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1 **Long lasting breeding performance differences between wild-born and**
2 **released females in a reinforced North African Houbara bustard**
3 **(*Chlamydotis undulata undulata*) population: a matter of release strategy.**

4 Léo Bacon^{a, b, *, **}, Alexandre Robert^b, Yves Hingrat^{a, c}

5 ^aEmirates Center for Wildlife Propagation, PO Box 47, 33250 Missour, Morocco.

6 ^bCESCO, UMR7204 MNHN-CNRS-Sorbonne Université, CP135, 43 Rue Buffon, 75005 Paris,
7 France.

8 ^cReneco International Wildlife Consultants LLC., Po Box 61741, Abu Dhabi, U.A.E.

9 *Corresponding author (bacon.leo@gmail.com)

10 **Orcid ID: 0000-0003-1200-9902

11 **Abstract**

12 The success of translocation programmes is reflected by the ability of translocated individuals
13 to survive and reproduce in their new environment. However, it has previously been reported
14 that translocated individuals have lower demographic performance than their wild-born
15 conspecifics, due to management and individual factors (such as release conditions or age).
16 Here, we study six breeding parameters in free-ranging females of the North African Houbara
17 bustard (*Chlamydotis undulata undulata*) and compare these parameters between captive-bred
18 released (n=204) and wild-born (n=101) birds, considering the age of individuals and the period
19 of release (autumn *versus* spring). Our results indicate that (1) captive-bred released females
20 successfully breed in the wild; (2) for three out of the six breeding parameters studied, released
21 females show lower performances than wild-born females; but, (3) Although we observed
22 consistently reduced breeding performances in one year old females relative to older females,

23 we did not uncover any interaction between age and the origin of females, suggesting that the
24 impairment of breeding parameters in released females is long lasting; and, (4) interestingly,
25 this impairment of breeding parameters depends on the period of release, with lower breeding
26 performances for spring releases compared to autumn releases. Overall, our study highlights
27 the capacity of captive-bred females to reproduce in the wild, contributing to the dynamics of
28 the population beyond their individual history. Our results also uncover complex variations of
29 breeding parameters in translocated birds, but suggest that these differences can be minimized
30 through an appropriate translocation strategy.

31 Key-words: Captive-breeding, post-release effect, reinforcement, reproduction, translocation

32 **Introduction**

33 The success of conservation translocation programmes is commonly defined as the capacity of
34 translocated populations to persist without further intervention (Ewen et al. 2012, IUCN 2013).
35 Assessment of success thus requires an understanding of the long-term dynamics and viability
36 of translocated populations (Robert et al. 2015a), which first and foremost requires a long-term
37 demographic assessment (Sutherland et al. 2010). However, such assessments are rarely
38 achieved, mainly due to a lack of resources to support appropriate monitoring and difficulties
39 associated with data analysis (Fischer & Lindenmayer 2000, Sutherland et al. 2010).
40 Translocated populations are complex, heterogeneous and unbalanced systems (Robert et al.
41 2007), and the assessment of demographic performances is required to encompass this
42 complexity. In particular, it is necessary to assess potential demographic variations among
43 translocated and wild-born organisms.

44 Previous knowledge indicates that the demography of translocated populations is likely to be
45 affected by a variety of genetic and non-genetic issues. Genetic issues include outbreeding
46 depression (Huff et al. 2011) and ill adaptation (Montalvo & Ellstrand 2001) as well as

47 inbreeding and drift loads (Robert 2009). In cases of translocations based on captive breeding,
48 adaptation to captivity (Frankham 2008) might be an important additional issue. In animals,
49 non-genetic issues are associated with captive-rearing and release strategies, leading to various
50 factors potentially affecting demographic rates in the wild. These include individual condition,
51 such as health status, physiology and behaviour (Champagnon et al. 2012, Dickens et al. 2010,
52 Hardouin et al. 2014, Tavecchia et al. 2009), proximity of the release site with other populations
53 (Mihoub et al. 2011), period of release (Hardouin et al. 2014), age at release (Sarrazin et al.
54 1996) or the size and composition of the animal group (Hardouin et al. 2014, 2015a).
55 Additionally, the potential impairment of demographic performances of translocated
56 individuals might be explained by the interaction of their phenotype with their new environment
57 and release conditions.

