth of unregulated hunting  
141 throughout the species range since the 1980's severely threatened wild populations (Goriup, 1997).  
142 Additionally, the intensification of pastoral activities (agricultural expansion, overgrazing of livestock),  
143 human presence and landscape fragmentation (road construction, infrastructure development) have  
144 accelerated its decline and the houbara is currently listed as "Vulnerable" on the IUCN Red List  
145 (Birdlife International/IUCN, 2016).

### 146 **Houbara population management**

147 The Emirates Center for Wildlife Propagation (ECWP) was created in 1995 (Lacroix *et al.*, 2003).  
148 Between 1998 and 2019, about 135,000 captive-bred houbara have been released in several regions of  
149 Morocco. The main intervention area of the ECWP is situated in Eastern Morocco and covers 50,170

150 km<sup>2</sup> (Fig. 1). The ECWP intervention area is divided in two types of areas according to their  
151 management: hunting areas, where hunting is allowed outside the breeding season only (October to mid-  
152 January), and protected areas, where hunting is totally prohibited. The partitioning into hunting and  
153 protected areas was driven by the following considerations: re-establishing hunting (falconry) on areas  
154 traditionally hunted and preserving the remnant wild populations in areas substantially large enough to  
155 allow their recovery. Preliminary surveys in the beginning of the programme helped locate remnant wild  
156 populations and protected areas were established in agreement with falconers, representing up to 47 %  
157 of the ECWP intervention area in 2017 (Appendix S3, Fig. A3-1). Regular releases of captive-bred  
158 houbara have been conducted every year in both areas since 1998, totaling 108,915 individuals by the  
159 end of 2019. As hunting occurs from October to mid-January, releases in hunting areas occurred in  
160 spring (see Fig. A1-1 Supporting Information Appendix S1) to avoid hunting newly released individuals.  
161 Releases in protected areas mainly occurred in fall. Before 2010, releases were conducted on eight main  
162 release sites every year and release group sizes were highly variable between sites and years (Hardouin  
163 *et al.*, 2014). From 2010, the release effort significantly increased numerically (Fig. A1-2 in Supporting  
164 Information Appendix S1) and spatially by releasing small groups (6 to 18 individuals) across a grid of  
165 5x5 km.

## 166 **Counting data**

167 The monitoring of the abundance of houbaras was carried out using the distance sampling method.  
168 Houbara were counted each year, beginning in 2000, between September and December. All counting  
169 sessions in protected areas were performed before releases and those in hunting areas were done before  
170 hunting. Our study focused on the 2010-2018 period. From 2010, following the significant increase in  
171 the release effort (Fig. A1-2 in Supporting Information Appendix S1), a standardized counting protocol  
172 was implemented. Each cell of the 5x5 km grid used for release (see above) was surveyed to identify a  
173 suitable counting location in the center of each cell. A total of 843 counting points were identified, each  
174 satisfying the following criteria: the location was accessible by car, and offered a 360° visibility for up  
175 to three km.

176 Individuals were counted using standardized circular point observations (within a 3 km radius during 20  
177 minutes, see details in Supporting Information Appendix S2). At the end of a counting session, observers  
178 visited locations where individuals or groups were sighted at first and recorded the exact coordinates  
179 using a GPS. This allowed the measurement of the accurate distance from the counting point to each  
180 bird (or group of birds) observed. At each counting session, the number of livestock animals present  
181 around the counting point was recorded.

## 182 **Abundance estimation**

### 183 *Correcting the observed abundances with the detection probability*

184 We used the “distance sampling” method (Buckland *et al.*, 2004) to estimate local abundances of  
185 houbaras over the study area. This method allows fitting a detection function to model the probability  
186 of detecting an individual at a certain distance from the observer. The approach assumes that the  
187 probability of detecting a bird decreases as its distance from the observer increases. We fit models with  
188 several key functions (Uniform, Half-normal, Hazard-rate), and several types of adjustments (cosine,  
189 simple polynomial, Hermite polynomial; for models with no covariates). Then, we assessed the effect  
190 of the following covariates: hunting (hunting versus protected area, binary covariate), the logarithm of  
191 the number of birds released during the year within a radius of 100 km around the counting point  
192 (quantitative covariate, see full description below), and the year (factorial covariate). All covariates were  
193 fixed effects. We chose the best model among the various combinations of covariates, key functions and  
194 adjustment models (n = 25 models) by using the Akaike information criterion (AIC, Burnham &  
195 Anderson, 2002). This analysis was performed using the “Distance” package version 1.0.0 (Miller *et al.*,  
196 2019) with R 4.0.2 (R core Team 2020). This best distance sampling model provided the abundances  
197 corrected with the detection function and accounted for the variability that could be explained by the  
198 covariates mentioned above. These abundance estimates were further used to analyze the environmental  
199 factors related to the spatial variation in abundance.

### 200 *Spatializing the abundances*

201 We used density surface modelling (hereafter: “dsm”) to spatialize abundance estimates from counts  
202 corrected by detectability and to produce maps of annual abundance distribution (see Supporting

203 Information Appendix S3 for detailed methods on dsm). From those maps we produced Hovmöller  
204 diagrams (Hovmöller, 1949) to examine whether houbara local abundances varied consistently over  
205 time (i.e. with no drastic change in local abundance (dsm pixel) from year to year). The Hovmöller  
206 diagrams illustrated the changes in houbara abundances according to latitude and longitude (by  
207 degree) and time (by year), by averaging all the values of a single column of longitude or a line of  
208 latitude. In our case, we averaged the abundance estimates per pixel by latitude and longitude bands  
209 for each year. We excluded the year 2010 because of its high uncertainty associated with the dsm  
210 abundance estimates (see results).

### 211 *Assessing the effects of releases on the abundance*

212 Although releases took place each year after the counting period, releases prior counting were likely to  
213 influence local abundances for the focal year. We therefore developed a covariate to quantify the number  
214 of individuals previously released near each counting point (hereafter, Nrel; see details in Supporting  
215 Information Appendix S4). Nrel corresponds to a number of individuals released since a date (n) within  
216 a certain radius (r) around a counting point. This covariate was included as an adjustment covariate in  
217 abundance models.

