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Ark or park: the need to predict relative effectiveness of *ex situ* and *in situ* conservation before attempting captive breeding

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Summary

1. When species face extinction, captive breeding may be appropriate. However, captive breeding may be unsuccessful, while reducing motivation and resources for *in situ* conservation and impacting wild source populations. Despite such risks, decisions are generally taken without rigorous evaluation. We develop an individual-based, stochastic population model to evaluate the potential effectiveness of captive-breeding and release programmes, illustrated by the critically endangered *Ardeotis nigriceps* Vigors great Indian bustard.

2. The model was parameterized from a comprehensive review of captive breeding and wild demography of large bustards. To handle uncertainty in the standards of captive-breeding performance that may be achieved, we explored four scenarios of programme quality: 'full range' (parameters sampled across the observed range), 'below average', 'above average' and 'best possible' (performance observed in exemplary breeding programmes). Results are evaluated examining: (i) the probability of captive population extirpation within 50 years and (ii) numbers of adult females subsequently established in the wild following release, compared to an alternative strategy of *in situ* conservation without attempting captive breeding.

3. Successful implementation of captive breeding, involving permanent retention of 20 breeding females and release of surplus juveniles, required collection of many wild eggs and consistent 'best possible' performance across all aspects of the programme. Under 'full-range' and 'above-average' scenarios, captive population extirpation probabilities were 73–88% and 23–51% respectively, depending on egg collection rates.

4. Although most (73–92%) 'best possible' programmes supported releases, re-establishment of free-living adults also required effective *in situ* conservation. Incremental implementation of effective conservation measures over the initial 10 years resulted in more free-living adults within 35 years if eggs were left in the wild without attempting captive breeding.

5. *Synthesis and applications*. For the great Indian bustard *Ardeotis nigriceps*, rapid implementation of *in situ* conservation offers a better chance to avoid extinction than captive breeding. Demographic modelling of threatened species should be used to examine whether captive breeding will bring net benefits to conservation programmes.

Key-words: *Ardeotis nigriceps*, captive breeding, counterfactual, great Indian bustard, Noah's ark, reintroduction, reinforcement, re-establishment

Introduction

Captive breeding can be a crucial intervention when species face imminent extinction, but its value to conservation depends on the ability to re-establish a population in the wild. This has proved successful for some high-profile species, but in many cases it has not (Snyder *et al.* 1996; Fischer & Lindenmayer 2000; Mathews *et al.* 2005). Captive-breeding ('*ex situ*') programmes involve multiple but often unappreciated risks, including delays in understanding

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the conditions required for reproduction, failure to reach self-sustaining levels or provide sufficient stock for release, loss of genetic diversity and poor success in reintroductions despite available captive-bred young (Martín *et al.* 1996; Snyder *et al.* 1996; Frankham 2008; Williams & Hoffman 2009; Lacy, Alaks & Walsh 2013). Crucially, favourable conditions must first be achieved in sites intended for reintroduction or wild population supplementation before captive-bred stock is released (IUCN/SSC 2013). Such vital '*in situ*' conservation interventions should not be delayed, since avoiding domesticity (selection for traits disadvantageous in the wild) requires minimizing the number of generations in captivity (Frankham 2008; Williams & Hoffman 2009). Where habitat restoration is required to mitigate agricultural intensification, delay may reduce opportunities and escalate costs, potentially consigning a species to indefinite, deleterious captivity. Conversely, if such action is taken early, it may remove the need for *ex situ* management altogether.

Wherever *in situ* conservation remains an option, the efficacy of adopting an *ex situ* programme needs careful evaluation (Snyder *et al.* 1996; Fischer & Lindenmayer 2000; IUCN/SSC 2013), yet no published studies appear to exist which, *prior* to embarking on a captive-breeding programme, analysed the likelihood that *ex situ* management and subsequent releases would succeed (though see Bretagnolle & Inchausti 2005). Showing that captive breeding does not compromise source population viability (IUCN/SSC 2013) and has a high probability of success is not sufficient to justify recourse to *ex situ* management; what could be achieved by an alternative management regime must also be evaluated (Bretagnolle & Inchausti 2005; IUCN/SSC 2013). For captive breeding and release, a key question is: Will the benefits from releases of captive-bred animals outweigh the loss of wild individuals captured to initiate the captive breeding (McCleery, Hostetler & Oli 2014)?

Here we demonstrate the importance of rigorously examining the evidence before deciding on captive breeding, taking as a case study *Ardeotis nigriceps* Vigors great Indian bustard, a critically endangered (BirdLife International 2014), ground-nesting polygynous species with long-lived adults, extended maternal care of precocial young and low productivity (Rahmani 1989). Once widespread in peninsular India, it is now restricted to a few disjunct areas where it faces major threats from agricultural intensification, power lines and hunting (Dutta, Rahmani & Jhala 2011; Dutta *et al.* 2013). Numbers declined from an estimated 1260 in 1969 to 100–300 by around 2010 (Dutta *et al.* 2013). Important *in situ* management options remain unimplemented (Rahmani 2012). Nevertheless, the government of India, cued by expert opinion (Dutta, Rahmani & Jhala 2011; Rahmani 2012), recently declared its intention to launch a 'conservation breeding programme' for the species (Dutta *et al.* 2013).

