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Survival rates of captive-bred Asian Houbara *Chlamydotis macqueenii* in a hunted migratory population

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Asian Houbara C*hlamydotis macqueenii* numbers are declining as a result of unsustainable levels of hunting and poaching, with the main conservation response being population reinforcement through the release of captive-bred birds. We assessed the contribution of captive breeding to the species' conservation by examining the fates of 65 captive-bred birds fitted with satellite transmitters and released during spring (March–May) and autumn (August) into breeding habitat in Uzbekistan. Of the released birds, 58.5% survived to October, the month favoured by Emirati hunters in Uzbekistan, but only 10.8% of those released survived the winter to return as subadults next spring. To mitigate and compensate for the loss of wild adults to hunting, the number of released birds needs to be an order of magnitude higher than hunting quotas (with a release of between 1640 and 1920 required for a hypothetical quota of 200), indicating that releases may be costly and do not remove the need for a biologically determined sustainable hunting quota.

Keywords: captive breeding, supplementation, sustainable hunting, translocation.

Migratory Asian Houbara *Chlamydotis macqueenii* are declining as a result of unsustainable levels of licensed hunting, unregulated poaching and trapping for trade (Combreau *et al.* 2001, Tourenq *et al.* 2005, Riou *et al.* 2011a). The persistence of the species will depend on its sustainable management as an exhaustible resource and will require coordinated collaboration between traditional hunters, states and conservationists throughout its range. However, the main (indeed virtually the only) conservation response so far has been the establishment of captive breeding centres in Kazakhstan, Uzbekistan and Arabian states to reinforce populations and compensate for wild individuals lost to hunting (Allinson 2014, Hardouin *et al.* 2014, Monnet *et al.* 2014). Even so, before a captive-bred released Asian Houbara recruits to the breeding population, it must survive the post-release period, subsequent migration and overwintering and a further period to breeding age. Males can breed at 2–3 years of age and females at 1 year, although they are unlikely to nest or rear chicks successfully until 2 years old (Maloney 2003, Bacon 2013, Dolman *et al.* 2015). Furthermore, although released captive-bred Houbara are known to have nested in the wild, it is possible that they achieve lower reproductive fitness as a result of the accumulation of maladaptive traits or loss of adaptive learned behaviour, as has been recorded in other species (Bagliacca *et al.* 2004, Buner *et al.* 2011).

To assess the contribution of captive-bred released stock to conserving migratory Asian Houbara populations, we examined the fates of 65 such birds to estimate how many are needed to (i) substitute for one captive-bred bird as quarry for the autumn hunt (mitigation) and (ii) replace one breeding-age adult lost to the hunt (compensation). We then estimated the annual number of released birds needed to hunt sustainably a quota of 200 birds in a concession through a combined

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strategy of mitigation and compensation, assuming that the relative density of captive-bred and wild birds during the hunt determines the composition of the bag.

METHODS

A self-sustaining captive population of Asian Houbara, derived from locally collected wild eggs, propagated through artificial insemination and maintained in exemplary conditions, was established in 2007 by the Emirates Bird Breeding Center for Conservation (EBBCC) in the Bukhara district of the Kyzylkum Desert, Uzbekistan (Collar *et al.* 2014). Each year since 2011, between 150 and 300 captive-bred birds have been released into suitable habitat within this district (Koshkin *et al.* 2014) in the expectation that they will integrate into an extant wild breeding population of migratory Asian Houbara. Although some individuals have been known to overwinter, almost all wild individuals migrate, leaving Bukhara from October, wintering in the deserts of Iran, Afghanistan and Pakistan, and returning to breed in Bukhara in March.

