1  **Captive breeding cannot sustain migratory Asian houbara *Chlamydotis***
2  ***macqueenii* without hunting controls**

3  **Running Title**: Captive breeding: reinforcement risks replacement

4

5  **ABSTRACT**

6  To evaluate the potential contribution of captive breeding to the conservation of exploited
7  migratory Asian houbara *Chlamydotis macqueenii*, we estimated release numbers required to
8  stabilise a population in a hunting concession (14,300 km$^2$), under scenarios of local licensed hunting
9  and flyway-scale protection. We developed a population model, initially 2350 adult females, re-
10  sampling parameters measured through fieldwork and satellite telemetry, over 1000 iterations. With
11  current flyway-scale unregulated harvest, and without any licensed hunting in the concession,
12  populations declined at 9.4% year$^{-1}$ (95% CI: –18.9 to 0% year$^{-1}$); in this scenario a precautionary
13  approach (85% probability $\lambda \geq 1.0$) to population stabilisation required releasing 3100 captive-bred
14  females year$^{-1}$ (131% x initial wild numbers). A precautionary approach to sustainable hunting of 100
15  females year$^{-1}$ required releasing 3600 females year$^{-1}$ (153% initial wild numbers); but if
16  interventions reduced flyway-scale hunting/trapping mortality by 60% or 80%, sustaining this quota
17  required releasing 900 or 400 females year$^{-1}$, 38% and 17% of initial wild numbers, respectively.
18  Parameter uncertainty increased precautionary numbers for release, but even with reduced
19  precaution (50% probability $\lambda \geq 1.0$), sustainable hunting of 100 females year$^{-1}$ required annual
20  releases of 2200 females (94% wild) without other measures, but 300 (13%) or no (0%) females
21  under scenarios of a 60% or 80% reduction in flyway-scale hunting/trapping. Captive breeding
22  cannot alone sustain migrant populations of wild *C. macqueenii* because it risks replacement and
23  domestication. Trade and exploitation must be restricted to avoid either extinction or
24  domestication. For exploited populations, supplementation by captive breeding should be used with
25  caution.

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## 1 Introduction

Captive breeding is increasingly used to re-establish or reinforce species' populations, but its effectiveness needs rigorous assessment (Converse et al. 2013a; IUCN/SSC 2013; Taylor et al. 2017). Inescapable behavioural and genetic risks (Frankham 2008; Snyder et al. 1996) become acute where large-scale releases reinforce exploited wild populations (Laikre et al. 2010). An understanding is therefore essential of the levels of release, relative to wild numbers, needed to render harvest sustainable (Burnside et al. 2016).

Despite best practices to minimise loss of genetic diversity (Frankham 2008; Williams and Hoffman 2009), long-term *ex situ* regimes inevitably select across multiple traits (Snyder et al. 1996). Traits can diverge rapidly (Christie et al. 2016) affecting fecundity and linked traits (Bagliacca et al. 2004; Chargé et al. 2014; Lacy et al. 2013), immune-genetics (Worley et al. 2010), digestive morphology (Moore and Battley 2006), temperament (Robertson et al. 2017), and intrinsic and learnt behaviours including anti-predator responses (Mathews et al. 2005; McPhee 2004; Rantanen et al. 2010). Despite higher mortality and lower productivity in captive-bred individuals, post-release selection may not purge maladaptive traits, which can introgress into wild populations (Ford 2002; Sanchez-Donoso et al. 2014; Söderquist et al. 2017), and wild-born descendants of captive-bred parents may exhibit substantially lower fitness than those of wild parents (Araki et al. 2009).

The primary cause of the Asian houbara *Chlamydotis macqueenii* Gray being listed as globally threatened (IUCN status Vulnerable) is hunting, which occurs across the semi-arid desert flyway linking China and Central Asia to wintering grounds in Iran and Pakistan, and involves Arab falconers and local communities (often using firearms) compounded by live-trapping for falcon-training (BirdLife International 2018). Asian houbara has suffered population losses and range contraction across its southern resident range in the Middle East, Arabia and Pakistan, as well as substantial declines in its migratory Central Asian populations (Tourenq et al. 2004). To date, the main conservation response has been supplementation by large-scale releases of captive-bred birds (Burnside et al. 2016; IFHC 2016). In the closely related African houbara *C. undulata*, however, selection in captivity has affected a range of physiological, reproductive and behavioural traits (Chargé et al. 2014), with unknown or unreported consequences. Captive-bred *C. macqueenii* released in Uzbekistan migrated shorter distances than wild counterparts (Burnside et al. 2017), but whether selection for docility, changes to immune-genetics and loss of learnt behaviours reduce fitness in the wild is unknown. Crucially, the release levels required to stabilise residual exploited populations remain unstudied.

Using a population model parameterised by extensive fieldwork and satellite telemetry, we estimate the current trajectory, and the potential for supplementation to stabilise it, in a population of migratory *C. macqueenii* that is targeted for small-scale harvest within a large hunting concession but is also exposed to exploitation elsewhere along its flyway. We assess whether the wild population possesses a harvestable surplus or, conversely, needs captive-bred supplementation or other mitigations within the flyway to stabilise it. We then calculate the additional releases required to offset licensed hunting, first under current conditions, then under management scenarios that limit hunting and trapping on the flyway and wintering grounds.

## 2 Materials and methods

### 2.1 Study area and population

We studied a migratory Asian houbara population in 14,300 km$^2$ of the southern Kyzylkum Desert, Bukhara province, Uzbekistan (39.34–40.56°N 62.21–65.20°E). The area supports c. 0.14 male houbara km$^{-2}$ (Koshkin et al. 2016b) and is managed as a hunting concession, licensed by the State Committee for Nature Conservation. A captive-breeding facility, founded with locally sourced birds, supports annual releases (mean 364 year$^{-1}$ during 2011–2017). Limited hunting (with falcons) occurs in October when, although released birds are still present, some adults have already left the area,

78 with numbers supplemented by migratory individuals from other breeding populations, including
79 Kazakhstan and China (Combreau et al. 2011). Thus, while our modelling assumes a closed
80 population, captive-bred individuals released to compensate for licensed harvest within a hunting
81 concession may bolster local numbers but not offset the depletion of populations breeding
82 elsewhere in the flyway.