To determine how feasible 'conservation breeding' might be for *A. nigriceps*, we reviewed life history, wild and captive-breeding demographic parameters for this and other large bustard species and undertook stochastic individual-based population modelling. We examined the probability that a programme of wild egg collection and captive breeding would establish a captive population capable of persisting in the face of sampling (e.g. egg hatching, chick and adult survival) and stochastic effects and provide sufficient surplus individuals for releases to re-establish breeding-age females in the wild. We evaluated outcomes across a 50-year period, comparing numbers of free-living adults in the wild that result from a programme of captive population establishment, breeding and release, against the numbers of breeding-age adults otherwise accruing in the wild from these eggs and their future offspring, if these eggs were not collected (hereafter referred to as the 'alternative strategy').

We compared outcomes under two scenarios: (i) current conditions, with poor demographic parameters owing to lack of appropriate *in situ* management (hereafter the 'current situation'), and (ii) effective conservation, with improved demographic performance through appropriate habitat management and regulation (hereafter 'effective conservation').

Materials and methods

QUANTIFYING EFFECTIVENESS OF CAPTIVE BREEDING AND *IN SITU* CONSERVATION

We developed three individual-based, age-structured, stochastic population models: for the captive population, released birds and wild birds under the alternative strategy (of not collecting eggs) across 50 programme years. In each modelled year, productivity (probability of breeding, repeat clutching, hatching rates, sex of hatched chicks and chick survival, each individually sampled from a binomial distribution evaluated against the parameter value) was followed by age-class-specific survival (again sampled individually), and the sex- and age-specific population matrix then incremented by 1 year. It is important that this model is stochastic because we are dealing with small populations, meaning there is a significant chance of stochastic extirpation, which could not be captured by a deterministic model.

The captive-breeding model incorporated phases of programme establishment (when wild individuals were acquired), subsequent survival, breeding and (once the population was sufficiently large) releases. Given the considerable risks involved in live capture and introduction of adult bustards to captivity (e.g. Ponjoan *et al.* 2008; O. Combreau pers. comm.), and the threatened status of the species, we considered scenarios whereby captive stock was established by collecting wild-laid eggs, hatching, rearing and recruitment of juveniles (as proposed for *A. nigriceps*: S. Dutta pers. comm.). We examined how egg harvest strategy (numbers per year, over how many years) affected likelihood of captive population persistence; however, only 5–10 eggs yr^{-1} may be achievable given current low nesting rates for *A. nigriceps* (S. Dutta pers. comm.). We assumed egg collection may continue for the first 5 years of the programme (although we also explored other establishment scenarios in Supplementary Materials). Until breeding commenced, recruitment was solely through egg harvest,

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after which captive reproduction and any further accessions contributed to productivity, but with separate hatching and survival rates.

A second individual-based model considered released birds. We assumed that only young of that year will be released from the captive-breeding programmes (following Combreau & Smith 1998; Burnside *et al.* 2012); among bustards habituated to captivity, greater post-release mortality has been observed in birds older than 1 year (R.J. Burnside unpublished data). Removing individuals from the captive stock must not jeopardize its persistence (IUCN/SSC 2013), so captive populations were managed to retain a minimum of 20 mature females (see Fig S1 in Supporting Information); releases occurred from the first year this was achieved.

Modelling consequences of egg collection for wild population viability was impossible, as the size of subpopulations targeted for egg collection is unknown. We compared subsequent numbers of free-living adults resulting from captive population establishment, breeding and release, or from the same eggs if left uncollected. For each scenario examined, demographic outcomes were examined across 1000 replicate model runs, in R software (v3.0.2; R Core Team 2013). Within each simulation run, these three models were linked: the state of the captive population defined annual numbers released, while during the years of captive population establishment, annual rates of wild egg harvest determined numbers of eggs considered in the alternative strategy.

PARAMETER COLLATION

Basic life-history parameters (clutch size, incubation length, age at sexual maturity and maximum breeding age) were available for *A. nigriceps* or the sister taxon *Ardeotis australis* Gray. For *A. nigriceps*, captive breeding has not been achieved. Therefore, captive-breeding and release parameters were collated from breeding or translocation and release programmes for other large bustards, including two species from the same genus. Nest success of wild *A. nigriceps* was estimated from monitored nests (Rahmani 1989; Rao & Javed 2005), accounting for exposure days (Aebischer 1999). Other wild demographic parameters were collated from studies of other large bustard species; details are in Appendix S1 in Supporting Information.

CAPTIVE-BREEDING SCENARIOS

At each stage of a captive-breeding programme, demographic performance depends on the levels of infrastructure (e.g. cages, incubators, biohazard containment, feed production and storage, laboratory and veterinary facilities); staff expertise and professionalism; husbandry and captive-breeding protocols; and overall institutional management and financial stability. As such performance cannot be predicted, we considered four scenarios of programme quality:

1. 'full-range' performance, where parameters were randomly sampled from a uniform distribution, defined by the minimum and maximum observed across captive-breeding programmes or ecological studies;

2. 'below-average' performance, sampling each parameter from the lower half of the observed distribution;

3. 'above-average' performance, sampling parameters from the upper half of the observed distribution; and

4. 'best possible' performance, where parameters relate to exemplary rates achieved in captive-breeding programmes of the highest professional standards, or the top quartile of the observed uniform parameter distribution.

For each demographic parameter, collated estimates and evidence for all species considered (see Table S1) were examined, to define minimum and maximum values under each scenario of captive-breeding programme quality. Preliminary ranges were independently reviewed by two individuals (K.M.S. and O. Combreau) possessing 42 years combined experience of captive breeding both *Chlamydotis undulata* Jacquin and *C. macqueenii* Gray, with adjustments made following their advice; resulting scenarios are summarized in Table 1.