58 *Post-release effects* have been defined as impairments of vital rates caused by translocation
59 conditions (Ewen et al. 2012). Such effects can be estimated either by assessing changes in vital
60 rates over time in a release cohort (e.g., Armstrong & Ewen 2001, Tavecchia et al. 2009) or by
61 comparing vital rates of translocated and resident animals over the same time period (e.g.,
62 Brown et al. 2006). A number of studies in translocated vertebrates have documented these
63 post-release effects, mostly in terms of survival probabilities (Armstrong et al. 2017, Bertolero
64 & Oro 2009, Hardouin et al. 2014, Sarrazin et al. 1994) but also in reproduction rates (Bertolero
65 & Oro 2009, Converse et al. 2013, Sarrazin et al. 1996, Tavecchia et al. 2009) and even in
66 dispersal behaviour (Le Gouar et al. 2008, Mihoub et al. 2011). In the particular cases of
67 translocated individuals originating from captive-breeding, any impairments of vital rates in
68 translocated individuals can result either from translocation conditions (i.e., post-release effects
69 *per se*), captivity conditions (including genetic and non-genetic issues), or the interaction of
70 translocation and captivity conditions.

71 However, disentangling the various sources of demographic variation in translocated
72 populations (and in particular those related to the translocation protocol from other sources of
73 variation) is challenging because (1) the comparison between translocated and wild-born
74 animals requires the monitoring of wild-born individuals; a difficult task often hindered by
75 several methodological and ethical issues, and (2) changes of vital rates over time in
76 translocated individuals can be confounded by other longitudinal sources of demographic
77 heterogeneity, such as age effects (Bacon et al. 2017a), or by inter-individual heterogeneity
78 (e.g., apparent improvement of survival due to the selection of the best survivors).

79 The North African Houbara bustard (*Chlamydotis undulata undulata*, hereafter Houbara – Fig.
80 1) is a medium-sized bird historically distributed from Northern Mauritania to Egypt. It is
81 threatened by over-hunting, poaching and habitat degradation, which have led to the decline of
82 the species during the second half of the twentieth century (Goriup 1997). This decline led to
83 the establishment of a reinforcement programme (the Emirates Center for Wildlife Propagation,
84 ECWP, see Material and Methods) which employs captive breeding and regular releases of
85 captive-bred individuals, combined with ecological research and hunting management, in order
86 to increase the population size of the threatened Houbara throughout its range and to maintain
87 viable populations in adequacy with traditional Arab falconry (Lacroix et al. 2003).

88 Importantly, captive-bred Houbara are released as juveniles (within their first year of life) either
89 before or during the breeding season (in autumn and in spring, respectively). Previous
90 researches on translocated Houbara indicate that (1) captive-bred juveniles exhibit reduction in
91 their short-term survival (the magnitude of which varies depending on the release season and
92 meteorological conditions), compared to long-term survival (Hardouin et al. 2014), and (2) one-
93 year-old released females have reduced breeding performance relative to older released females
94 (Bacon et al. 2017a). These results suggest that translocated individuals may experience
95 changes of vital rates over time. However, in these previous assessments of demographic rates,

96 potential changes caused by translocation conditions, captivity conditions and their interactions
97 may have been confounded with age effects. Thus, a rigorous assessment of these potential
98 captivity and translocation effects requires formal comparison between captive-bred released
99 and wild-born individuals of different ages. Hereafter, demographic effects occurring only in
100 the first year following release (i.e., in one-year-old individuals) are referred to as short-term
101 differences and effects occurring independently of the time since release (i.e., in individuals of
102 any age) are referred to as long lasting differences.

103 Here, we investigate potential differences in breeding performances between wild-born and
104 released captive-bred females, while controlling for age, period of release, and temporal and
105 individual effects. The Houbara is a ground-nesting, gyneparental incubating species. In Eastern
106 Morocco, females breed from mid-February to mid-June. They lay generally two to three eggs,
107 at intervals of 2.5 days, which they incubate for an average of 23 days (Gaucher 1995). In case
108 of nest failure, females generally initiate a replacement clutch. Houbara chicks are nidifugous
109 but still rely on their mother for food during the first 10 days after hatching (Saint Jalme & van
110 Heezik 1996) and fledge at a mean age of 60 days (Hardouin et al. 2012). Maximum longevity
111 observed in the wild was at least 13 years old for a wild-born female and 10 years old for
112 captive-bred released females (Bacon et al. 2017a). The diet of the Houbara bustard is generalist
113 and opportunistic and present strong seasonal variation in animal (e.g. Coleoptera,
114 Hymenoptera) and vegetal (e.g. Asteraceae, Brassicaceae, Chenopodiaceae – Bourass et al.
115 2012) proportion.

116 We used data collected from a longitudinal nest survey conducted between 2002 and 2016 in
117 the reinforced Houbara population in Eastern Morocco.