218 To include Nrel in the model it was first necessary to select the most relevant buffer value (Bnr, i.e. a  
219 choice of r and n) around counting points. For this, we tested the relationship between the estimated  
220 abundance and various spatio-temporal buffers (Bnr). Buffers included a log-transformed number of  
221 released individuals within a radius r around the counting point, over the n days prior to the counting  
222 date. We considered two values of n. The first value of n corresponded to “1 year before the count” and  
223 the second corresponded to the period between “January 1st of the counting year and the counting date”.  
224 We investigated four spatial radii r: 10km, 20km, 50km and 100km. We then obtained eight different  
225 combinations of temporal and spatial distances from the counts. We fitted the models with these different  
226 combinations and ranked them using the Akaike Information Criterion (AIC) and selected the best model  
227 (see details in Supporting Information Appendix S4). Analyses of the relative importance of the  
228 parameters and model-averaged coefficients of the best models allowed us to select a buffer (Brn) with

229 the most relevant  $r$  and  $n$  values. The *Nrel* variable used in the abundance model corresponded to log-  
230 transformed numbers of released individuals within the selected spatio-temporal buffer.

### 231 *Spatial and temporal environmental covariates*

232 For each counting point the following explanatory covariates were used to assess the effects of the spatial  
233 heterogeneity of the area on abundances: the type of management (Hunting as binary covariate), the  
234 mean annual temperature (Temp; in Kelvin) and annual total precipitation (Prec) over the nine years of  
235 the study, the type of habitat (three level factor, see below), the log-transformed nearest distance to a  
236 town (Town), the log-transformed nearest distance to a road (Road) and the log-transformed livestock  
237 density (Livestock). The livestock density was obtained from counts made at the counting points and  
238 log-transformed. We used livestock density to estimate the potential disturbance of pastoral activities  
239 and/or direct disturbance due to the presence of livestock animals (Le Cuziat *et al.*, 2005).

240 Temperature and precipitation covariates were derived from the Noah Land Surface Model, GLDAS  
241 data (Beaudoin & Rodell, 2016), which gave a value of mean temperature and total precipitation per  
242 day. We calculated an average daily mean temperature value (Temp), and an average daily total  
243 precipitation value (Prec) over the nine years of the study, for each geolocalized counting point.

244 To assess the effects of the temporal heterogeneity on abundances, we computed meteorological  
245 anomalies. For each counting session, we computed the temperature anomaly ( $T_{anom}$ ) as the difference  
246 between the average temperature of the year of the count and the average temperature of the focal  
247 counting point calculated over nine years. A positive anomaly corresponded to a year with a warmer  
248 than average temperature for the counting point. We used the same protocol for precipitation ( $P_{anom}$ ).

249 We extracted the type of habitat (Habitat) of each counting point from Globcover 2009 data (Bontemps  
250 *et al.*, 2011), using observations from the MERIS satellite with a resolution of 300 m. The study area  
251 included three different habitats: mosaic vegetation/croplands ( $Hab_{mosaic}$ ), sparse vegetation ( $Hab_{veg}$ ) and  
252 bare area ( $Hab_{bare}$ ). Distances to the nearest town and road were calculated from Open Street Map data  
253 (data © OpenStreetMap contributors, under ODbL license).

254 For the analyses, all covariates were rescaled: centralized and standardized.

## 255 **Abundance modelling**

256 We modelled the temporal and spatial variation in houbara abundances using  $N_c$  (the local abundance  
257 during a counting session corrected by the probability of detection) as the response variable. This  
258 variable  $N_c$  included a very large quantity of zeros: among the 10,071 count data, more than 70%  
259 corresponded to non-observation.

260 We used zero-inflated models to account for over-dispersion of these data and excess of zeros in a better  
261 way than their conventional counterparts (e.g. Poisson regression). Zero-inflated models consider that  
262 the response variable contains more zeros than expected and fitted models are thus divided into two  
263 parts: a conditional model, which corresponds to the abundance/count modelling, and a zero-inflation  
264 part, which corresponds to the absence (see details in Supporting Information Appendix S5). Using a  
265 single conditional model including all the main fixed-effect covariates listed above (Year, Town, Road,  
266  $N_{rel}$ , Hunting, Livestock, Habitat,  $T_{anom}$ ,  $P_{anom}$ , Temp and Prec), we tested several zero-inflated models  
267 with different distributions (Poisson or negative binomial) and various covariate combinations in the  
268 argument to model extra zeros: Hunting, Year and  $N_{rel}$ . This resulted in eight main models (see  
269 Supporting Information Appendix S7). We then added some interactions to the conditional part of each  
270 of these eight models: (i) between the precipitation anomaly and the mean precipitation at the focal pixel  
271 ( $P_{anom}$ :Prec) following the expectation that a positive precipitation anomaly would have a positive  
272 effect on abundance, especially in sites associated with low average precipitation (Ficetola and  
273 Majorano, 2016; Ogutu et al., 2008); (ii) between temperature anomaly and the mean temperature at the  
274 focal pixel ( $T_{anom}$ :Temp) following the expectation that positive temperature anomalies would have a  
275 negative effect on abundance, especially in sites associated with high average temperatures (Ficetola  
276 and Majorano, 2016; Hardouin et al., 2014); and (iii) between the management of the zone and the  
277 number of releases (Hunting: $N_{rel}$ ) to examine whether the effect of the number of individuals released  
278 on local abundance varies according to area management (hunted or protected area; Hardouin et al.,  
279 2015). We used AIC to select the most parsimonious model between the 48 models tested (see  
280 Supporting Information Appendix S7). Zero-inflated models were implemented with the “glmmTMB”  
281 package version 0.2.3 (Magnusson et al., 2017) of R.

## 282 **Results**

### 283 **Temporal variation in abundance**

284 The best detection function model was the hazard-rate with year and number of releases as covariates  
285 (in a buffer of 100 km, since the 1st January of the year of the count; see details in Supporting  
286 Information Appendix S4). The integrated probability of observing an individual that was actually  
287 present within a radius of 3 km, was  $p = 0.082$  (cv: 0.021, se: 0.001) according to the best distance  
288 sampling model. The average density estimated over the nine years for the 38,628 km<sup>2</sup> area was 0.442  
289 houbara per km<sup>2</sup> and the average abundance was estimated to 16,918 individuals (95% CI [13,629 –  
290 21,027]) with substantial variation over the study period (Fig. 2 and Table A6 in Supporting Information  
291 Appendix S6).