Early in captive-breeding programmes, particularly involving species new to *ex situ* management, demographic performance commonly dips until managers adapt protocols (see Appendix S1). We therefore included a 2- to 4-year initial phase when maximum values were restricted for hatch rate, chick survival to 1 year (e.g. due to diet optimization, hygiene), adult survival and proportion of females breeding per year (Table 1). Learning was also incorporated as a delay (duration depending on programme quality) between the first females reaching sexual maturity and successful captive breeding (Table 1).

Breeding programmes are vulnerable to stochastic events (see Appendix S1). Captive bustards commonly suffer musculoskeletal disorders, disease outbreaks and trauma (van Heezik, Seddon & Maloney 1999; Bailey & Flach 2003; White 2012; Hanselmann *et al.* 2013). Bad weather, cage failure and predator incursions cause injuries or mortality (K.M. Scotland unpublished data). We used expert experience to estimate stochastic risk, in terms of likely frequency and severity of 'infrequent, high-impact' and 'frequent, low-impact' event classes (Tables 1, S1). Events were modelled independently each year for (i) adult survival (accidents, predators); (ii) juvenile survival (diet, disease, developmental problems); and (iii) proportion of females breeding (reduced, e.g., by weather or renovations). While a naïve programme may be exposed to severe 'high-impact' risks, we assumed that after one severe adult mortality event, severity of subsequent stochastic events was reduced following adjustments to protocols or infrastructure (Table 1), but that moderate risks persist as stochastic events resulting in lower levels of adult or juvenile mortality may occur for multiple reasons. Severity and probability of stochastic adult mortality or of breeding problems were assumed to be lower in 'best possible' programmes (Table 1).

Within each scenario explored, each run of the population model represents a hypothetical captive-breeding programme for which each demographic parameter was independently and randomly sampled from the uniform distribution defined by the relevant scenario of programme quality (Table 1). To examine the sensitivity of programme extirpation probability to changes in programme performance, for each demographic parameter in turn we substituted a value drawn from the 'full-range' into the 'best possible' scenario. In recognition of parameter uncertainty for stochastic mortality and stochastic reductions in breeding performance, these parameter values were increased or reduced by 25% and 50%. Outcomes of captive-breeding programme scenarios were assessed against three criteria: (i) the proportion of model runs (simulated captive populations) extirpated, with no females in the population, by programme year 50; (ii) whether they provided surplus individuals to attempt release; and (iii) numbers of breeding-age adult females subsequently established

Table 1. Demographic parameters for models of *Ardeotis nigriceps* captive breeding and release under four scenarios of programme quality ('full range', 'below average', 'above average' and 'best possible') and *in situ* conservation under two scenarios ('current situation' and 'effective conservation'), showing minimum (Min) and maximum (Max) values from which each programme iteration was sampled. Whether the parameter is restricted during the learning phase is also shown (Y, yes; N, no; n/a, not applicable)

		Scenario of captive-breeding programme quality:							
		Full range		Below average		Above average		Best possible	
Parameter	Learn	Min	Max	Min	Max	Min	Max	Min	Max
Learning for husbandry (hatchability, survival)	n/a	2	4	3	4	2	3	2	2
Proportionate adjustment of relevant parameters during learning period	n/a	0·6	1	0·6	0·8	0·8	1	0·85	1
Hatch rate of collected wild-laid eggs (with artificial incubation)	Y	0·5	0·75	0·5	0·6	0·55	0·75	0·6	0·75
Juvenile survival to 1 year of wild-laid captive-reared chicks	Y	0·45	0·85	0·45	0·7	0·7	0·85	0·75	0·85
Adult survival in captivity (same for wild laid and captive laid)	Y	0·83	0·97	0·83	0·88	0·88	0·97	0·92	0·97
Age of male at first breeding (years)	N	3	7	5	7	3	5	3	4
Age of female sexual maturity and potential for first breeding (years)	N	3	5	4	5	3	5	3	4
Learning lag (years) between first females reaching sexual maturity and breeding in the programme	N	1	7	4	7	1	4	1	2
After first breeding, subsequent annual probability that an adult female will again breed	Y	0·6	0·9	0·6	0·70	0·65	0·9	0·7	0·9
Clutches female^{-1} yr^{-1}, for first 2 years of breeding age	N	1	1	1	1	1	1	1	2
Mean clutches female^{-1} yr^{-1}, for subsequent breeding	N	1	3	1	1·3	1·15	3	1·3	3
Hatching rate of captive-laid eggs (with artificial incubation)	Y	0·45	0·78	0·45	0·6	0·65	0·75	0·68	0·78
Survival of captive-bred juvenile to 1 year old	Y	0·6	0·78	0·6	0·67	0·67	0·78	0·72	0·78
Prior to first stochastic adult event: annual probability of severe adult mortality event*	N	0·05	0·167	0·125	0·167	0·1	0·167	0·05	0·1
First stochastic adult event: severe additive adult mortality	N	0·25	0·8	0·3	0·8	0·25	0·8	0·25	0·5
Prior to first stochastic adult event: annual probability of moderate adult mortality*	N	0·2	0·5	0·333	0·5	0·2	0·5	0·2	0·333
First stochastic adult event: moderate additive adult mortality	N	0·1	0·2	0·15	0·2	0·1	0·15	0·1	0·15
After first stochastic adult event: annual probability of stochastic adult mortality†	N	0·2	0·5	0·333	0·5	0·333	0·5	0·2	0·5
After first stochastic adult event: additive adult mortality	N	0·1	0·2	0·15	0·2	0·1	0·15	0·1	0·15
Annual probability of stochastic juvenile mortality (e.g. through disease, diet or developmental problems)‡	N	0·2	0·5	0·333	0·5	0·2	0·5	0·2	0·333
Additive chick or juvenile stochastic mortality	N	0·08	0·15	0·08	0·15	0·08	0·15	0·08	0·15
Annual probability of stochastic reduction in proportion of females breeding	N	0·1	0·333	0·25	0·333	0·1	0·333	0·1	0·2
Reduction in proportion of adult females breeding	N	0·15	0·2	0·15	0·2	0·15	0·2	0·15	0·2
Juvenile survival to release	N	0·45	0·88	0·45	0·66	0·58	0·88	0·75	0·88
Juvenile survival post-release to 1 year	N	0·1	0·3	0·1	0·3	0·1	0·3	0·1	0·3
		In situ Conservation for wild and post-release							
		Current situation						Effective conservation	
Annual probability that an adult female will breed	n/a	0·4	0·9					0·8	0·98
Wild nest survival	n/a	0·4	0·68					0·71	0·83
Re-nesting rate after failure	n/a	0·1	0·5					0·5	0·8
Wild juvenile survival to 1 year	n/a	0·1	0·3					0·4	0·6
Adult survival	n/a	0·85	0·9					0·88	0·95