118 We focused on six breeding parameters: nesting effort (number of nesting attempts per breeding
119 season per female), nest initiation date, clutch size, egg volume, daily nest survival and brood

120 survival. We hypothesized that potential short-term reduction of performance in released
121 Houbara are related to their potentially low condition and limited experience with their new
122 environment (Bertolero & Oro 2007, Bertolero et al. 2009). Thus, potential differences between
123 released and wild-born individuals should decrease with increasing age, reflecting both
124 individual (i.e., gain in experience within an individual, Mauck et al. 2012) and population-
125 scale processes (i.e., death of lower-quality individuals, assuming that survival and breeding
126 performance may positively covary, Robert et al. 2015b). We thus hypothesize that the
127 difference in breeding performances of wild-born and captive-bred released females will
128 decrease with their age (which is confounded with the time since release for released females).
129 In other words, we expect to find an interaction between the origin of females (released vs.
130 wild-born) and their age.

131 **Material and methods**

132 *Study area*

133 The study was conducted in Eastern Morocco, in the ECWP intervention area (Fig. 2). The
134 study area encompasses approximately 50 000 km² and is characterized by an arid climate
135 marked by irregular rainfalls (less than 200 mm/year). Mean temperatures vary from 6.80°C in
136 winter (December to February) to 26.64°C in summer (June to August). The habitat in the study
137 area is characterized by sparse, shrubby vegetation. **Vegetation cover in the plains mainly**
138 **comprises Chenopodiaceae such as Salsola spp., Hamada spp. and Compositae such as**
139 **Artemisia herba-alba. In clay and silt-rich areas created by seasonal runoff waters, Salsola sp. is**
140 **often associated with Atriplex spp. Drainage courses and wadis are characterized by Zizyphus**
141 **lotus (Rhamnaceae) and Retama sp. (Leguminosae). On the high plateaux and slopes, from the**
142 **extreme east to the Oran region of Algeria, the vegetation is dominated by Stipa tenacissima**
143 **(Gramineae). The core of the study area is used for nomadic pastoral activities, herding and**

144 grazing. Mixed herds are generally composed of 100–300 heads of sheep and goats. Nomads
145 settle camps within the study area, whereas some shepherds come from surrounding villages
146 (Le Cuziat et al. 2005).

147 *Emirates Center for Wildlife Propagation and reinforcement programme*

148 The EWCP was established in 1995 to mitigate the severe decline in Houbara populations
149 occurring in the second half of the 20th century. Two ECWP breeding stations were built for
150 captive breeding (in Missouri in 1995 and in Enjil in 2005, see online appendix A). Detailed
151 descriptions of the captive breeding programme can be found in Lesobre et al. (2010) and
152 Chargé et al. (2010, 2014). From 1996 to 2016, 108 486 birds were released in North Africa
153 (94 374 in the study area). Locally, these intensive releases may induce density dependent
154 process leading to deleterious biotic interactions (intraspecific competition, disturbance,
155 predation) and negatively impact life history parameters (Azar et al. 2016, Bacon et al. 2017b).

156 Within the study area, the overall number of birds released progressively increased over the
157 years (from 28 in 1996 to 9 084 in 2016, see online appendix B), with an increase in the number
158 of release sites and a decrease in the group size per release (Hardouin et al. 2014). The release
159 group size varied between sites (from four to 498 individuals, median = 18 individuals).
160 Houbara were released at an average of 6 ± 3 (standard deviation) months of age in autumn
161 (August to December), and an average of 9 ± 1 months of age in spring (February to May).
162 Autumn releases were managed to avoid direct mortality and disturbance due to hunting. In
163 addition, since 2003, some birds were released in summer (June) at an average of 3 ± 0.6 months
164 of age, but they represent only 8% of total releases in the study area. As such, in this study, we
165 only focused on captive-bred females released in spring and autumn.

166 Hunting was banned between 2000 and spring 2005, and subsequently restricted to the
167 autumn/winter period (October–January) confined within an area comprising 60% of the

168 intervention area. Since 2014, it is estimated that on average 2000 birds are harvested every
169 year, with captive-bred individuals representing 85% of the hunting bags (ECWP unpublished
170 data).