## 2.2 Parameterisation of adult female re-nesting model

84 Breeding productivity, $F$, was estimated from an individual-based re-nesting model (following
85 Dolman et al. 2015) coded in R. Propensity to nest and first clutch dates were determined from
86 returning adult satellite-tagged females (2013–2017). Clutch size, nest outcomes and hatching rates
87 were measured from wild nests (2012–2017) monitored using protocols in Koshkin et al. (2016a).
88 Incubating females were confirmed as wild at 74% of nests, and since few remaining nesters were
89 likely to have been captive-bred (95% probability ≤5 nests: Appendix A) the likelihood of
90 confounding effects was considered negligible. Nests were treated as independent observations
91 since nest predation is spatially unpredictable (Koshkin et al. 2016a) and most were from different
92 individuals. Nest success was date-dependent, declining mid-season before partially recovering
93 (Appendix A and Fig. A.1) in response to the phenology of a key nest predator (Koshkin et al. 2016a).
94 Following nest failure, date-dependent re-nesting probability, re-nesting interval and clutch size
95 were determined from satellite-tagged females (Appendix A and Fig. A.2; sample sizes in Table 1). As
96 negative effects on reproduction are largely associated with neck collars (Bodey et al. 2017),
97 breeding parameters derived using backpack-mounted telemetry were not adjusted.

## 2.3 Age-specific survival

99 Chick survival (over 35 days) to fledging, $S_{chick}$, was measured for replicate broods of satellite-tracked
100 adult females (some tracked over multiple years: Table 2) that had hatched at least one egg. Early
101 long-distance flights indicated complete brood loss; other females were relocated 34–38 days post-
102 hatch and the numbers of surviving chicks were recorded (details in Appendix A). Chick daily survival
103 probability, *chick.dsr*, estimated using a binomial trials Generalised Linear Model (GLM) (which
104 considers the number of repeated trials, here exposure days, leading to the outcome of each
105 sample), was independent of hatching date (Table A.2). Juvenile survival from fledging to October
106 was examined by satellite telemetry of individuals captured at 34–38 days (details in Appendix A).
107 The fledging-date-specific daily survival rate declined for later broods, such that earlier-fledged
108 juveniles were more likely to survive to October (Fig. A.3 and Tables A.3, A.4).

109     A binomial trials GLM was used to estimate subsequent first-winter survival of wild satellite-
110 tagged juveniles that survived to October. Survival of satellite-tagged wild adults (following protocols
111 in Burnside et al. 2017) considered two periods: winter (including outward and return migration),
112 and summer (including settlement, breeding, post-breeding dispersal and moult). Survival of captive-
113 bred houbara to 01 October was similar for yearlings released in spring (March–May) and young-of-
114 the-year released in August (Burnside et al. 2016). To examine underlying demography, when
115 analysing survival probabilities individuals killed by licensed hunting within the concession were
116 coded as surviving up to that date; hunting quotas were then applied in population management
117 scenarios (see below).

118     Transmitters may reduce avian survival, particularly when backpack-mounted on species with
119 flapping flight, using tags that exceed 1% of body mass, although mean effect size is small (Bodey et
120 al. 2017). As we cannot exclude satellite-tag effects on houbara survival, we adjusted all transmitter-
121 derived survival parameters (captive-bred released, wild juvenile from fledging to October, first
122 winter, adult summer and adult winter) by the mean effect size on avian survival from meta-analysis
123 (Bodey et al. 2017). Mean effect sizes reported as the Fisher-transformed correlation coefficient ($Zr$
124 = –0.064) were converted to Cohen's d, a measure of the difference between means ($d$ = –0.128),
125 following Nakagawa and Cuthill (2007). All mean survival parameters were increased by this

126 proportion of the parameter's standard error (SE), as an estimate of the pooled SD of the original
127 and adjusted parameter.

128 *2.4 Population model*

129 Age-specific female cohorts were modelled, coded in R, assuming: equal sex ratio at hatching
130 (Dolman et al. 2015), breeding unconstrained by male availability, and maximum age 20 years
131 (Preston et al. 2015). Table 1 summarises demographic parameters. The initial distribution of age-
132 classes was determined from a Leslie matrix model using mean demographic parameters, which
133 stabilised at 35 years. Population trajectories over 20 generations were examined using a population
134 model, applied to an initial population of 2350 adult females, estimated from spring male point
135 count data (Appendix B). At each of 1000 iterations, each demographic parameter was randomly
136 sampled: for survival rates from a beta distribution bound by limits of 0 and 1, defined by the mean
137 and its SE; for clutch size and incubation start-date from a normal distribution defined by the mean
138 and observed standard deviation (SD); and for other parameters from a normal distribution defined
139 by the mean and SE. Parameter estimates pooled data across individuals and years, and iteration-
140 specific resampling combined both inter-annual variability and empirical sampling error. Individual
141 probabilistic events (probability of breeding, daily nest survival during incubation, egg hatching
142 probability, date-dependent re-nesting probability after clutch loss, and individual chick, juvenile and
143 adult survival) were assessed as random binomial trials against the iteration-specific parameter
144 threshold.

145 As few one-year-old females attempt to breed (Azar et al. 2018; Maloney 2003), we assumed
146 first breeding at two years. We further assumed that subsequent breeding performance was
147 independent of age; however, as breeding propensity and success increase up to three years (Bacon
148 et al. 2017; Maloney 2003) the contribution of second-year birds to productivity was slightly over-
149 estimated. Reproductive senescence was not incorporated. For captive-bred *C. undulata*,
150 reproductive senescence is negligible, with only subtle reductions in chick hatching by 18 years
151 (Preston et al. 2015) and, for released birds, in clutch size and egg volume after eight years (Bacon et
152 al. 2017). Furthermore, our monitoring of wild nests and broods sampled performance across the
153 current female age structure.