### 292 **Predictors of abundance**

293 The selected model was the negative binomial zero inflation model with the *Year* as the covariate in the  
294 *ziformula* (covariate related to the excess of zeros). The model outputs can be divided into two distinct  
295 parts: the zero-inflation part that explains presence-absence (see Supporting Information Appendix S5)  
296 and the conditional part that explains abundance per se. The conditional model (Table 1) showed that  
297 the abundance increased with the number of individuals released within 100 km around the count point  
298 since the 1st January of the year of the count session (Table 1 and Fig. 3a). Abundances were also  
299 positively correlated with the presence of livestock animals and negatively correlated with the mean  
300 temperature of the site (i.e. average temperature over the study period, Table 1 and Fig. 3b). Further,  
301 higher abundances were found in hunting areas and lower abundances were found in habitat composed  
302 of mosaic vegetation and croplands. Other covariates and interactions among covariates were not  
303 significantly related to houbara abundances.

### 304 **Spatial distribution of abundances**

305 The distribution map of abundances provided by the density surface modelling showed that the  
306 distribution of houbara abundance was highly heterogeneous over the study area (Fig. 4). The density  
307 of houbara was markedly higher in the west, in the north-east and in the south of the Eastern part of the

308 study area. The higher uncertainty of predicted abundances was related to areas with the lowest counting  
309 effort over the study period (only one or two years out of the nine years of the study) (see Supporting  
310 Information Appendix S10). Visual examination of annual abundance maps also indicated that some of  
311 these "hotspots" of abundance last several years (see Fig. A10-1 and A10-2 in Supporting Information  
312 Appendix S10). To examine whether local abundances of Houbaras varied consistently over time (i.e.  
313 without drastic changes in local abundance (dsm pixel) from one year to the next), we used Hovmöller  
314 diagrams. Examination of the latitudinal (left) and longitudinal (right) change of abundances over time  
315 showed that changes in abundance were gradual (Fig. 5), although abundances were much more self-  
316 correlated in space than in time at this space-time scale.

## 317 **Discussion**

318 Our study provides the first estimates of density and annual abundance of the houbara in Eastern  
319 Morocco in relation to the 22-year population reinforcement programme for the species. The associated  
320 distribution maps highlight a non-uniform distribution of individuals over the study area. This spatial  
321 heterogeneity is statistically linked to local climatic conditions (temperature) as well as the management  
322 of the area (hunting and reinforcement).

323 Beyond the estimation of the total houbara abundance in the study area in Eastern Morocco, our study  
324 reveals high variation of abundance in space and time. In terms of spatial variability, from an  
325 evolutionary point of view, an attractive environment is expected to correspond to high demographic  
326 rates and a high percentage of species occurrence (i.e. a high habitat suitability). However, habitat  
327 suitability is not systematically correlated with the distribution of a species' abundance (*VanDerWal et*  
328 *al.*, 2009; *Acevedo et al.*, 2017) and a triangular relationship is often observed: poorly suitable habitats  
329 are associated with low abundance, while highly suitable habitats are associated with both low and high  
330 abundance.

331 The temporal variability in abundance is just as complex as spatial variability, because it strongly varies  
332 depending on the metrics, the method of analysis and/or the temporal and spatial scale used (*Gaston &*  
333 *McArdle*, 1994; *Heath*, 2006; *Brown, Brown, & Roche*, 2013). Density dependence and environmental

334 stochasticity interact to influence population dynamics and it is often difficult to dissociate their  
335 respective effects. Further, temporal variation in population size (and the resulting changes in observed  
336 abundance) are related to demographic parameters in complex ways. There are direct causal  
337 relationships between survival, reproduction and dispersal parameters and population size, but the  
338 strength of these relationships is highly dependent on the elasticities of the asymptotic population growth  
339 rate to the demographic parameters, which themselves depend on the life history of the species (Caswell,  
340 2001). In houbara, preliminary analyses of the population dynamics of wild-born individuals indicate  
341 that the generation time of this population is about eight years, and that the houbara exhibits high  
342 elasticity of the growth rate to adult survival probabilities (sum of elasticities for survival probability of  
343 adult females  $\approx 0.88$ , Bacon, 2017c). It is therefore expected that variations in adult survival will have  
344 strong consequences on the growth rate and thus on the population size.

345 Beyond the direct causality of demographic parameters on population size, population size also  
346 potentially exerts a causal effect on the parameters through density-dependent processes on survival,  
347 reproduction and dispersal (Tavecchia *et al.*, 2007; Knipe *et al.*, 2013). These processes are still  
348 insufficiently characterized for houbara, but a recent study suggests the existence of density-dependent  
349 regulation on the survival of released individuals in the most suitable habitats (Monnet *et al.*, 2015a). In  
350 a close species, the MacQueen's bustard (*Chlamydotis macqueenii*), Azar *et al.*, (2016) have also  
351 highlighted density dependence processes, where the long-term survival of individuals is negatively  
352 affected by the local increase in densities linked to the reinforcement strategy. Thus, in the case of the  
353 complex system of reinforced population of houbara in Eastern Morocco, it is likely that the observed  
354 temporal variations in global abundance also depend on the release effort (Bacon, 2017c, last chapter).  
355 This release effort has been highly variable globally (with the total number of individuals released  
356 annually varying from 6,722 to 13,224) and locally. Further, beyond the variation in the number of  
357 releases, it is also the short-term survival of these released individuals that was highly variable between  
358 years (e. g. post-release three-month survival of individuals released in fall varied from  $0.92 \pm 0.06$  in  
359 2006 to  $0.19 \pm 0.07$  in 2009, Hardouin *et al.*, 2014).