*For stochastic adult mortality, in each year we sampled the probability of a programme-wide event occurring. We first compared this sample to the threshold for a low-probability 'severe' consequence event; if this did not occur, we compared the sample to the threshold for a higher-probability 'moderate' consequence event.

†After the first stochastic adult mortality event, we assumed that adjustments to protocols or infrastructure would limit the magnitude, but not the probability, of subsequent events in that programme.

‡Risks of stochastic juvenile mortality and stochastic effects on the proportion of females breeding were not reduced by learning as each subsequent event can be novel and unpredictable.

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in the wild. Annual numbers (N_t) are back-transformed values of the geometric mean of $\ln(N_{ti} + 1)$ across replicate programme runs i.

RELEASE AND ALTERNATIVE SCENARIOS

Outcomes of captive-bred releases and of the alternative strategy were examined over the same 50-year period, for 'current situation' and 'effective conservation' scenarios. As expert opinion (S. Dutta pers. comm.) indicated it may take 5–10 years to implement necessary conservation measures, demographic parameters under 'effective conservation' were initially set at the 'current situation' scenario and then increased (by equal annual increments) achieving 'effective conservation' at year 10.

The parameter range for the 'current situation' was informed by the lower range observed for the large bustard species examined and by recent nest success rates of *A. nigriceps* (Rao & Javed 2005). Parameter values for 'effective conservation' were estimated from greater nest success rates of *A. nigriceps* observed in the 1980s (Rahmani 1989) and demographic parameters for wild *Otis tarda* Linnaeus in Iberia (Morales, Alonso & Alonso 2002; Alonso *et al.* 2004; Martín *et al.* 2007), where numbers are reportedly stable or increasing (Palacín & Alonso 2008). Wild juvenile survival rates are unknown for *Ardeotis* species and poorly known for *O. tarda* (Table S1). As this scenario was predicated on achieving favourable conservation status through appropriate interventions, we set juvenile survival as sufficient to give a self-sustaining wild population (i.e. finite population growth rate >1; see Fig. S2) at realistic rates of adult survival (Martín *et al.* 2007).

Lacking contrary empirical evidence, we applied the same wild demographic parameter values used for wild and captive-bred released birds that had survived to at least 1 year. If captive-bred released birds have lower adult survival, productivity or subsequent juvenile survival, this would bias results in favour of captive breeding. For released birds and the alternative strategy, we assumed adult females could breed after reaching sexual maturity without Allee effects through male availability for copulation, due to the presence of a residual wild population.

Results

The full-range scenario, sampling parameters across the range reported for bustard captive-breeding programmes, led to a high probability of breeding programme extirpation (73–88% within 50 years, at egg harvest rates of 5 or 10 yr^{-1} for 5 years, Fig. 1). For the 'below-average' scenario, all breeding programmes became extirpated within 50 years (Fig. S3); this scenario is not considered further. At these egg harvest rates, probability of programme extirpation was substantial (23–50%) for the 'above-average' and non-trivial (3–17%) for the 'best possible' scenario (Fig. 1). For the full-range scenario, probability of captive programme extirpation remained substantial (>50%) even when established by collecting greater numbers of wild-laid eggs (e.g. 10 yr^{-1} for 10 years or 15 yr^{-1} for 7 years; see Fig. S4). For the 'above-average' scenario, probability of extirpation remained high (>30%) with moderate (e.g. 10 yr^{-1} for 4 years) levels of egg collection; substantial egg harvest (e.g. 10 yr^{-1} for 8 years) was required for a good (>90%) chance that populations persist. For the 'best possible' scenario, high (approximately 95%) chance of population persistence was achieved with levels of egg collection of 5 yr^{-1} for 9 years or 10 yr^{-1} for 5 years (Fig. S4).

Under the 'best possible' scenario, likelihood of captive population extirpation was particularly sensitive to adult survival: sampling from the full range of observed values increased extirpation rates to >20% (Fig. 2). Elasticity analysis of stochastic adult risk also increased extirpation rates (to >10%). Outcomes were also sensitive to captive hatching rates, lag between first females reaching sexual maturity and first breeding, and juvenile survival (Fig. 2). Sampling any of these parameters from the full range increased extirpation rates to approximately 5%.