154 For computational efficiency, a single matrix of potential breeding outcomes was populated by
155 running the re-nesting model for 10,000 independent female breeding seasons. Within the re-
156 nesting model, individual probability of breeding was assessed and, if breeding, the first-egg date of
157 the first nesting attempt was determined by randomly sampling the observed distribution (Table 1).
158 Initial clutch size was sampled from the distribution of known first attempts (rounded to an integer,
159 bounded 1–5), incremented by 1.5 days for each additional egg (Saint Jalme and van Heezik 1996) to
160 determine incubation start-date. As the primary cause of nest failure is predation (Koshkin et al.
161 2016a), which is considered spatially unpredictable, nest success was sampled independently for
162 each attempt (rather than individual). A vector of date-specific daily nest survival probabilities
163 ($clutch.dsr_d$) and their SE was generated from a binomial trials model of monitored nests. For each
164 nesting attempt, the beta distribution of the first day's $clutch.dsr_d$ was sampled to determine a nest-
165 attempt-specific adjustment that was applied (as a Z score relative to the date-dependent SE) to
166 each subsequent $clutch.dsr_d$ that formed the basis of iterative daily binomial trials, until the clutch
167 failed or hatched. Females hatching eggs were assumed not to re-nest during that season. Whether
168 a female re-nested after failure was determined by a binomial trial performed on the date-
169 dependent re-nesting probability, sampling the re-nesting interval to determine the subsequent
170 first-egg date, sampling the distribution of known second clutches to determine the re-nesting clutch
171 size, and then modelling success as above. The re-nesting model yielded a matrix of outcomes for
172 each female-season.

173 The population model randomly sampled the matrix of nesting outcomes for each breeding-age
174 female in each breeding season. For each successful nest, the matrix provided clutch size and

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175 hatching date; the iteration-specific hatching probability was then applied (by binomial trial for each
176 egg) to determine chick numbers. Chick survival to fledging was tested by an individual binomial
177 trial, against the iteration-specific value of $S_{chick}$. For each juvenile, survival from fledging to October
178 was determined by an iteration-specific adjustment (by Z score) of the relevant fledge-date-
179 dependent $juv.dsr_{fd}$, with daily binomial trials repeated according to the number of exposure days to
180 01 October.

181 Following breeding, adult summer survival was tested by individual binomial trials against the
182 iteration-dependent probability, together with surviving juveniles providing total numbers at the
183 October hunt. Individual over-winter survival to spring (31 March) was tested against the iteration-
184 specific, age-dependent probability and survivors then incremented in age, providing spring
185 breeding numbers.

186 *2.5 Demography*

187 Population trajectories were considered in terms of mean population growth rate ($\lambda$, the linear
188 regression of log population size across years 1–20). The value of each demographic parameter
189 (breeding productivity, first-winter, adult winter and adult summer survival) at which $\lambda = 1$ (holding
190 other parameters at their mean) was predicted from a series of GLMs (with normal error) which
191 related iteration-specific $\lambda$ to the iteration-specific parameter value.

192 *2.6 Population management / mitigation scenarios*

193 To examine the magnitude of releases required to stabilise the exploited population within the
194 hunting concession, we considered scenarios of releasing between 0 to 4000 captive-bred female
195 houbara year$^{-1}$, under different levels of regulated hunting, ranging from 0 to 200 females year$^{-1}$. For
196 captive-bred *C. undulata*, susceptibility to hunting did not vary between sexes or with time since
197 release (Hardouin et al. 2015). We treated wild adult, wild juvenile and captive-bred released
198 females as equally susceptible to hunting, with their mortality dependent on the ratio of the hunting
199 quota to total female numbers alive in October. Subsequent individual winter survival was tested by
200 a binomial trial against the iteration-specific, cohort-specific survival probabilities and survivors
201 incremented in age next spring. We assumed (perhaps generously: see Discussion) that, after their
202 first year, captive-bred released birds performed as wild birds.

203 For each release and hunting scenario, we examined release numbers required to stabilise the
204 population ($\lambda \geq 1$). We examined two scenarios: an 'average approach' based on the mean $\lambda$, thus
205 giving a 50% probability of stability or increase, and a more rigorous 'precautionary approach' based
206 on the lower 15% confidence interval of the mean $\lambda$ (85% probability $\lambda \geq 1$).

207 Despite extensive ecological study (Koshkin et al. 2016a; Koshkin et al. 2016b; Koshkin et al.
208 2014), no opportunity exists to enhance *in situ* breeding productivity to offset mortality. We reject
209 predator control across breeding landscapes because: (1) the key predator, *Varanus griseus*, is
210 vulnerable and protected (Anon 2009); (2) poison-bait is indiscriminate; (3) disrupting predator/prey
211 dynamics risks unforeseen consequences; (4) predator reduction may affect selection on wild
212 houbara traits (e.g. Guilherme et al. 2018); and (5) no evidence exists that anthropogenic factors
213 inflate predator numbers in areas remote from agriculture or settlements.

214 Actions to limit illegal trapping and sustainably regulate hunting have long been advocated as
215 conservation measures (CMS 2005; Combreau et al. 2005) and may reduce dependence on captive-
216 bred supplementation. We therefore examined the demographic consequences of scenarios that
217 reduced anthropogenic mortality. The proportion of mortality in each cohort (wild adults in summer;
218 wild adult, wild first-winter and captive-bred birds in winter) attributable to hunting/trapping, was
219 estimated from PTT location and engineering data (Burnside et al. submitted). A similar proportion
220 of wild adult winter and wild first-winter mortalities were attributed to hunting/trapping, at 53%
221 (Table 1), less than an earlier estimate of 74% of over-winter mortality attributable to hunting for
222 adult-sized migrant Asian houbara (Combreau et al. 2001). Hunting/trapping pressure may have

223 reduced, alternatively more hunters or trappers may now simply remove and discard rather destroy
224 a PTT, in which case anthropogenic mortality will be underestimated. We therefore consider our
225 estimates of the proportion of total winter mortality attributed to hunting/trapping, and thus the
226 extent to which limiting this offers a reduction in captive-bred numbers needed for release, as
227 conservative. Fewer (23%) captive-bred first-winter mortalities were attributed to hunting/trapping
228 (Burnside et al. submitted). Of wild adult summer mortalities, 23% were attributed to
229 hunting/trapping (Burnside et al. submitted). Using this information, we incrementally reduced
230 hunting/trapping mortality according to:

231 $$S_{j.2} = S_{j.1} + mort.red.(P_{j.1}).(1 - S_{j.1}) \qquad \text{eqn. 1}$$

232 where $S_{j.1}$ and $S_{j.2}$ are the original and improved winter or summer survival probabilities of cohort $j$,
233 $mort.red$ the proportionate reduction in hunting/trapping (by 0.1 increments) and $P_{j.1}$ the proportion
234 of mortality attributable to hunting/trapping.