171 *Monitoring of captive-bred released females*

172 Prior to 2006, released Houbara were tagged on the left tarsus with an aluminium ring
173 displaying a unique ID number. Beginning in 2006, all released individuals were
174 subcutaneously tagged with a unique radio-frequency identification (RFID) microchip
175 (TROVAN LID100 implantable transponder, DorsetID; see Hardouin et al. 2015b for details).
176 In Eastern Morocco, 3 014 released birds (49% females) were equipped with transmitters (1
177 937 with VHF transmitters, 933 with satellite transmitters and 144 with GSM transmitters). The
178 VHF transmitters used in this study were battery-powered necklace units with mortality signals
179 (11 g model RI-2B-M, 20 g model RI-2D-M, Holohil System Ltd., Carp, Ontario, Canada) and
180 solar-powered backpack (19 g model, Merlin Systems Inc., Boise, Idaho, USA). During the
181 breeding season, females fitted with VHF transmitters were searched for at least once per week.
182 The satellite and GSM transmitters used in this study were backpack solar-powered
183 transmitters: PTT-100 30 or 45 g Solar GPS PTT and 30 g solar GSM (Microwave Telemetry,
184 Inc., Columbia, Maryland, USA). To identify breeding events of individuals equipped with
185 satellite transmitters, individuals' movements were remotely monitored. When stationary
186 locations were recorded, the last location was checked in the field to confirm whether the
187 individual was dead or nesting.

188 *Trapping and identification of wild-born nesting females*

189 Trapping of wild-born females was performed during egg-collection campaigns in the breeding
190 season of the periods 1997-1998, 2001-2009 and 2015-2016 (see details in online appendix C).
191 Egg collection campaigns were aimed at building the founder population of the ECWP captive-

192 breeding program (Lesobre et al. 2010, Chargé et al. 2014). Females were caught using nylon
193 snares around their nest or around their recently hatched chicks. In total, 143 wild-born females
194 were caught while nesting and were equipped with a transmitter or transmitter replacement. In
195 addition, 10 wild-born females captured and equipped with VHF/PTT transmitters as juveniles
196 were found nesting in later years (see Hardouin et al. 2012 for more details of the capture and
197 monitoring procedures).

198 *Data collection*

199 *Breeding parameters*

200 Six breeding parameters were assessed from breeding survey data collected from 2002-2016:
201 the nesting effort (number of nesting attempts per breeding season per female), the clutch size,
202 the egg volume, the nest initiation date, the daily nest survival rate and the daily brood survival
203 rate. The number of years for which survey data was available varied slightly between breeding
204 parameters, this is detailed in online appendix D.

205 - Nest survey

206 Nests were located from a collaborative survey with shepherds and from individually tracked
207 females. Because of the bias inherent to the trapping and egg-collection campaigns (all wild-
208 born non-equipped nesting females had their eggs collected if not already hatched and were
209 caught) and to avoid confounding factors between transmitter presence and female origin (wild-
210 born and captive-bred), we only selected those nests for which the nesting female was equipped
211 with a transmitter at nest initiation. In total, 703 nests from 305 females were selected for this
212 study. For wild-born females, 300 nests were from 91 wild-born females first captured on their
213 nest, and 21 were from 10 females captured and marked at the juvenile stage. For captive-bred
214 females (n nests = 382), we selected nests from cohorts of females that were released in their

215 first year of life from August to November (in autumn, before the breeding season, n nests =
216 122, n females = 74) and from February to May (in spring, during the breeding season, n nests
217 = 260, n females = 130). Nests were visited on average every 6 ± 3.60 days. In addition, since
218 2013, camera traps were deployed at some of the monitored nests (n=45), providing a
219 continuous survey effort and more accurate assessments of nest fate. Nests equipped with
220 camera traps were visited on average every 8 ± 5.07 days. Preliminary unpublished results did
221 not highlight any deleterious effects of the camera trap monitoring on nest survival in our study
222 area (Bacon 2017a). The use of camera traps gave great details on the guild of species predated
223 on Houbara nests. It is composed of the red fox (*Vulpes vulpes*), the golden jackal (*Canis*
224 *aureus*), stray dogs (*Canis lupus familiaris*), desert hedgehog (*Paraechinus aetiopicus*),
225 common raven (*Corvus corax*) and brown-necked raven (*Corvus ruficollis*). Nest failure was
226 recorded for a visit interval if the clutch disappeared without signs of hatching (Mabee 1997)
227 or was abandoned. We considered a nest to have survived if at least one egg hatched (Mayfield
228 1975).

229 The clutch size was defined as the maximum number of eggs observed in the nest. Since 2003,
230 the length, width (to the nearest hundredth of a centimetre) and mass (to the nearest tenth of a
231 gram) of each egg were measured. The width and length of eggs were then used to calculate the
232 egg volume (Vol) in cm^3 (see details in Bacon et al. 2017a). The nest initiation date was
233 estimated from the calculation of the eggs' incubation stage (in days) at the time of
234 measurement (based on the egg weight loss equation from Hoyt 1979, see details in Bacon et
235 al. 2017a).