Although the 'best possible' scenario predicted low rates of population extirpation over 50 years, resulting populations were often small, taking 20–30 years to reach a geometric mean of 20 breeding-age adult females (Fig. 1). Under the full-range scenario, 91–96% of programmes failed to release any juvenile females within 50 years (Fig. 3), and under the 'above-average' scenario, 53–73% failed to release. Even with 'best possible' management, with low rates of wild egg harvest (5 yr^{-1} for 5 years) during the establishment phase, 28% of programmes failed to release any juvenile females within 50 years (Fig. 3). Outcomes were similar when the captive population management threshold was reset to a minimum of only 15 instead of 20 breeding-age adult females.

For numbers of mature adult females re-established in the wild, outcomes primarily depended on quality of breeding programme, with geometric mean numbers close to zero for full-range and above-average scenarios irrespective of *in situ* scenario (Fig. 3). With 'best possible' management, releases by some programmes established small numbers of adults in the wild after approximately 30 years, with higher numbers predicted with effective *in situ* conservation. However, for the alternative strategy under the *in situ* 'current situation' scenario, numbers declined to zero after 'foregone harvest' ceased, indicating wild demography was not self-sustaining. Thus, the small numbers in the wild from captive-breeding and release programmes under current *in situ* conditions are a sink population dependent on reinforcement by ongoing releases. For the alternative strategy, under the *in situ* 'effective conservation' scenario, despite our assumption that conditions would only gradually improve over 10 years, mean numbers of free-living wild adults resulting from uncollected eggs were consistently higher than under captive-breeding programmes of only full-range or above-average quality (Fig. 3). Crucially, even in the 'best possible' scenario, numbers of free-living adults were still higher under the alternative strategy until around year 35 of the programme. Results were similar for collection rates of either 5 or 10 eggs yr^{-1} over 5 years (Fig. 3); for scenarios established by egg collection sustained over

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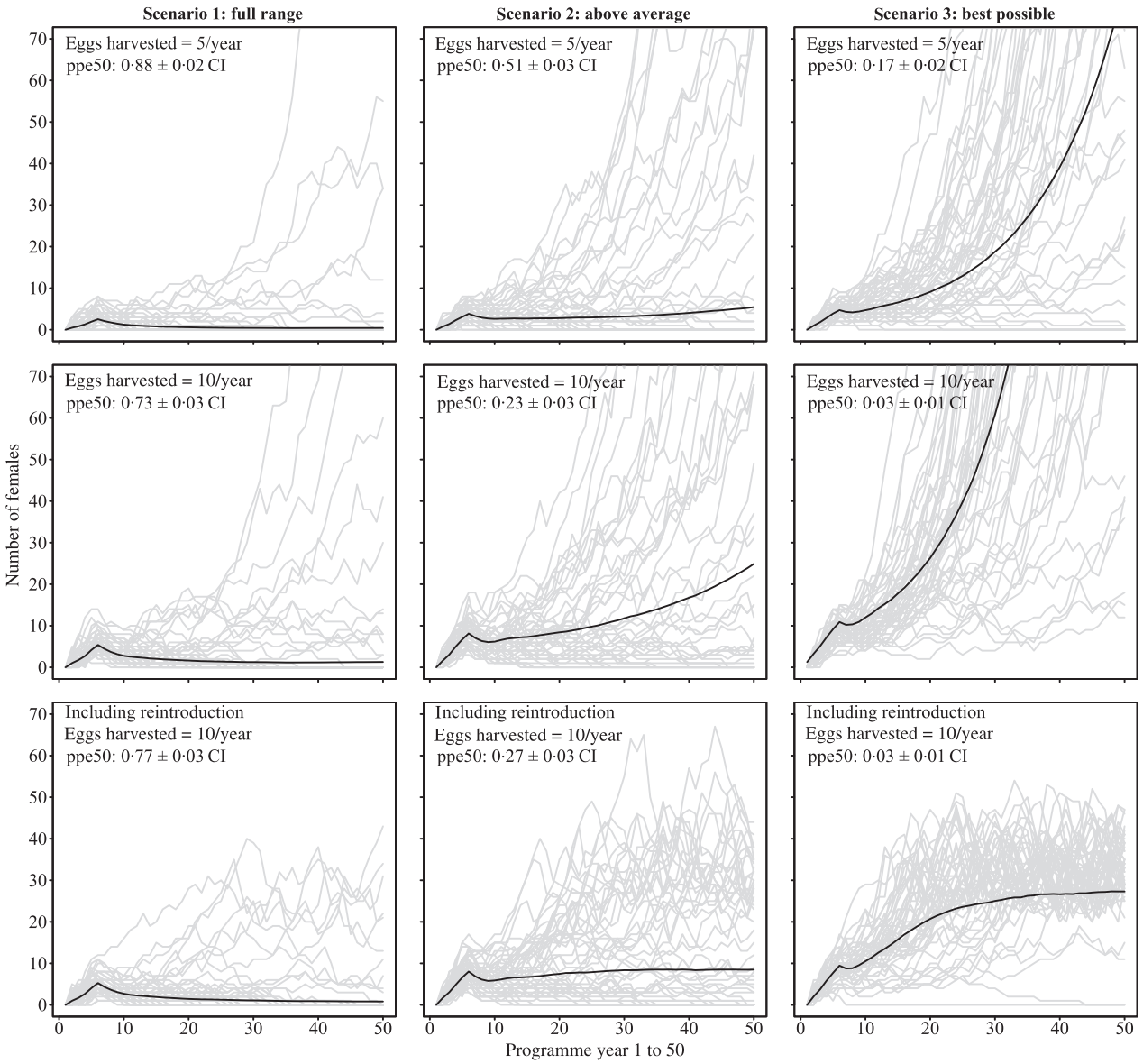

Fig. 1. Captive demography for three scenarios of programme quality (1: 'full range'; 2: 'above average'; 3: 'best possible') and two rates of egg harvest (5 or 10 eggs yr^{-1}, both for 5 years). For the latter, demography is shown with and without removal of juveniles for release. For each panel, annual numbers of adult females (≥1 year) are shown in 50 replicate programme runs (pale lines), with their geometric mean (thicker continuous line) based on 1000 iterations and mean and 95% limits of the probability of programme extirpation (ppe) by year 50.