## 3 Results

### 3.1 Demographic performance

### 3.1.1 Productivity

238 Nesting propensity was high, and nest success relatively high (52% overall), with most eggs in
239 successful nests hatching (Table 1). Mean annual productivity, estimated from the re-nesting model
240 for a starting population of 2056 breeding-age (≥2 years) females and applying date-independent
241 chick mortality and date-dependent juvenile mortality, was 0.334 (0.037 SD) female recruits in
242 October per breeding-age female (Table A.5).

### 3.1.2 First-winter and adult survival

244 The mean number of wild female yearling recruits returning the following year was 0.132 ± 0.016 SD
245 (breeding-age female)$^{-1}$ (Table A.5). First-winter survival of released captive-bred houbara did not
246 differ ($t_{67}$=1.235, P=0.221) from that of wild first-winter birds (Table 1). Adult annual survival
247 (excluding licensed hunting within the concession; estimated for 58 individuals over 132 individual-
248 years 2011–2018) was 0.8030± 0.0346 SE, and similar between winter and summer periods (Table
249 1).

### 3.1.3 Population trend

251 The wild population, examined in the absence of licensed hunting in the concession or release of
252 captive-bred birds (Fig. 1), was estimated to be declining at 9.4% year$^{-1}$ (mean $\lambda$, 0.906, 95% CI
253 0.811–1.00), with only 2.7% of population iterations increasing. The trajectory was similar without
254 adjustment of survival parameters to compensate for potential transmitter effects (mean $\lambda$ = 0.904,
255 0.818–0.985 CI; 0.9% iterations increasing). To achieve population stability ($\lambda$ = 1.0) required large
256 increases in demographic parameters: for productivity, to 0.599 (95% CI 0.583–0.616) female
257 recruits in October per breeding-age female, substantially beyond the upper quartile of current
258 productivity (Fig 2a); for first-winter or adult winter survival, to 0.70 (95% CI 0.69–0.72) and 0.996
259 (95% CI 0.992–1.0) respectively, again substantially beyond their current upper quartiles (Fig. 2b, 2c).
260 Stability could not be achieved solely through increased summer survival (to >1.0) (Fig. 2d).

### 3.2 Scenarios for population stabilisation and creating a huntable surplus

262 With no licensed hunting occurring in the concession, stabilising population trajectories required, on
263 average (50% probability $\lambda$ ≥ 1.0), annual releases of 1700 females (Fig 3a), 72% of the initial wild
264 female numbers. Under this 'average approach', compensating for an annual hunting quota of 100
265 females within the concession would require annually releasing 2200 females, approaching (94%)
266 initial wild numbers, while a quota of 200 females required annually releasing 2700 females,
267 exceeding (115%) wild numbers. However, a precautionary approach (85% probability $\lambda$ ≥ 1.0)
268 required annually releasing 3100 females (132%) with no hunting, and 3600 (153%) or >4000

269  (>170%) females for sustainable annual quotas of 100 or 200 females respectively. Total numbers of
270  houbara hunted or released would, assuming an equal sex ratio and no differential hunting
271  susceptibility, be double these levels.

272  In scenarios where the hunting/trapping component of winter mortality was reduced by 30%, a
273  quota of 100 females could, on average, be sustained by annually releasing 1100 females, half those
274  required without wider regulation but still 47% relative to wild numbers (Fig 3b); or under a
275  precautionary approach by annually releasing 2200 females (94% wild numbers). If winter
276  hunting/trapping mortality were reduced by 60%, a quota of 100 females could, on average, be
277  sustained by annually releasing 500 females (21%), while a precautionary approach required
278  annually releasing 1200 females (33% of those required without wider regulation but still 51% of
279  wild numbers). Concerted action to reduce winter hunting/trapping mortality by 80% would allow
280  sustainable hunting of 100 females by annually releasing only 200 (on average) or 700
281  (precautionary) females, 9% and 30% initial wild numbers respectively.

282  If both summer and winter hunting/trapping mortality were reduced similarly by 30%, a quota
283  of 100 females could be sustained by annually releasing 900 (on average) or 1900 (precautionary)
284  females (Fig. 3c), 38% and 81% of initial wild numbers respectively. If annual hunting/trapping
285  mortality were reduced by 60%, a quota of 100 females could be sustained by annually releasing 300
286  (on average, 13%) or 900 (precautionary, 38%) females. However, if annual hunting/trapping
287  mortality were reduced by 80% a sustainable hunt would require no (0%) or 400 (17%) females
288  under average and precautionary scenarios, respectively.

**4 Discussion**

Population modelling indicated the *C. macqueenii* population in the Kyzylkum of Uzbekistan is declining by 9.4% year$^{-1}$ (95% CI: −18.9% year$^{-1}$ to 0% year$^{-1}$), despite strong breeding productivity, due to unsustainable mortality. With no harvestable surplus, population stabilisation required a reduction in mortality and/or the release of captive-bred birds; licensed hunting within the concession then required additional releases. However, if captive breeding and release was the sole conservation measure, under a precautionary approach (85% probability of stabilising the population) numbers that must be released annually exceed the wild population: 132% of initial wild numbers in the absence of licensed hunting within the concession; 153% or >170% with a modest hunting quota of 100 or 200 females respectively (200 or 400 houbara). Unless action to regulate hunting and limit trapping across the flyway was extremely effective (e.g. reducing annual hunting/trapping mortality by 80%), annual numbers of captive-bred releases required for population stabilisation remained substantial relative to wild numbers.