236 The nesting effort was calculated as the number of nests initiated per breeding season per
237 female, including females initiating no nest. We selected females that were continuously
238 monitored during the breeding season. Even if all females were fitted with monitoring devices,
239 technical limitations could cause gaps in their monitoring, which could cause the non-detection

240 of nesting attempts. To increase the detectability of nesting attempts, we only selected females
241 that were fitted with VHF and monitored from February to the end of June, with at least one
242 individual sighted every two weeks (resulting in 173 monitoring histories from 141 females
243 from 2002 to 2014).

244 Trapping of nesting females causes systematic nest abandonment; thus, female trapping and
245 egg collection have a positive effect on overall nesting effort, as they promote replacement
246 clutches. However, replacement clutches are initiated later in the breeding season, affecting the
247 distribution of nest initiation dates. Therefore, for those two parameters, we excluded females
248 from the years where their eggs were collected (see online appendix D).

249 - Brood survey

250 Assessing breeding success after hatching and before fledging in species with nidifugous chicks
251 is difficult. It requires the marking and close monitoring of all individuals; a delicate operation
252 that may affect chick survival at this very sensitive stage of life (Barron et al. 2010). As such,
253 we chose to not mark chicks and instead assessed the fate of broods through the monitoring of
254 brooding females. Therefore, between 2002 and 2014, nesting females fitted with VHF
255 transmitters that successfully hatched at least one egg were then searched for at least once per
256 week. Brood failure was considered for a female at a given monitoring interval if the entire
257 brood disappeared before 60 days of age (Hardouin et al. 2012). In total, we monitored 201
258 broods from 133 females. A few females (n=12) were captured while rearing chicks, at the nest
259 or after leaving the nest, either to take measurements or to replace the transmitter.

260 *Statistical analyses*

261 *Nest and brood survival analyses*

262 We used the logistic exposure approach of Shaffer (2004) to estimate the daily nest survival
263 rate (defined as the probability of a living nest to not fail in one day). Egg collections and female
264 trapping cause the end of the nest history and produce an unknown “natural” final fate.
265 Theoretically, in occasional cases where they represent a subset of the sample of nests
266 monitored, nests with an unknown final fate are right truncated at the last date they are known
267 to be active for daily nest survival analysis. In our study, the number of clutches collected was
268 relatively important and biased towards wild-born females. Therefore, nests with an unknown
269 final fate were not representative of the sample of the nests monitored and could lead to an
270 overestimation of the daily nest survival of wild-born females relatively to released females.
271 Thus, we excluded all nests with an unknown final fate from the analysis (following Manolis
272 et al. 2000 and personal communication from Stephen Dinsmore). Finally, as records of
273 periodic nest visits were only standardized beginning in 2003, we discarded data collected prior
274 to 2003.

275 The same statistical approach was used to study brood survival, with the exception that the
276 exposure period starts at hatching and ends 60 days later for successful broods (mean age at
277 fledging, Hardouin et al. 2012, but see details in Bacon et al. 2017a).

278 *Clutch size, egg volume, nest initiation date and nesting effort*

279 The nesting effort was analysed using a generalized linear mixed effects model with a Poisson
280 distribution and a log link function. The clutch size was analysed based on ordinal regression
281 using cumulative linked mixed-effects models (CLMMs). Egg volumes and nest initiation dates
282 were analysed using linear mixed-effects models (LMMs) fitted by maximum likelihood with
283 a Gaussian distribution and an identity link function.

284 *Origin and age factor*

285 We grouped nests into categories based on female origin (wild-born, captive-bred released in
286 autumn and captive-bred released in spring). In addition, we assigned to each nest the age of
287 the nesting female: one-year-old or at least two years old (see online appendix E). For wild-
288 born females, only those captured as juveniles could be aged precisely. A previous study
289 focussing only on released females indicated that one-year-old females had lower breeding
290 performance than older individuals (Bacon et al. 2017a). In addition, the percentage of one-
291 year-old released females initiating at least one nest is low (8%, ECWP unpublished data).
292 Based on this information, we assumed that all wild-born females with unknown age were at
293 least two years old at their first identification on a nest.