10 years, the advantage of not collecting eggs over captive breeding and release was magnified (Fig. S5).

Discussion

DEMOGRAPHIC MODELLING TO INFORM *EX SITU* CONSERVATION

The systematic, objective and evidence-based approach developed here provides a support framework to inform decisions at key junctures in the conservation of highly threatened species, by modelling probability outcomes for *ex situ* and *in situ* conservation. We explored the implications of taking individuals into captivity not in terms of the viability of source populations, but by contrasting the numbers of free-living adults subsequently established in the wild under different management scenarios. The modelling also establishes benchmark criteria for the demographic performance required if captive populations are to be self-sustaining, allowing adaptive management of underperforming breeding programmes.

The model structure captures important biological stages of the process of captive population establishment, breeding and release and, with appropriate parameterization, is potentially transferable to any proposal to establish a captive bird population for subsequent release. For *Ardeotis nigriceps*, we modelled captive population establishment through egg collection and rearing, but acces-

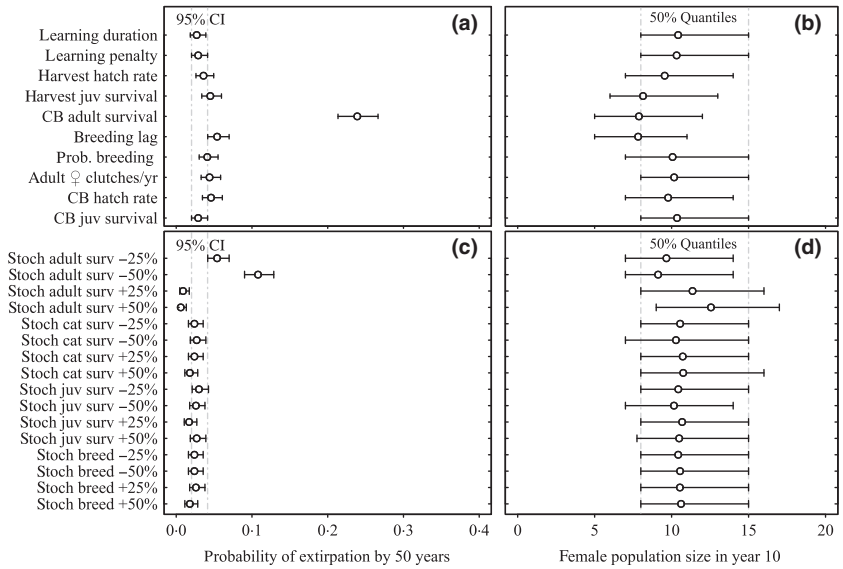

Fig. 2. Sensitivity of (a) mean extirpation probability and (b) geometric mean numbers of adult females, to aspects of captive-breeding performance, under the 'best possible' programme quality scenario substituting each parameter in turn with a value drawn from the 'full-range' scenario. Error bars represent 95% limits for extirpation probability and upper and lower quartiles for numbers of females in year 10; vertical dashed lines show the 95% intervals or 50% quartiles of 1000 iterations prior to sensitivity analysis. Sensitivity to stochastic parameters was examined for the 'best possible' scenario, by varying the magnitude of impacts on survival or breeding by ±25%. Captive populations are established by initial harvest of 10 eggs yr^{-1} for 5 years.