*4.1 Wild performance*

Nesting propensity of satellite-tagged females was high (98%), while overall nest success (52%) and hatching probability (86%) were similar to those of wild houbara in China (59% and 84% respectively, Combreau et al. 2002). Wild chick survival probability to five weeks (50%) exceeded that of wild chicks in China (39% to 8 weeks, Combreau et al. 2002), and wild juvenile survival was high from fledging to 01 October (71%). Thus predicted population declines cannot be attributed to poor productivity, and population stabilisation would require an unfeasible increase above current levels of recruitment.

Wild adult annual mortality (19.7%) was below the 28.3% (18.6–40.4% CI) for adult-sized houbara (possibly including some first-winter birds) migrating between China and Pakistan, 1994–2000, when mortality was 11.2 times higher in winter than the breeding season (Combreau et al. 2001). Although wild first-winter mortality (63%) was greater, the proportion attributable to hunting/trapping was similar to that of wild adults. However, in the absence of hunting/trapping mortality, wild first-winter mortality may be less than 45%. Although houbara remain at risk on migration and wintering grounds in Pakistan, Afghanistan and Iran, adult summer mortality (including unlicensed hunting and powerline collisions: Burnside et al. submitted; Burnside et al. 2015) was similar to that in winter. Conservation measures should therefore address threats of infrastructure and hunting on breeding grounds as well as the widely recognised threat (CMS 2005; Combreau et al. 2005) of unsustainable harvest in wintering areas.

We consider these results robust, although further parameter refinement may narrow confidence limits and refine predictions. In two aspects, our modelling was conservative and thus may have under-estimated numbers of releases needed to stabilise populations. First, it will have slightly over-estimated productivity by not allowing for lower output of two-year-old females and senescent birds. Second, it assumed that, after surviving their first winter, captive-bred birds performed as well as wild adults (see below). Conversely, any transmitter impacts may over-estimate numbers of releases required. However, we adjusted survival estimates upward by the mean transmitter effect from recent meta-analysis (Bodey et al. 2017). Moreover, given that transmitter effects are more detrimental for nesting propensity than survival (Barron et al. 2010), the high (98%) nesting propensity of returning satellite-tagged adult females suggests transmitters minimally affected condition. Indeed, where protocols have been tested and expertly adapted to bird species, satellite transmitters commonly have minimal effects (e.g. Ashbrook et al. 2016; Sergio et al. 2015). Nevertheless, a concern is whether transmitters affected juvenile or first-winter survival if not properly fitted to allow for growth. Accepting that development, growth and thus harness adjustments may differ for active wild birds, 4 captive-bred juveniles, fitted with transmitters at c.35 days using identical protocols to tagged wild juveniles, and kept over winter to the following spring, showed normal growth and mobility, no lesions and no signs of musculoskeletal problems.

## 4.2 Captive-bred released performance

Initial survival of captive-bred houbara from release to October was higher (56%) than for houbara bred in the UAE and released in Saudi Arabia, Kazakhstan and Pakistan (to 3 months: 25%, 25%, 29% respectively IFHC 2017). Houbara released in Central Asia face challenges in their first migration, through exposure to hunting and trapping. Overall first-year survival was, unsurprisingly, lower (12.9% from release to spring return) than that of non-migratory captive-bred houbara released into protected areas in the UAE (48% for their first year, Azar et al. 2016) and Morocco (44%, IFHC 2016).

First-winter captive-bred birds were more susceptible to natural mortality from starvation, disease or predation than wild juveniles (Burnside et al. submitted), potentially indicating poorer fitness in terms of physiological condition, immunity to pathogens, anti-predator behaviours or foraging ability. Our estimates of captive-bred survival were derived from cohorts reared in earlier years of the facility; subsequent refinement of diet and rearing protocols may improve performance. If post-release survival were improved by rearing and pre-release protocols such as exercise (Rymešová et al. 2013), or predator-aversion training (Gaudioso et al. 2011; Van Heezik et al. 1999), numbers needed for release could perhaps be reduced.

Uncertainty in long-term demographic performance of released individuals is common when planning reintroduction or reinforcement programmes (e.g. Converse et al. 2013b; Dolman et al. 2015). As noted above, a critical uncertainty in our model concerns the subsequent demographic performance of surviving captive-bred released birds that returned to the breeding grounds. We assumed this matched that of wild birds and, additionally, that their wild-hatched progeny were indistinguishable from wild individuals. However, even after reaching 3+ years, annual survival of captive-bred *C. undulata* (67%) is substantially below that of wild adults (89%, IFHC 2016), suggesting persistent effects of long-established captive-breeding programmes on fitness. We lack robust data on returning captive-bred *C. macqueenii* due to high first-winter mortality rates, but initial data suggest annual survival (12 individuals, over 20 individual-years, 0.40 ± 0.1096 SE) may be substantially less than for wild adults (0.8030 ± 0.0346). More generally, captive-reared gamebirds released to reinforce wild populations commonly achieve substantially poorer productivity and survival than wild counterparts (Buner et al. 2011; Hill and Robertson 1988; Madden et al. 2018; Rymešová et al. 2013). The conventional response to this poorer performance is to release larger numbers of birds (Robertson et al. 2017; Söderquist et al. 2017), the unintended consequences of which we have reviewed in the Introduction.

## 4.3 Conservation of migratory Asian houbara

For migratory Asian houbara, the sheer scale of captive breeding and release needed to stabilise exploited populations—approaching or annually exceeding initial wild numbers—could itself become a destabilising and unsustainable measure, owing to the known and predictable dangers from various adverse heritable or acquired traits (see Introduction). Such scaling-up of supplementation would risk replacement and domestication of wild stock rather than conservation reinforcement, with unknown population consequences. While our modelling assumed a closed population, localised compensatory release of captive-bred individuals may supplement local numbers but will not offset hunting pressure on other populations during their migratory stop-over in the hunting concession. Moreover, a flyway-wide programme of captive breeding and release, currently under development, poses even greater risks of wild replacement. Only by substantially reducing mortality along the flyways can the decline of *C. macqueenii* be halted and releases of captive-bred birds moderated to levels at which the dangers to wild populations are minimised.