360 Previous works also indicated that post-released survival is related to weather conditions, which have a  
361 strong impact on the availability of food resources in this arid environment (Hingrat *et al.*, 2007). The  
362 survival of released individuals is negatively affected by extreme temperatures, as a warmer than  
363 average year will have a negative impact on houbara survival (Hardouin *et al.*, 2014). Temperature also  
364 has a positive effect on the dispersal distance of released individuals (Hardouin *et al.*, 2014). In  
365 agreement with these demographic results, our results highlight the effect of temperature on spatial  
366 variations in abundance over the Eastern region. Lower abundances are associated with sites with higher  
367 mean temperatures.

368 Beyond these climatic and meteorological effects, spatial variations in abundance in the eastern region  
369 are statistically associated with the management of the area in which the counting site is located (hunting  
370 area vs. protected area) and pastoral activities around the counting sites. The observed positive  
371 relationship between pastoral activity and the abundance of houbara can be explained by the fact that  
372 during the counting period (in fall), houbaras and livestock animals share similar habitats to forage. Our  
373 results also indicate that hunting areas are associated with higher abundance. A previous study showed  
374 that certain demographic parameters were distinct between hunting areas and protected areas. In  
375 particular, there is a higher probability of movement from protected areas to hunting areas, and survival  
376 is lower in hunting areas, but this difference is not only due to hunting per se as it persists when hunting  
377 activity does not occur (Hardouin *et al.*, 2015). In the end, our results indicate that houbara movement  
378 is oriented towards areas associated with higher abundances and lower survival, suggesting (1) an  
379 important role for habitat selection (Pulliam & Danielson, 1991) or conspecific attraction (Stamps, 1988;  
380 Mihoub *et al.*, 2011) to the most suitable areas in terms of habitat, which explains the spatial variations  
381 in abundance that we observe; (2) a negative effect of density (Johnson *et al.*, 2012) on houbara survival.  
382 The ability to assess the benefit of recovery programmes is a major conservation issue (Brichieri-  
383 Colombi & Moehrensclager, 2016; Thévenin *et al.*, 2018), as is the definition of the success of these  
384 programmes (Seddon, Armstrong & Maloney, 2007), which ultimately must be linked to the long-term  
385 viability of the restored populations and their contribution to the viability of the species (Sarrazin, 2007;  
386 Robert, 2009; Robert *et al.*, 2015). Faced with the difficulty of assessing the viability of a population,

387 the increase in population size or geographic distribution are often used as positive facts of the  
388 assessment of the recovery of a species, making abundance monitoring a major criterion (Carlson,  
389 Osborne & Schmidt, 2007; Thévenin, 2019). Akçakaya *et al.*, (2018) proposed an assessment of species  
390 recovery and conservation success to develop an IUCN Green List of Species. Their objective was to  
391 compare the current status of a population with the status that would have been expected if there had  
392 been no restoration or protection measures, i.e. the "counterfactual state". The difference between the  
393 current status of a population and its counterfactual state allows the assessment of the impact of past  
394 conservation actions.

395 Globally, historical counts in the mid-1990s estimated the population of houbara bustard at about 10,000  
396 birds in North Africa, of which more than 50% were in Algeria, 30% in Morocco and 10% in Libya  
397 (Goriup, 1997). More recently, it has been assumed that the population would range between 20,000  
398 and 50,000 birds, with 13,000 to 33,000 mature individuals in North Africa (BirdLife International,  
399 2020). However, no reliable abundance estimates were so far available for the North African Houbara  
400 bustard.

401 In this context, the results of the present study, in conjunction with previous ecological studies, allows  
402 to draw three types of conclusions on the current state of conservation of the houbara and the  
403 contribution of the restoration and protection programme initiated 25 years ago.

404 Firstly, before any real quantification of the probability of extinction of the species, we provide the  
405 estimation of two important demographic properties: population size and population trend, which are  
406 two major proxies used to define conservation status (IUCN, 2012). For the period 2010 - 2018, we  
407 estimated the average abundance over the study area at around  $16,918 \pm 1,875$  individuals, which  
408 corresponds to an average density of  $0.44 \pm 0.05$  houbara per km<sup>2</sup>. This estimate suggests that the  
409 population is large enough to avoid problems related to demographic stochasticity and short-term  
410 genetic deterioration (Frankham, Ballou & Briscoe, 2002), as the species exhibits little genetic  
411 differentiation over its range (Lesobre *et al.*, 2010). In addition, the relative stationarity of numbers (Fig.  
412 2) suggests that with continuity of current management, the risk of extinction in the short term is  
413 moderate.

414 Second, in the framework of the evaluation of a counterfactual state that would allow to quantify the  
415 benefits of conservation actions, our analysis suggests that the programme put in place had beneficial  
416 effects on the numbers and trend of the houbara, and thus presumably on the risk of extinction. Following  
417 several decades of population decline (Birdlife International/IUCN, 2016), density estimates had been  
418 made for three areas in the Eastern region of Morocco in 2001, at the beginning of the reinforcement  
419 programme. These 2001 estimates ranged from 0.05 to 0.1 individuals per km<sup>2</sup> depending on the type  
420 of management of the area considered, hunted or protected (ECWP, unpublished data). In 2009 new  
421 estimates indicated an average density of  $0.45 \pm 0.08$  houbara per km<sup>2</sup> in these three areas. Maximum  
422 densities were observed in 2010 in protected areas, with 0.76 houbara/km (Hardouin *et al.*, 2015). These  
423 maximum densities are similar to our estimates (2010 is associated with maximum densities with  $0.84$   
424  $\pm 0.12$  houbara per km<sup>2</sup>).