294 *Adjustment variables*

295 In monitored animals, events such as trapping and marking are stressful and may have some
296 effect on subsequent behavioural and demographic patterns (e.g. unusual movements, increased
297 mortality, cessation of breeding) once released (Casas et al. 2015, Ponjoan et al. 2008). For
298 nesting female Houbara, trapping causes nest abandonment (direct effect) but may also have a
299 carry-over effect on subsequent breeding performance. For females trapped on live chicks,
300 trapping may have a direct effect on brood survival by affecting either the female or the chicks.
301 Therefore, we considered an intra-seasonal carry-over effect of trapping for the following
302 parameters: clutch size, egg volume, daily nest survival and daily brood survival rate, when
303 measured on the replacement clutch consecutive to the trapping of the female (carry-over
304 trapping). In addition, specifically for the daily brood survival rate, we considered a direct effect
305 of trapping (direct trapping) on the brood when trapping of the females occurred while rearing
306 chicks. Carry-over trapping and direct trapping effects were implemented as binary adjustment
307 variables. To account for the temporal variation of breeding performance values within the
308 breeding season, we included a date covariate (in Julian days, 1st of January = 1, implemented
309 as the nest initiation date for egg volume and clutch size, as the median date between two nest

310 visits for the daily nest survival rate, and as the hatching date of the nest for the daily brood
311 survival rate, Grant & Shaffer 2012). Finally, we considered temporal variation of the daily
312 survival rate of the nest and brood by including, respectively, a binary factor describing whether
313 the nest was in laying or incubation stage and a continuous covariate indicating the age of the
314 brood since hatching (Grant & Shaffer 2012).

315 *Model selection*

316 For each breeding parameter analysis, covariates were rescaled, centralized and standardized
317 by two times the standard deviation (Gelman 2008), and factors with two levels were
318 transformed into binary dummy variables (0-1).

319 We examined the relationship between the breeding parameters and their corresponding
320 variables by developing sets of candidate models that included additive terms of explanatory
321 variables, quadratic terms of continuous temporal covariates ($date^2$ and $brood\ age^2$) and the
322 interaction between the age of the nesting female and its origin. To adjust for potential effects
323 of trapping, we kept the trapping carry-over effect and the direct trapping effect in all candidate
324 models of the concerned breeding parameters. Additionally, current year, female identity and
325 nest identity nested under female identity (only for egg volume analyses) were incorporated as
326 random intercept effects in all models. Random intercept effects were included to avoid pseudo-
327 replication and to account for potential heterogeneity among years, females and nests (Zuur et
328 al. 2009).

329 Thus, the starting (most complex) statistical models were of the following form:

$$330 \quad Y = Female\ Age + Female\ Origin + Female\ Age \times Female\ Origin + Adjustment\ variables$$
$$331 \quad \quad \quad + random\ intercepts$$

332 where Y was the dependent variable (the breeding parameter). Details of specific adjustment
333 variables (mentioned in the section *Adjustment variables*) implemented in the starting model of
334 each breeding parameter can be found in Appendix F.

335 Starting from this generic structure, models were simplified to develop all possible
336 combinations of explanatory variables (including additive, polynomial terms and the
337 interaction, see all model combinations in Appendix G). This procedure was applied to our six
338 breeding dependent variables. For each breeding dependent variable, we ranked models using
339 the Akaike Information Criterion corrected for small sample size (AICc). The best model
340 ($\Delta\text{AICc} = 0$; Burnham & Anderson 2002) was selected to estimate β coefficients and associated
341 95% confidence intervals for fixed-effect covariates. All analyses were conducted using R 3.3.3
342 (R Development Core Team, 2017) and the packages lme4 1.1-12 (Bates et al. 2015), Ordinal
343 2015.6-28 (Christensen 2015), MuMIn 1.13.4 (Barton 2015), and nest survival (Herzog 2009).
344 Normality and homoscedasticity of the random residuals were checked graphically from the
345 starting models, and no overdispersion (Zuur et al. 2009) was observed for the Poisson
346 distribution model.

347 **Results**

348 On average, females were monitored over 2.97 ± 1.50 years (3.58 ± 1.76 years for wild-born
349 females and 2.70 ± 1.25 years for released females) and 86% of females were monitored over
350 more than 1 year (88% for wild-born females and 85% for released females).

351 We analysed the effects of dependent covariates on our six breeding parameters based on a
352 common statistical approach. To keep the presentation of the results clear and straightforward,
353 we directly present the coefficients from the best selected models ($\Delta\text{AICc} = 0$) in Table 1. AICc
354 based model ranking selections, which compiled six tables, can be found in online appendix G.

355 According to the best models (Table 1), clutch size and egg volume declined along the breeding
356 season. Daily nest survival was higher during the nest initiation stage than during the incubation
357 stage, while daily brood survival increased with the age of the brood. For all breeding
358 parameters concerned (clutch size, egg volume, daily nest survival and daily brood survival),
359 the carry-over trapping effect had 95% confidence intervals overlapping 0, whereas direct
360 trapping of females while rearing chicks had a very strong negative impact on the daily survival
361 of the brood (Table 1). For all breeding parameters (with the exception of the daily nest survival
362 rate), the Age effect was selected in all best models, indicating that one-year-old females had
363 poorer breeding performances than older ones (Table 1).