Conservation success can, therefore, only be achieved by interested parties committing jointly to a scientifically informed, strictly observed and fully integrated system of legal enforcement, quotas, concessions and supplementations (CMS 2005) to reverse the current downward trajectory of the wild population and allow truly sustainable hunting. Extending the supply of captive-bred birds for falcon training has the potential to reduce markets for wild-caught houbara (Combreau et

al. 2005), although losses from powerline collisions (Burnside et al. 2015) may be costly to mitigate. Considerable resources are already invested by Gulf states in the captive breeding of houbara and in falcons, logistics for falconry and hunting expeditions, and the social and economic support provided to host countries. Given the level of this investment, the move to a sustainably managed hunting regime should represent not a threat to the deep tradition of falconry but the only means of ensuring its long-term survival. Host countries and conservation agencies will surely find common cause in helping develop and implement this now imperative strategy.

## 5 Conclusions

This study adds to the mounting evidence of potential long-term risks to wild populations from supplementation and reinforcement through the release of captive-bred animals. Where the fitness reduction of captive-bred relative to wild individuals is heritable, as has been frequently demonstrated (e.g. Araki et al. 2009; Christie et al. 2016), release of even slightly less-fit individuals may cause long-term reduction in the size, genetic diversity and viability of wild populations (Lynch and O'Hely 2001; Willoughby and Christie 2018), particularly where captive-born individuals are released for more than a few years (Willoughby and Christie 2018). The use of repeated annual supplementation to reinforce exploited populations over the long-term is, therefore, a high-risk strategy. For hunted populations, a further unintended consequence of releasing captive-bred stock is that, instead of reducing pressure on wild individuals through a dilution effect, perceptions of high abundance and effective mitigation can lead to greater hunting pressure on wild stock (Casas et al. 2016). Although it is important to develop strategies to reduce genetic adaption in captivity and to increase survival and performance after release, without adequately addressing *in situ* threats, over-reliance on supplementation risks domestication and replacement.

Supplementary data to this article can be found online.

19   Table 1

20   Parameters of migratory Asian houbara *Chlamydotis macqueenii* population model, showing sample sizes. Breeding components (probability of nesting, clutch size, nest
21   success, hatching probability, chick survival to fledging) were measured using nest monitoring, and satellite and UHF tracking of adult females with broods. Subsequent survival
22   was measured using satellite telemetry. Distributions of clutch size and first-egg date were defined by mean and SD; other parameters by the mean and SE.

| Demographic parameter (*units*) | N, details of replication | Parameter estimate |
|---|---|---|
| Probability of breeding (starting incubation) after spring return | 52 returns of 23 satellite-tagged adult females to the breeding grounds (2012–2017); mean estimated from binomial GLM treating arrivals as independent events: outcome 0/1, did-not-breed, bred. | 0.981 ± 0.019 SE |
| First-egg date of first nesting attempt (*Jday*) | 51 first-egg dates from 23 satellite-tagged adult females returning to the breeding grounds (2012–2017); mean and variance sampled across individuals and years. | 92.4 *Jday* ± 6.8 SD |
| Clutch size in first nesting attempt (*number of eggs*) | 41 known first clutches (23 individuals) 2012–2017, from Koshkin et al. (2016a) supplemented by this study. | 3.32 eggs ± 0.65 SD |
| Clutch size reduction from first to second attempt | 38 re-nesting events (25 individuals) 2013–2017. | mean –0.56 eggs, ± 0.15 SE (median = –1) |
| Date-dependent daily nest survival probability, *clutch.dsr$_d$* | 249 nests monitored over 3025 exposure-days over 6 years (2012–2017); *clutch.dsr$_d$* related to *Jday*; for details see Fig. A.1 and Table A.1. | *clutch.dsr$_d$* = 1 – inverse logit(5.604642 (SE 0.89) – 0.08789 (se 0.039726) * (*Jday* – 68) + 0.000836 (SE 0.000424)* (*Jday* – 68)$^2$) <br> Per attempt (23 days)$^{-1}$ = 52.3% ± 3.6% SE |
| Hatching probability egg $^{-1}$ (accounting for partial predation, infertile eggs and embryo death) | 339 eggs laid in 110 successful nests (2012–2017) hatched 294 chicks; hatching probability estimated in a known-fate binomial trials Generalised Linear Model (GLM). | 0.855 ± 0.019 SE |
| Date-dependent re-nesting probability | Outcome following 99 nest failures (with known failure day) of 36 satellite-tagged females where it was known whether subsequent incubation was initiated (65 re-nesting events). | inverse logit(43.5389 (SE 9.43) – 4.0366 (SE 0.88) * sqrt(day of failure)) <br> mean 0.657 ± 0.048 SE |
| Re-nesting interval (*days*) | 65 paired nest failure and re-nesting events of satellite-tagged females, with both dates known. | 8.57 days ± 0.30 SE |
| Chick survival probability from hatching to fledging (35 days), *S$_{chick}$* | 40 broods (initially comprising 104 hatched chicks) from 24 satellite-tagged females that successfully hatched one or more clutches during 2013–2017; broods relocated at 34–38 days. Chick daily survival probability, *chick.dsr*, was estimated using a binomial trials GLM, treating broods as the unit of replication. Survival from hatching to fledging; *S$_{chick}$* estimated as *chick.dsr* [35]. | 0.500 ± 0.049 SE |