425 Our results also indicate that, in our study area, releases are locally associated with higher abundances  
426 when considering large spatial and temporal range (100 km around the counting points and several  
427 months prior to counting, starting in January of the year of counting considered). This result suggests  
428 that releases have a positive impact on population dynamics, and that this increase in density is not  
429 simply related to a very short-term effect following release but can be interpreted in terms of dispersal,  
430 habitat selection, and survival of released houbara. In other words, individuals do not leave the areas  
431 where they were released, settle in suitable habitat and their survival is sufficient to ensure that local  
432 abundances reflect the local release effort even several months after release. This hypothesis is supported  
433 by results from previous ecological and demographic studies conducted on this reinforced population  
434 showing: (1) a relatively low dispersal distance from release sites (below 20 km after 90 days, Hardouin  
435 *et al.*, 2014), (2) a relatively high survival of released individuals under certain weather conditions (high  
436 and consistent spring short-term survival rate, i.e. three months after release:  $0.86 \pm 0.02$  between 2001  
437 and 2009, Hardouin *et al.*, 2014). Over the 2001-2010 period, the post-release survival probability over  
438 six months averaged  $0.82 \pm 0.02$  in protected areas whatever the season. In hunting areas, it was constant  
439 between years and averaged  $0.74 \pm 0.01$  during the breeding season, and varied among years (ranging  
440 from  $0.30 \pm 0.07$  to  $0.76 \pm 0.04$ ) during the non-breeding season (Hardouin *et al.*, 2015); (3) breeding  
441 parameters of released individuals similar to wild-born individuals (Bacon, Robert, & Hingrat, 2019),

442 and an average clutch size of 2.44 eggs [2.41, 2.48] (Bacon, Hingrat & Robert, 2017b); (4) a pattern of  
443 reproductive senescence (Bacon *et al.*, 2017b) comparable to that observed in captivity (Chantepie *et*  
444 *al.*, 2016), highlighting that some released individuals live long enough to complete their life history.  
445 Further, wild-born and captive-born individuals share much of the ecological space (Monnet, Hingrat,  
446 & Jiguet, 2015b) and the diet of released houbara is similar to that of wild-born individuals (Bourass &  
447 Hingrat, 2015), suggesting successful integration of captive-bred individuals. Overall, demographic and  
448 ecological data collected since the start of the reinforcement through an intensive monitoring programme  
449 suggest that the population reinforcement strategy and the management of the area have led to an  
450 increase in the population size since the early 2000s. Without these actions, the population would have  
451 continued to decline at a critical level or have become extinct, as is the case in other parts of its range  
452 (Chammen *et al.*, 2003 and 2008).

453 Thirdly, our results question the self-sustainability of the houbara population in its current environment,  
454 the dependence of its dynamics on the continuity of the reinforcement, and highlight the need to better  
455 understand density-dependent and density-independent processes that influence these dynamics. Over  
456 the 108,915 individuals released in the Eastern region since 1998, about 90% have been released after  
457 2009. (i.e. over the study period). In spite of this large release effort, our results indicate that the observed  
458 densities in the last years stagnate around 0.38 individuals per km<sup>2</sup> (average of the densities estimated  
459 from 2016 to 2018). In the last two decades, several studies have indeed revealed the importance of  
460 additional natural and anthropogenic threatening factors on the reinforced houbara population and its  
461 habitats, such as climate change (Frenette-Dussault *et al.*, 2013; Monnet, 2014), carrying capacity and  
462 density dependence mechanisms (Monnet *et al.*, 2014), human disturbance and habitat degradation (Le  
463 Cuziat *et al.*, 2005), and even the management strategy itself (Hardouin *et al.*, 2015; Bacon *et al.*, 2019).  
464 All these elements concerning the diagnosis of the state of conservation of the houbara population and  
465 the effects of the restoration programme directly impact the directions to be followed in terms of  
466 management and research. In particular, the comparison of the current state of the population (population  
467 size and trend) with its probably very unfavorable counterfactual state justifies the existence and interest  
468 of the programme (i.e. its contribution to the conservation of the species). Furthermore, the dependence  
469 of the free-ranging population on the continuity of the reinforcement programme is an argument for not

470 stopping the releases. It rather encourages towards a fine tune of the release strategy in close link with  
471 the research to assess in situ functioning of the reinforced houbara population. More specifically, the  
472 data on spatial variation in abundance will be integrated into the ongoing studies on density-dependent  
473 regulation mechanisms in relation to habitat quality (Bacon *et al.*, 2017a). They can also guide releases  
474 toward the areas with the greatest deficits in relation to the carrying capacity of the environment (see  
475 Acevedo *et al.*, 2017). Finally, an attempt has been made in the past to estimate viability based on  
476 individual-based demographic monitoring and population dynamics models (Bacon 2017c). This work  
477 has highlighted the lack of information on initial numbers, carrying capacity, and the links between  
478 density and demography. In this context, the acquisition of reliable abundance data will allow (a) to  
479 quantify density-dependent relationships in mechanistic population models, (b) to combine individual-  
480 based population monitoring data (Hardouin *et al.*, 2012, 2015) with the abundance data from the present  
481 study within an integrated modeling framework (Schaub & Abadi, 2011) to construct robust viability  
482 estimators.

#### 483 Conclusion

484 This and previous studies on abundance, demographic parameters and dynamics of this restored  
485 population suggest that it still does not meet the criteria for viability and self-sufficiency (Seddon *et al.*,  
486 2007; IUCN/SSC, 2013; Robert *et al.*, 2015; Akçakaya *et al.*, 2018). However, they also show that  
487 applied ex and in situ practices offered large scale restoration opportunities. They stopped the population  
488 decline (Bacon, 2017c) and secured captive and free ranging populations by preserving the genetic  
489 diversity and evolutionary resilience of the species (Lesobre *et al.*, 2010; Rabier *et al.*, 2020). In terms  
490 of species/global restoration, the reinforced population also does not meet the criteria of  
491 representativeness (i.e. the presence of the species in a representative set of ecosystems and communities  
492 throughout its range, Akçakaya *et al.*, 2018), as eastern region of Morocco represents only a portion of  
493 the species' range (Monnet *et al.*, 2015b), which extends across North Africa.

494 Although the programme to protect and restore the North African houbara bustard has proven its  
495 beneficial effects on recent population dynamics in eastern Morocco, future dynamics, viability and  
496 recovery of the species throughout its historical range are still dependent on continued global  
497 conservation efforts.