364 The origin factor was selected in the best model sets for nesting effort, egg volume and daily
365 brood survival rate. In Table 1, for the female origin factor, the results show the differences
366 with respect to a reference level at the intercept. We defined wild-born females as the reference
367 level at the intercept in Table 1, but all levels of the female origin factor were set as the reference
368 level at the intercept in order to assess potential significant differences. Captive-bred females
369 initiated fewer nests and produced smaller eggs than wild-born females (Figs 3A, B). However,
370 confidence intervals of these effects did not overlap 0 only for captive-bred females released in
371 spring relative to wild-born females (Table 1). Captive-bred females released in autumn had
372 intermediate values of nesting effort and egg volume, but with confidence intervals difference
373 to the two other groups overlapping 0 (Table 1). Finally, captive-bred females released in spring
374 had lower daily brood survival than wild-born females and captive-bred females released in
375 autumn (Fig. 3C, Table 1), and the confidence intervals of the difference between captive-bred
376 females released in spring and wild-born females was close to negative (Table 1).

377 We were particularly interested in the interaction term of the age of nesting females and their
378 origin, which quantifies whether any effect of origin depends on age (i.e., short-term) or not
379 (i.e., **long lasting**). However, none of the best models (Table 1) included this interaction,

380 providing no support for a more marked effect of the origin in one-year-old females as
381 compared to older females.

382 **Discussion**

383 The assessment of the breeding performances of released individuals is of major importance in
384 translocation programmes (Bertolero et al. 2009). In this study, we investigated the differences
385 of breeding parameters between wild and captive-bred released Houbara females and revealed
386 how release strategies may influence the magnitude of this differences. This is a prerequisite to
387 adapting and improving translocation strategies and thus to increase the chance of translocation
388 success (Armstrong & Seddon 2008).

389 Most breeding parameters (except nest survival) consistently showed age-specific variation,
390 suggesting that **one-year-old females have reduced performances** compared to older ones, in
391 agreement with a previous study (Bacon et al. 2017a). Individual heterogeneity was taken into
392 account in our statistical framework (see Nussey et al. 2006, van de Pol & Verhulst 2006). This
393 suggests that the observed effect of age is best explained by longitudinal improvement of
394 individuals (increased breeding experience or an increase in breeding investment, Curio 1983),
395 than by population level processes (e.g., selection of the best individuals over time). The lack
396 of age effects on the daily nest survival may be explained by the weight of external factors,
397 such as environmental conditions (Morales et al. 2002) or predation, which is a prominent cause
398 of nest failure in birds (Martin 1995), including Houbara (Bacon et al. 2017a, Koshkin et al.
399 2016), potentially overriding any age-dependent effects.

400 Regardless of age effects, our results indicate that, for some of the breeding parameters studied,
401 wild-born individuals performed slightly better than individuals translocated in autumn and
402 better than individuals translocated in spring. More precisely, wild-born females initiated more
403 nests with larger eggs when compared to captive-bred females released in spring. In addition,

404 the daily brood survival of captive-bred females released in spring was lower than for wild-
405 born females. These differences have a marked size effect. It corresponds to a decline of ~47%
406 in nesting effort and a decline of ~40% in brood survival (from hatching to fledging) when
407 considering adult females released in spring relative to wild-born adult females (Figs 3A, C).

408 Conversely to our expectations, we did not observe any interaction between the age of the
409 female and its origin. This result is consistent with the **long lasting** (i.e., permanent) negative
410 post release effect on breeding parameters observed in other translocated species (see, e.g.,
411 Sarrazin et al. 1996). It is also consistent with previous findings in Houbara that released
412 captive-bred females exhibit age-dependent patterns of variation in breeding performance,
413 similar to those observed in many vertebrate populations in the wild (i.e., a bell-shaped trend
414 divided into youth, adulthood and senescence; see discussion in Bacon et al. 2017a).

415 As differences between wild-born and captive-bred individuals were **long lasting**, we cannot
416 exclude the possibility that genetic causes related to captive-breeding issues partly explain the
417 observed differences. However, strong and restrictive guidelines are conducted in the ECWP
418 captive breeding programme (Chargé et al. 2014). These guidelines aim to minimize the loss of
419 genetic variation and to minimize the adaptation to captivity in the captive population in order
420 to maximize the fitness of individuals released into the wild, while reducing the genetic
421 consequences of the reinforcement programme on wild populations (Chargé et al. 2014).
422 Nevertheless, the relaxation of sexual and natural selection and adaptation to captivity may
423 partly explain the lower breeding performances of captive-bred individuals in the wild (Araki
424 et al. 2007, Frankham 2008). Beside, owing to the substantial translocation effort (see online
425 appendix B), a substantial proportion of wild-born individuals may be offspring from
426 translocated birds (see general discussion in Barbanera et al. 2010), which may explain why the
427 breeding performances of released and wild-born females are relatively similar. Therefore, it is
428 likely that most differences between the two groups are related to non-genetic issues.