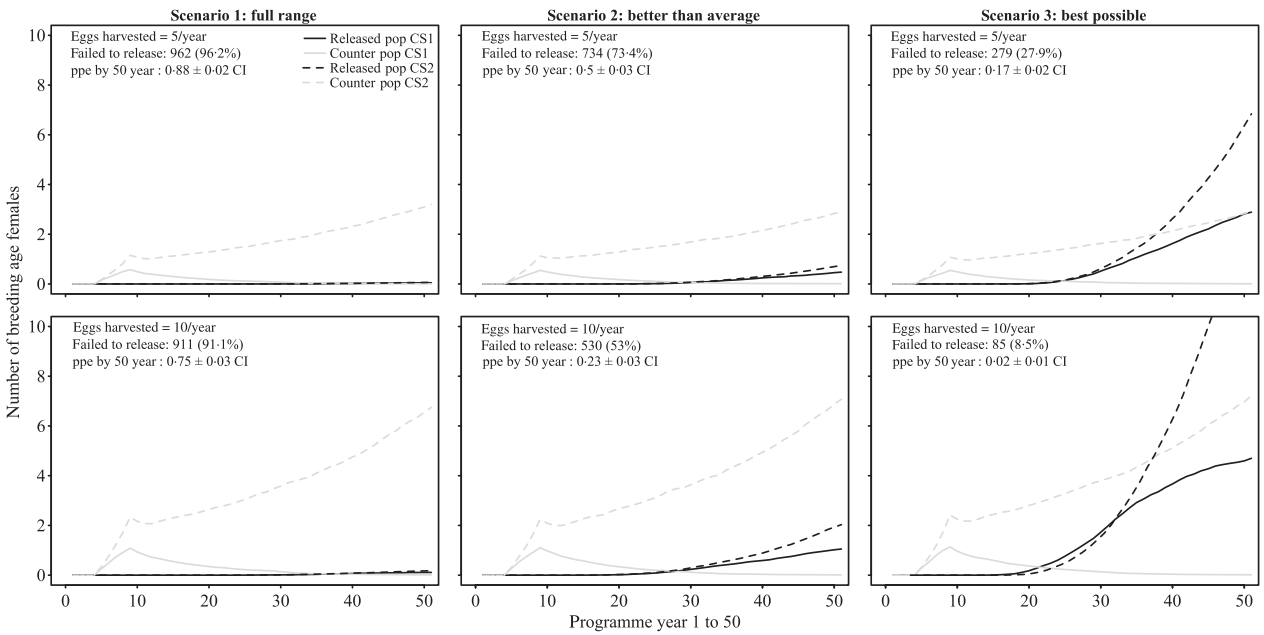

Fig. 3. Numbers of free-living adult females established by captive breeding and release ('released pop', comprising surviving released birds and their adult progeny) or by the alternative strategy ('counter pop', comprising adults resulting from uncollected eggs and their progeny) alive in each programme year, 1 to 50. Geometric mean numbers of breeding-age adult females (net result of recruitment plus subsequent breeding, offset by mortality) are shown for three scenarios of captive-breeding programme quality ('full range', 'above average' and 'best possible') under two scenarios of *in situ* conservation, the 'current situation' (cs1, continuous lines) and 'effective conservation' (cs2, dashed lines) and for two scenarios of egg harvest (5 or 10 eggs yr^{-1}, both for 5 years). We also show the number of programmes that failed to release any individuals (from 1000 iterations) and the probability of captive population extirpation (ppe).

sions of adults or juveniles would require only minor modifications to the model. Parameterization was possible for *Ardeotis nigriceps*, although we needed to draw on evidence from other large bustard species and use expert judgement to validate parameter ranges. Collated evidence revealed high variance in performance of captive-breeding programmes, requiring a scenario modelling approach. The frequency and severity of stochastic events represented further areas of uncertainty. Although population viability modelling (e.g. by Vortex software) routinely

includes demographic stochasticity, underlying biological mechanisms may remain opaque; here we attempted to estimate explicit stochastic risks affecting chick rearing, adult survival or probability of breeding.

For the parameter space explored here, comprising delayed maturity and low fecundity, and captive-breeding performance relevant to large bustards, many populations did not persist in captivity. The level of demographic performance achieved was crucial, with extirpation probability also dependent on establishment from numerous individuals collected from the wild. The full-range model, sampling across the range of parameters observed in relevant captive-breeding programmes, predicted a high chance of captive population extirpation within 50 years. Low rates of programme extirpation required the highest level of performance simultaneously across all aspects of rearing, establishment and breeding protocols, as in the 'best possible' scenario. Elasticity and uncertainty analysis showed small changes in adult mortality were particularly influential on outcomes; sampling from the full range instead of guaranteeing the best possible values increased extirpation risk by approximately 20%. This is of concern for large bustard species, which are susceptible to accidents and fractures in captivity. Population persistence was also sensitive to changes in breeding delays, hatching and juvenile survival rates. It is therefore essential to maintain standards across *all* aspects of a programme, but the scope and scale of the resulting institutional challenges should not be underestimated. Encouraging results achieved with tractable species like vultures (Bowden 2009) is no guarantee of success with challenging stress- and injury-prone species like large bustards.

However, even if this scenario of consistently 'best possible' programme performance were achievable, many captive populations failed to provide surplus birds for release, while even those that did failed to release more than a few individuals within the first 30–40 years. In part this was because IUCN guidelines prohibit releases if they undermine the longer-term viability of the captive population: retaining at least 20 breeding-age adult females protected the demographic viability of the captive population in the medium term. However, much larger numbers (e.g. 100 individuals) must be maintained to minimize genetic losses (Witzenberger & Hochkirch 2011). The accumulation of deleterious genetic traits and loss of important learnt behaviours were unconsidered in our analysis. Captive-bred released female *Perdix perdix* Linnaeus had lower survival (Parish & Sotherton 2007) and lower breeding success than wild females (Buner, Browne & Aebischer 2011), and breeding parameters diverged between hen-brooded and artificially incubated lines (Bagliacca *et al.* 2004), suggesting captive breeding may select for traits potentially suboptimal in the wild. In a captive-breeding programme for *Chlamydotis undulata*, reproductive traits, including ejaculate size and egg-laying rates, underwent rapid genetic and phenotypic change (Chargé *et al.* 2014); fitness consequences in the wild are unknown.

Importantly, release of captive-bred individuals cannot establish meaningful numbers of adults in the wild unless effective *in situ* conservation is achieved; if *in situ* conservation remains ineffective, releasing captive-reared birds is pointless (IUCN/SSC 2013). Crucially, even programmes establishing breeding-age adults in the wild provided less conservation benefit over the first three decades than solely focusing on *in situ* conservation, without removal of eggs into captivity.