| | | |
|---|---|---|
| Wild juvenile survival probability from fledging to 01 October (mean 116 days), $S_{juv.oct}$ | 37 satellite-tracked juveniles fitted (2013–2017) at fledging (35 days) monitored to October. Survival from fledging to October, $S_{juv.oct}$, was estimated as: $S_{juv.oct}$ = $juv.dsr_{fd}$ $^{(days)}$ where $juv.dsr_{fd}$, is fledging-date-specific daily survival probability and *days* the brood-specific number of exposure days from fledging to 01 October; details in Fig. A.3 and Tables A.3, A.4. | $juv.dsr_{fd}$ = (1 – inverse logit[–19.59017 (SE 5.298) + 0.08341 (SE 0.031) * $fd$] mean 0.9965 ± 0.0012 SE $S_{juv.oct}$ = 0.7113 ± 0.0766 SE |
| Wild first-winter survival probability from 01 October to 31 March (183 days), excluding hunting in the concession, $S_{juv.wtr}$ | 27 juveniles satellite-tracked (2013–2017) beyond October. | 0.3704 ± 0.0929 SE |
| Wild adult summer (01 April to 01 October) survival probability, $S_{adult.su}$ | 58 satellite-tracked wild adults (15 adult males, 35 adult females, plus 8 adults originally caught as juveniles) monitored for 135 over-summer periods. | 0.9037 ± 0.0254 SE |
| Wild adult winter (01 October to 31 March) survival probability, $S_{adult.wtr}$ | 52 satellite-tracked adults (both sexes) monitored for 123 over-winter periods. | 0.8926 ± 0.0282 SE |
| Captive-bred survival probability from release to 01 October, $S_{cbr.oct}$ | Total of 75 captive-bred released individuals monitored by satellite transmitters, 65 from Burnside et al. (2016) plus 10 released April 2015. | 0.560 ± 0.057 SE |
| Captive-bred released, first-winter survival probability from 01 October to 31 March, $S_{cbr.wtr}$ | 42 captive-bred released individuals, alive at October, monitored by satellite transmitters, 38 from Burnside et al. (2016) plus 4 released April 2015. | 0.231 ± 0.068 SE |
| Proportion of winter mortality attributed to hunting/trapping (excluding licensed hunting in the concession) | 13 wild adult winter, 17 wild first-winter, 30 captive-bred first-winter and 13 wild adult summer mortalities, respectively, from (Burnside et al. submitted). | 0.538 ± 0.138 SE; 0.529 ± 0.121 SE; 0.233 ± 0.078 SE; 0.231 ± 0.117 SE, respectively |

23

**Figure legends:**

**Fig. 1.** Demography of Asian houbara *Chlamydotis macqueenii* populations, showing the number of females in spring (yearlings plus adults) over 20 years, and the geometric mean trajectory (continuous line) and SD (dashed lines) across 500 model iterations (pale lines).

**Fig. 2.** Mean rate of wild Asian houbara *Chlamydotis macqueenii* population change ($\lambda$) across 5000 model iterations, related to (a) productivity: female recruits in October per breeding-age female; (b) wild first-winter survival; (c) adult over-winter survival and (d) adult over-summer survival. Vertical lines show median (solid line, x axis value) and inter-quartile range (shaded, dashed lines) of parameters re-sampled across iterations, and the fit (red solid line) and 95% CI (red dashed lines) of a GLM relating $\lambda$ to recruitment or survival. The vertical dashed line and x axis value show the parameter value for which $\lambda$ = 1.0 (horizontal dashed line).