429 At the phenotypic level, previous research into captive breeding/rearing in birds has suggested
430 that demographic differences between released and wild-born individuals can be explained by
431 the lack of exposure of chicks hand-reared in captivity to adult behaviour (Roche et al. 2008),
432 permanently decreasing their fitness in the wild (Buner & Schaub 2008, Buner et al. 2011, Pérez
433 et al. 2015, Sánchez-García et al. 2011). Although wild-born and released captive-bred Houbara
434 females have a similar diet (Bourass & Hingrat 2015) and exploit equivalent ecological niches
435 (Monnet et al. 2015), released females may be less efficient at finding and exploiting resources
436 (Champagnon et al. 2012). This could explain the lower investment of captive-bred females in
437 reproduction (e.g., egg production), which may subsequently affect the survival of the chicks.
438 In species with precocial chicks (including nidifugous chicks), smaller eggs generally contain
439 less yolk, giving rise to chicks that are in lower condition with lower nutrient reserves at
440 hatching and that are more prone to early mortality (Amundsen & Stokland 1990, Blomqvist et
441 al. 1997, Galbraith 1988, Williams 1994). The differences observed between wild-born and
442 translocated females must be interpreted while taking into account that all individuals were
443 fitted with transmitters. Markings devices can have significant impacts on some demographic,
444 physiological and behavioural parameters (Barron et al. 2010, see discussion in Le Maho et al.
445 2014). However, because wild-born and released females are unlikely to exhibit differential
446 responses to transmitter fitting, our main conclusions are unlikely to be affected by transmitter
447 effects.

448 Our results indicate that the difference observed between wild-born and released females varies
449 according to the period of release (autumn versus spring). Captive-bred females released in
450 autumn had consistently higher nesting effort, egg volume and daily brood survival values than
451 females released in spring (Table 1). Assuming that survival and reproductive parameters
452 positively covary (e.g., "fixed heterogeneity", Cam et al. 2016), such a pattern may be related
453 to the death of the less performant females between their release and the breeding season among

454 females released in autumn. This hypothesis is supported by previous findings showing that
455 harsh environmental conditions in autumn and winter lower short-term survival rates compared
456 to spring releases (Hardouin et al. 2014), representing a stronger environmental filter that
457 primarily affects weak individuals.

458 It is important to note that not all breeding parameters differed between wild-born and captive-
459 bred females. The origin of females was not selected in the best models for clutch size, nest
460 initiation date and daily nest survival analysis. Similar heterogeneous responses of multiple
461 breeding parameters to female origin were observed by Hill & Roberston (1988) for a reinforced
462 ring-necked pheasant (*Phasianus colchicus*) population, where wild-born and captive-bred
463 released females had similar nesting effort and nesting success, yet chick survival to fledging
464 and total productivity were higher for wild-born females.

465 **Management implications**

466 We observed consistent, permanent impairments in some breeding parameters of captive-bred
467 released females relative to wild-born females. The magnitude of these differences highlights
468 the importance of assessing demographic impacts of captivity and post release effects in
469 translocated populations. In our study, the observed differences between wild-born and released
470 females appears to be dependent on the translocation strategy (period of release), which implies
471 that it could be buffered by adapting translocation strategies (favouring autumn releases).
472 Nonetheless, the current strategy (spring and autumn releases) seems suitable regarding the
473 multiple objectives of the reinforcement programme, i.e., reinforcement of the wild population
474 and supplementation for hunting (falconry). For autumn releases, environmental stochasticity
475 may select individuals in good condition (Hardouin et al. 2014) that will later breed with
476 relatively better parameters (as suggested by the present results). On the other hand, although
477 outcomes from spring releases will be less certain in terms of breeding performances, higher

478 survival rates in this season will help to maintain the population size at a level that can sustain
479 hunting pressure (Hardouin et al. 2015a) and population growth rate. Finally, although
480 differences were observed between wild-born and captive-bred females, our results confirm the
481 capacity of captive-bred females to reproduce in the wild and to contribute to the dynamics of
482 the population beyond their individual history. This partially supports the success of the
483 reinforcement programme (Bertolero & Oro 2009) and provides a strong basis for more
484 integrative and quantitative assessment of translocation success (Robert et al. 2015a).

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