Modelling likely outcomes is particularly important before initiating any captive-breeding programme for species with delayed reproductive maturity, low fecundity and or vulnerability to stress or injury. Results for the parameter space explored here support an approach of solely *in situ* interventions. Nevertheless, a bet-hedging approach, of *in situ* conservation backed-up by captive breeding, or opportunistically collecting eggs in threatened nests to rear and release chicks into the wild, may seem sensible insurance measures. However, such approaches have not been effective for large bustards, through three aspects: low availability of source individuals, high post-release mortality and equivocal evidence of subsequent breeding ability. Captive-reared *Otis tarda* derived from wild-laid eggs and released over 10 years in England have successfully hatched chicks, but no chick has yet survived to recruit into the population, and the population is predicted to decline when juvenile releases cease (Ashbrook *et al.* in press). For *Otis tarda* reinforcement in Germany, collection of at-risk nests, chick rearing and release may have helped the population to persist (Langgemach & Bellebaum 2005). However, as adult mortality is not high, persistence can occur despite low recruitment rates; survival rates of released juveniles are unquantified but population recovery has been negligible because unfavourable conditions persist in the wild. For mixed reinforcement strategies for the smaller, more fecund bustard *Tetrax tetrax* Linnaeus in France, post-release survival and population contribution of captive-reared birds were unknown (Bretagnolle & Inchausti 2005); released birds have possibly nested (C. Attié in litt.), but wild population recovery was attributed to *in situ* agri-environmental measures (Bretagnolle *et al.* 2011). Elsewhere, effective *in situ* management without recourse to captive breeding has proved successful in recovering *Otis tarda* populations, with western Pannonian populations doubling in *c.* 15 years (Raab *et al.* 2010).

It might be posited that a captive population is preferable to no population and that at some stage in the unspecifiable future, ways may be found first of overcoming the inbreeding and domestication that will inevitably characterize a long-term captive stock (Snyder *et al.* 1996; Frankham 2008) and then of restoring birds to the wild. Our evidence suggests that the maintenance of such stock is, in the most propitious of circumstances, a possibility. However, we know of no release programme that has demonstrated a self-sustaining population of a large bustard, and a concern is that setting up such facilities may

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divert attention and resources from urgent *in situ* efforts. We are reluctant to speculate about costs, but as effective *in situ* conservation is a necessary component of successful *ex situ* conservation, costs of any worthwhile captive-breeding programme must be additive.

IMPLICATIONS FOR CONSERVATION OF *ARDEOTIS NIGRICEPS*

For *Ardeotis nigriceps*, 'successful' captive breeding and release provided fewer and delayed conservation benefits than effective *in situ* conservation over three decades of programme management. Modelling predicted that egg collection and captive rearing could conceivably establish an *ex situ* population capable of persisting at least 50 years, but only in the most propitious and restrictive conditions, requiring substantial investment in materials, expertise and management. Those inclined to attempt captive breeding should therefore reflect deeply on the human, financial and physical resources they will need to command for half a century into the future. Even assuming 'above-average' performance across all aspects and stages of the programme, the modelling predicted high extirpation probability unless large numbers of eggs (e.g. 10 yr^{-1} for 8 years) were collected. For *A. nigriceps*, such rates of egg collection are unlikely, with 5 yr^{-1} achievable (S. Dutta pers. comm.). Even with 'best possible' programme performance, for captive populations established by collecting 10 wild eggs yr^{-1} for 5 years, 16·8% (and with 5 wild eggs yr^{-1} for 5 years, 39·1%) failed to reach 50 females within half a century. Thus, further loss of genetic diversity (already comparatively low in *A. nigriceps*: Ishtiaq *et al.* 2011) would be likely in captivity.

Implementing effective *in situ* conservation measures within the next decade plus not removing wild eggs will recruit more adult females to the wild within 30 years than a captive-breeding and release programme, even with the 'best possible' standards of captive breeding and assuming that released birds breed as well as wild birds. Although not implemented, the measures needed for effective *in situ* conservation of *A. nigriceps* are well known (Rahmani 1988; Dutta, Rahmani & Jhala 2011; Dutta *et al.* 2013) and similar to those that have allowed population increases for *Otis tarda* (Palacín & Alonso 2008). *In situ* conservation of extensive habitat should be achieved soon; future opportunities to restore habitat will be compromised by pressures of infrastructure development (Dutta, Rahmani & Jhala 2011; Dutta *et al.* 2013), human population growth (for India projected to continue over the next three decades, Raftery *et al.* 2012), rising demands for agricultural products, agricultural intensification and land-use change (Tilman *et al.* 2011). Our recommendation to the Indian government is unequivocal: the future of *A. nigriceps* can only be secured by serious immediate investment in *in situ* conservation.

This study adds to the growing body of cautionary evidence for captive breeding and release. It has become standard to undertake some form of feasibility study of the likely persistence of individuals released into the wild; however, models of release strategies generally assume sufficient stock for release. We know of no previous study to model potential outcomes objectively prior to embarking on a captive-breeding and release programme. Modelling after systematically reviewing the biology of a target species and its close relatives shows success is not guaranteed and that, for the parameter range explored, captive breeding is likely to be a worse strategy than solely implementing *in situ* conservation. This adds to a growing body of literature showing conservation breeding and releases are not a panacea for conservation, but rather an arduous, difficult and unpredictable course to take when alternatives exist. We emphasize that modelling should be used to explore and inform every stage of supplementation, not just of released individuals, and that a captive-breeding programme entered into without appropriate evaluation could potentially divert resources away from much-needed conservation action towards an extremely challenging endeavour which has a significant probability of failure.

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Data accessibility

R scripts: uploaded as online supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Retention of minimum breeding stock under release management.

Fig. S2. Juvenile survival required for positive population growth.

Fig. S3. Captive demography for below-average programme quality.

Fig. S4. Egg collection rates required for captive population establishment and persistence.

Fig. S5. Demography of captive breeding and release and of uncollected wild birds, under various scenarios of egg collection and captive population establishment.

Table S1. Evidence base to estimate *Ardeotis nigriceps* demographic parameters.

Appendix S1. Supplementary details of model parameterization and structure.

Appendix S2. R code (model).

Appendix S3. R code (figures).

Appendix S4. parameter csv file for R model.

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