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## 678 Supporting information

679 Additional Supporting Information may be found in the online version of this article at the publisher's  
680 web-site:

681 **Appendix S1:** Release effort of captive bred houbaras from 1998 to 2018 in the ECWP intervention  
682 area

683 **Appendix S2:** Counting effort

684 **Appendix S3:** Spatializing the abundances using density surface modelling

685 **Appendix S4:** Releases effort variable

686 **Appendix S5:** Zero Inflated models

687 **Appendix S6:** Houbara abundance estimation per year, from 2010 to 2018

688 **Appendix S7:** Model selection

689 **Appendix S8:** Factors related to abundance

690 **Appendix S9:** Uncertainty of density surface modelling (dsm)

691 **Appendix S10:** Annual density surface modelling (dsm)

692 **Appendix S11:** Correlation assessment and univariate models

693 Table 1: Summary of the best generalized linear mixed effects model regressing corrected abundances  
694 of houbara against spatial and temporal covariates; with a negative binomial distribution and the Year  
695 as zero-inflation parameter. Only the conditional part of the model is presented (i.e. the slopes of  
696 abundances for non-zero observations). For clarity, the Year effect is not shown here, see Supporting  
697 Information Appendix S8 for the complete table (conditional and zero-inflated part). CI is the 95%  
698 confidence interval.

	<i>Estimate</i>	<i>Lower CI</i>	<i>Upper CI</i>	<i>Standard Error</i>	<i>z value</i>	<i>p-value</i>
<b><i>Town</i></b>	0.023	-0.014	0.059	0.019	1.21	0.225
<b><i>Road</i></b>	-0.009	-0.045	0.028	0.019	-0.47	0.642
<b><i>N<sub>rel</sub></i></b>	0.08	0.026	0.133	0.027	2.93	0.003
<b><i>Hunting</i></b>	0.436	0.358	0.514	0.04	10.96	< 10 <sup>-3</sup>
<b><i>Livestock</i></b>	0.041	0.022	0.061	0.01	4.14	< 10 <sup>-3</sup>
<b><i>Hab<sub>mosaic</sub></i></b>	-1.928	-3.69	-0.165	0.899	-2.14	0.032
<b><i>Hab<sub>vege</sub></i></b>	-0.05	-0.135	0.036	0.044	-1.13	0.257
<b><i>T<sub>anom</sub></i></b>	0.029	-0.036	0.093	0.033	0.87	0.384
<b><i>P<sub>anom</sub></i></b>	0	-0.05	0.049	0.025	-0.01	0.991
<b><i>Precip</i></b>	-0.037	-0.085	0.01	0.024	-1.53	0.125
<b><i>Temp</i></b>	-0.129	-0.172	-0.086	0.022	-5.86	< 10 <sup>-3</sup>

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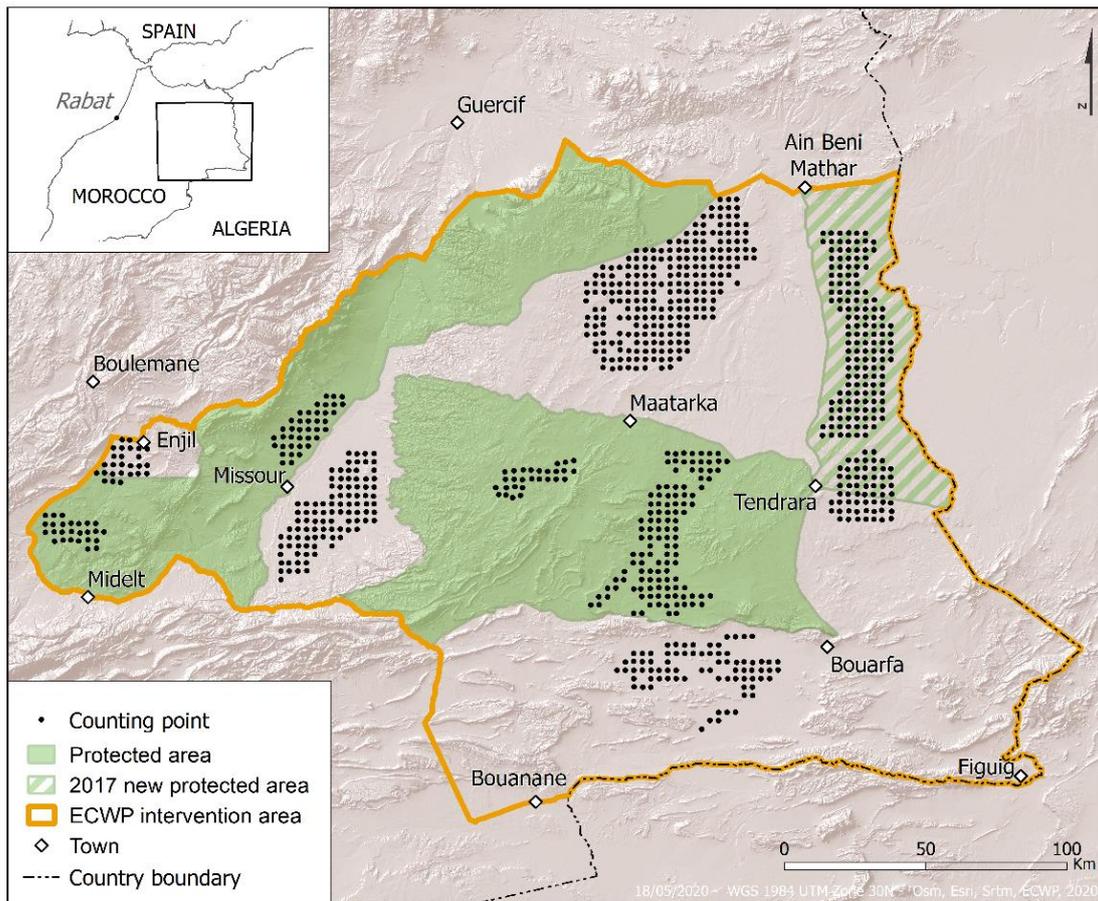
701 Figure 1: Location of the counting points of houbara fall counts from 2010 to 2018 within the ECWP  
702 intervention area, Morocco.