**Fig. 3.** Mean and 95% CI of population growth rate ($\lambda$), across 1000 iterations for each release/hunt scenario, shown in relation to (a) numbers of female captive-bred houbara released year$^{-1}$ for different annual hunting quotas (numbers of females hunted), and (b, c), maintaining an annual quota of 100 females, but with proportionate reductions (0 to 1.0) in (b) adult and first-winter hunting/trapping mortality, (c) adult winter, first-winter and adult summer hunting/trapping mortality. Assuming an equal sex ratio, total numbers released and hunted will be twice the values shown.
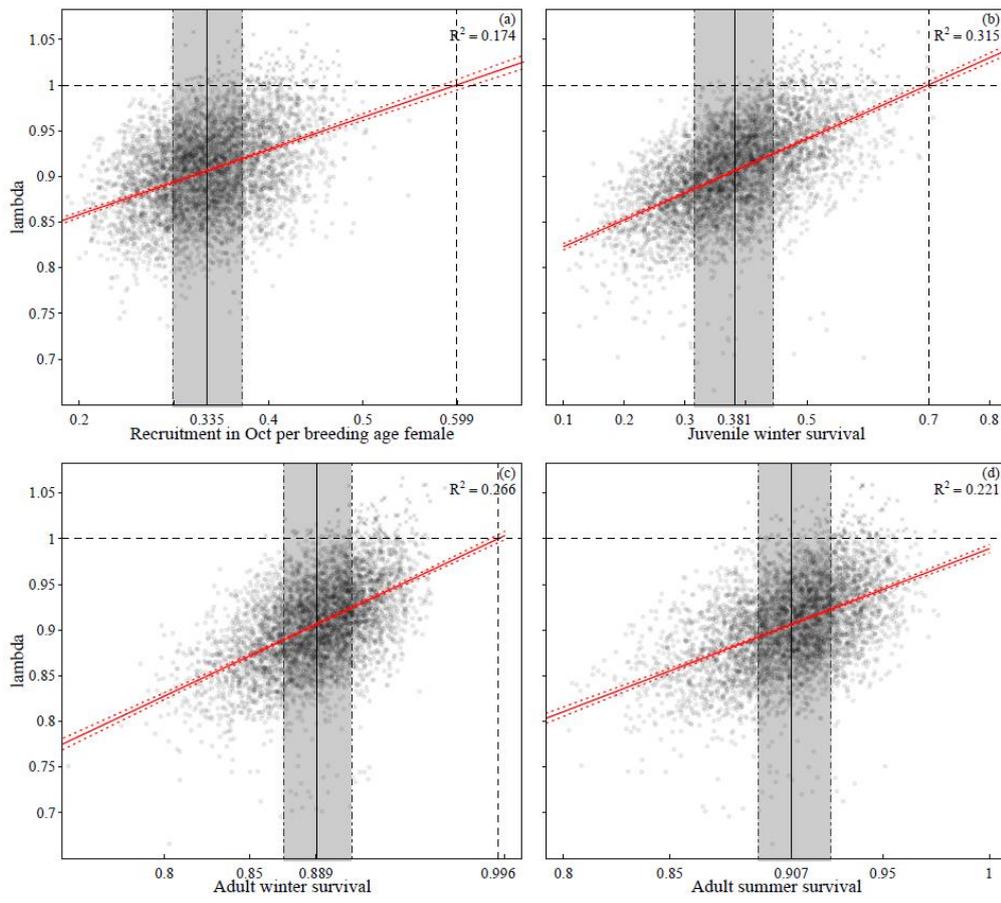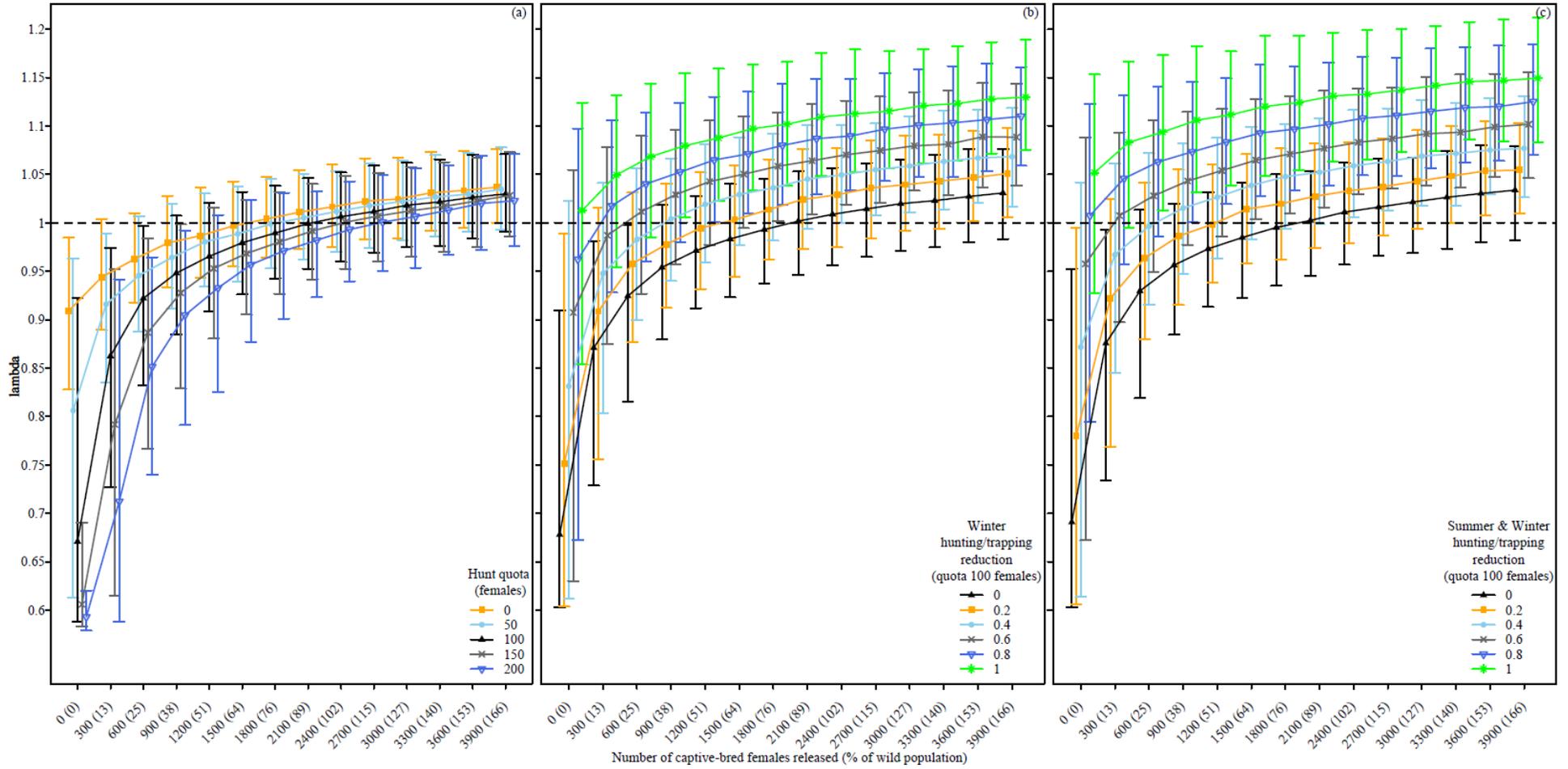
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**Fig. 1.**

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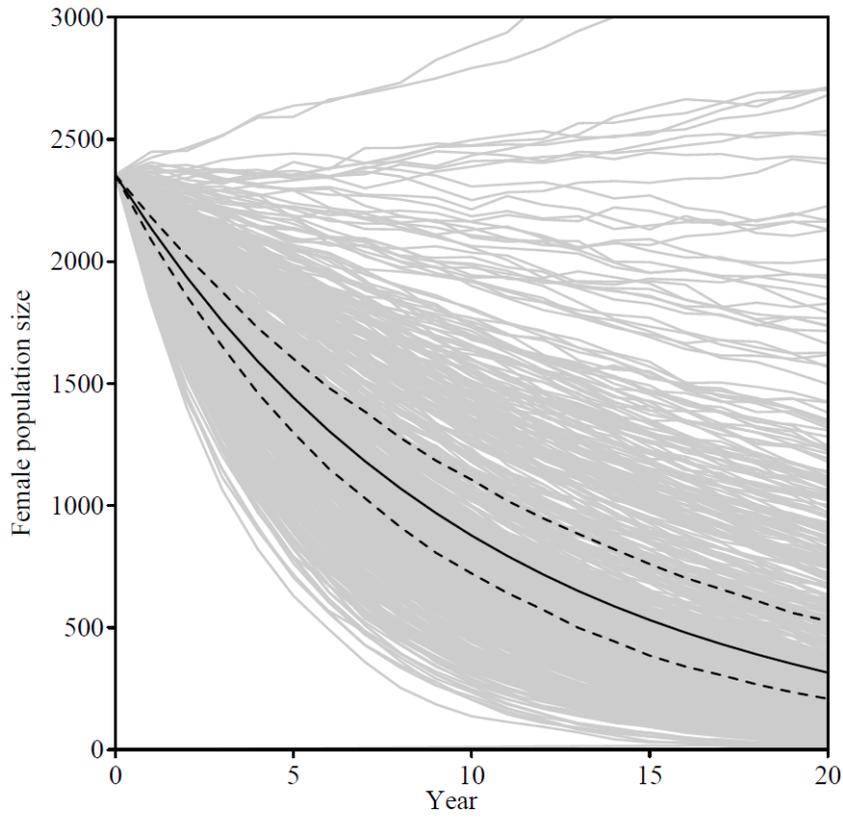
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449  **Fig. 2.**

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453 **Fig. 3.**

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