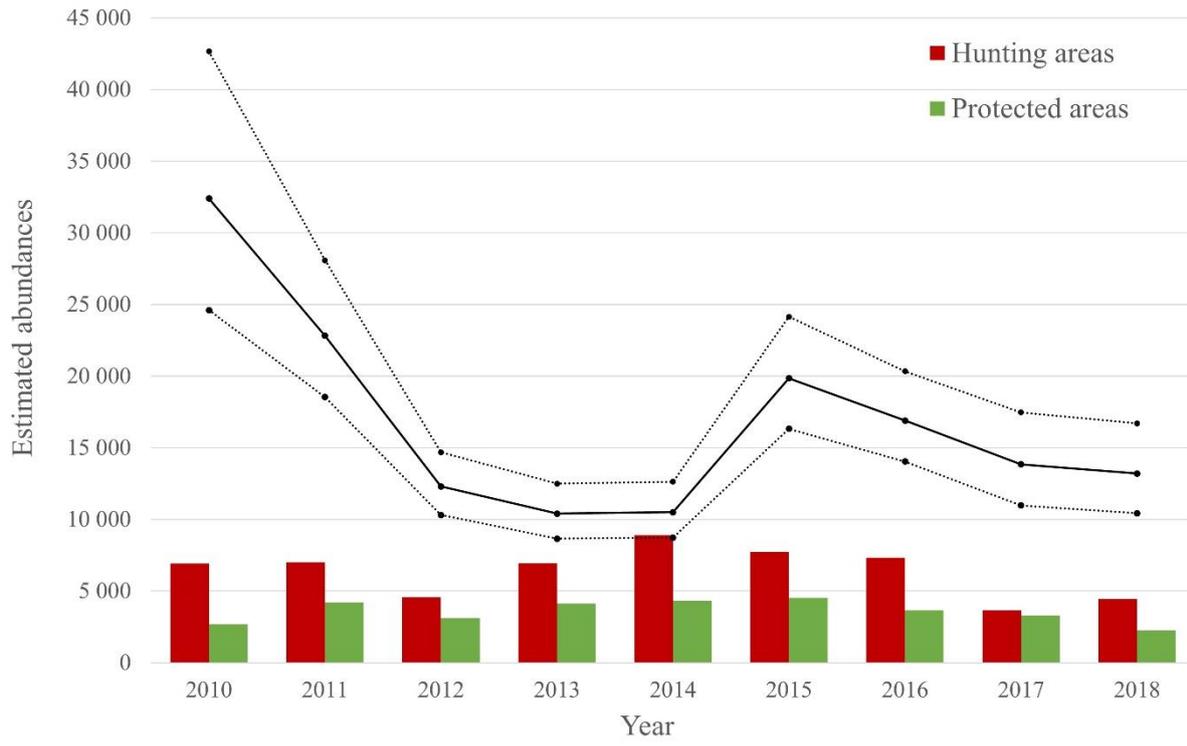
703 Figure 2: Variation in houbara abundances in the ECWP intervention area between 2010 and 2018.  
704 The blue dashed lines represent the upper and lower bounds of the 95% confidence interval. Red bars  
705 represent releases in hunting areas and green bars represent releases in protected areas.

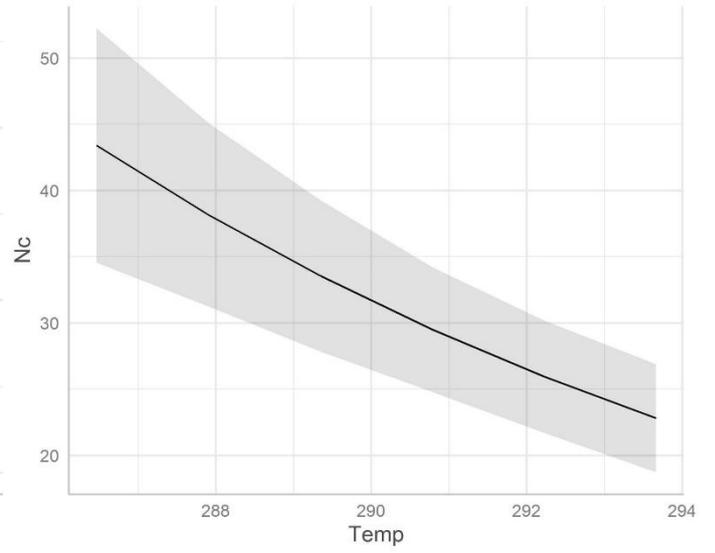
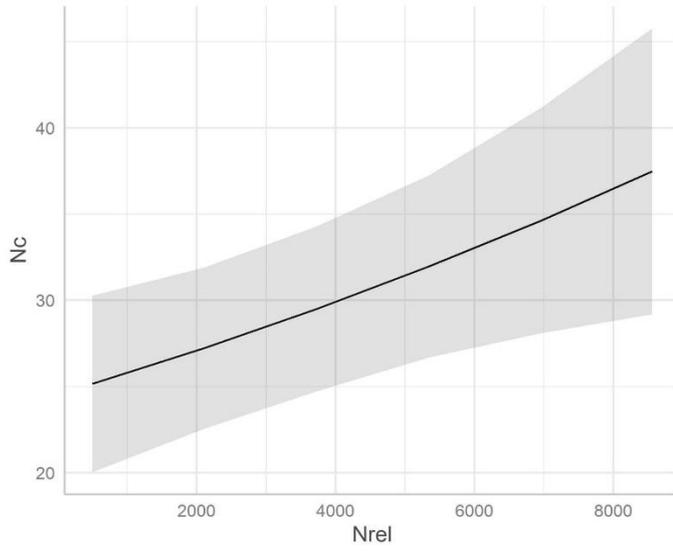
706 Figure 3: Illustrations of the effects of a) the release effort and of b) the average temperature (in  
707 Kelvin) in a counting site on the houbara abundance ( $N_c$ , the local abundance of houbara observed at a  
708 counting session corrected by the probability of detection).

709 Figure 4: Spatial variation in the abundance of houbara in the ECWP intervention area, Morocco.  
710 Abundance is given in terms of absolute density by pixel of 75km<sup>2</sup>, projected in an area of 38 268 km<sup>2</sup>  
711 excluding some areas identified as unsuitable for the houbara (see Fig. A3-1 in Supporting  
712 Information Appendix S3). Black dots represent the counting points.

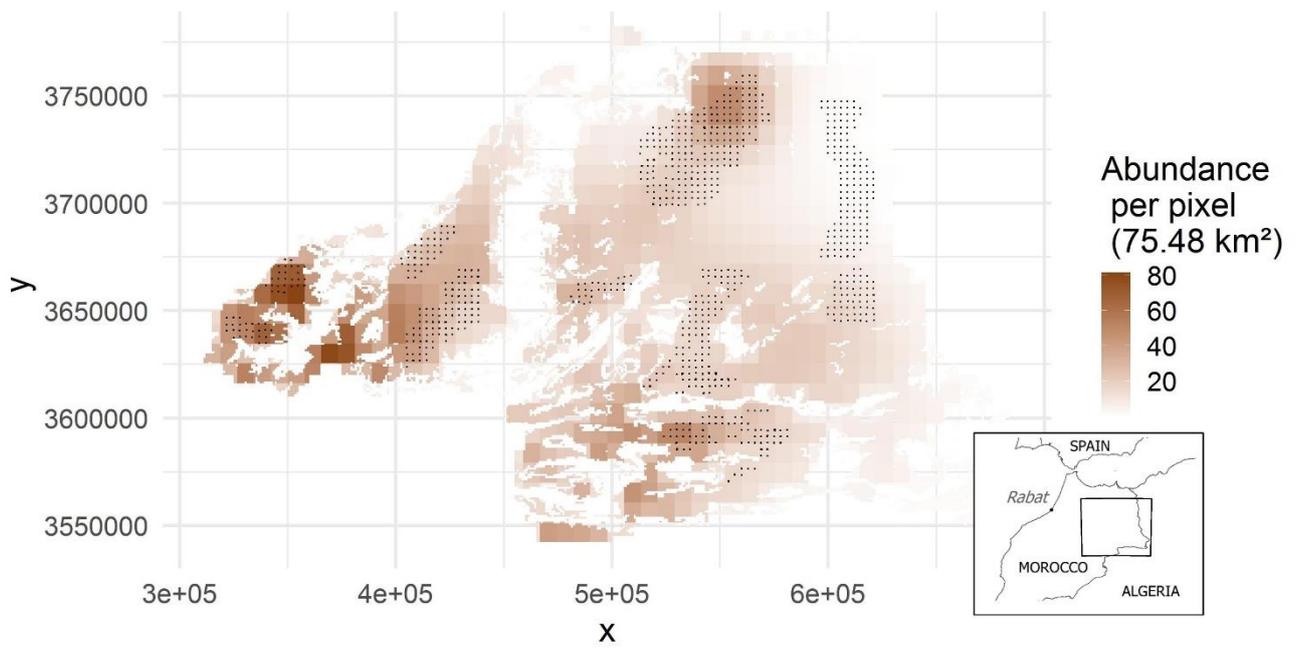
713 Figure 5: Hovmöller plots for the latitude (left) and the longitude (right) coordinates for abundance  
714 estimates. The color denotes the abundance per pixel estimated by the dsm. The year 2010 is not  
715 represented due to the high uncertainty associated with abundance estimates.

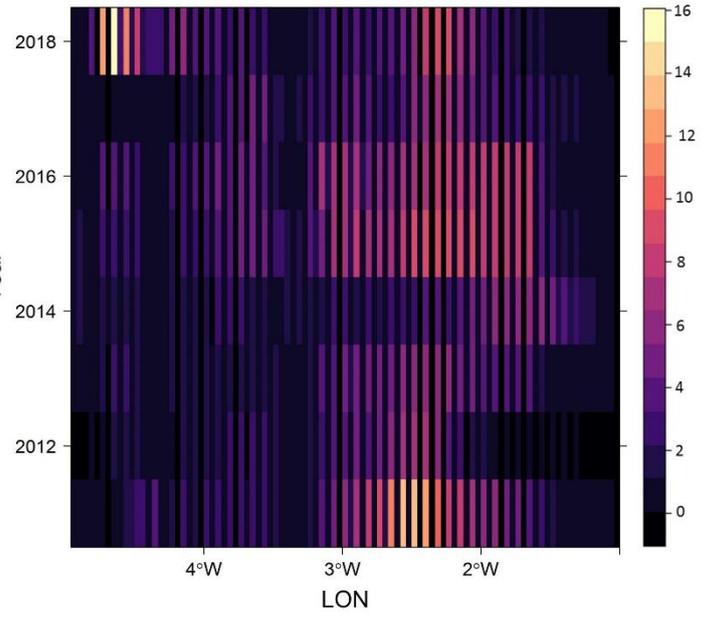
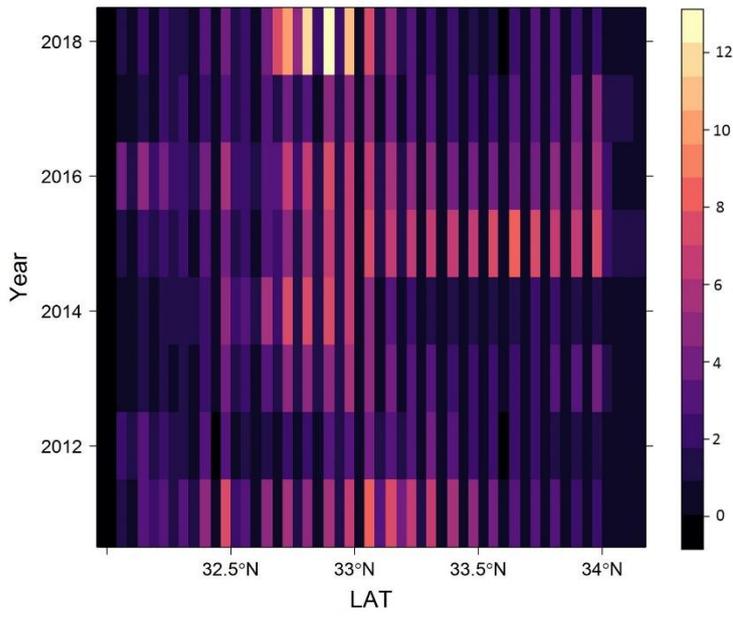






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