We monitored the fates of 65 captive-bred birds (38 females and 27 males) released between April 2012 and August 2014 (Table 1) within 12 groups of approximately 50 birds, each containing three to four individuals with transmitters, although in spring 2014 logistical constraints restricted releases to a total of only four individuals, each with a transmitter (Table 1). To avoid biases in survival estimates introduced by unconsciously selecting better individuals, those chosen for monitoring were randomly selected by their ring numbers from a list of the entire release cohort. Experimental protocols compared survival rates of 'overwintered' (denied first migration opportunity) 1-year-old birds released in spring to those of fully fledged young-of-the-year released in August. Most spring releases occurred in April or May following vegetation growth and the passage of large eagles; a March release in the Navoi district 100 km north of other release sites is considered separately. Release points were positioned more than 30 km from agricultural areas, at sites judged to be high-quality habitat based on spring densities of displaying males (Koshkin *et al.* 2016).

Survival was monitored using solar-powered satellite GPS platform telemetry transmitters (PTTs) equipped with activity, temperature and mortality sensors. Transmitters were permanently attached using Teflon tubular ribbon backpack harnesses, tied and glued so that the unit would remain on unless removed manually or after predation. Attachment protocols were trialled successfully on Bengal Florican *Houbaropsis bengalensis* (Packman 2011) and adult wild Asian Houbara (R. J. Burnside unpubl. data), with tags surviving over multiple years. Although the survival probability of released, captive-reared Great Bustards *Otis tarda* in the UK was unaffected by harness-mounted PTTs (Ashbrook *et al.* 2015), PTTs may have some residual effect on survival (e.g. if birds are more visible or vulnerable to aerial predators). Mortality was assumed when one or more of the following applied: location data indicated a static location for multiple days, the activity sensor remained static and/or the unit's temperature dropped. Abrupt cessation of transmissions where engineering data had been regular with no indication of voltage deterioration was also attributed to mortality, with associated

Table 1. The fates of captive-bred Asian Houbara released and monitored by satellite transmitter in Uzbekistan. All values are numbers of individuals; 'Alive in October' is the number of birds alive at 1 October. 'Available to migrate' denotes birds that survived the hunting period in Uzbekistan.

Year	Release month	Released	Alive in October	Hunted in concession	Available to migrate	Migrated	Surviving to April
2012	April	12	9	1	8	8	1
2012	August	10	6	1	5	4	3
2013	March	10	6	0	6	3	1
2013	April	10	7	0	7	4	0
2013	August	10	5	0	5	2	1
2014	May	4	2	1	1	0	0
2014	August	9[a]	3	0	3	0	1[b]
Totals		65	38	3	35	21	7

[a]One bird was hunted by falconers before the start of October. [b]Did not migrate but successfully overwintered in Bukhara.

destruction, burying or covering of the solar panel. In contrast, transmitter failure was typically preceded by progressive deterioration of the battery voltage and increasing gaps in location and engineering data. When possible, mortalities were visited in the field to assess the cause and confirm engineering data interpretation methodology. PTTs were new or recently refurbished with an expected transmission lifespan of 3–4 years, and were tested prior to fitting. We analysed the 1-year period post-release; the possibility of PTT failure was therefore minimal and no failures were suspected to have occurred. Consequently, all individuals had a known fate, allowing direct measures of mean survival per cohort, with variance estimated by binomial error. Differences between treatment groups, release years and sexes were modelled using generalized linear models (GLMs), candidate models were ranked by corrected Akaike information criteria (AICc) and the change in deviance between the top model and lower models was examined by χ^2 test.

We analysed survival during two periods: (i) from release until the end of September ($S_{september}$), before hunting within the concession (hereafter 'summer'); (ii) from 1 October until the end of the following March; S_{march} is survival encompassing the hunt in Uzbekistan, plus outward and return migration with birds exposed to hunting and trapping during winter and migration (hereafter 'winter'), and S_{winter} is survival in the same period but excludes birds hunted in Uzbekistan. Migration onset varied among individuals and years, with birds leaving from early October. Southward movement into neighbouring Turkmenistan was classified as migration, with surviving birds wintering in Iran, Afghanistan or Balochistan (Pakistan). Any bird returning to Turkmenistan or Uzbekistan (by the end of March) was classified as a successful migrant.

We used survival estimates to calculate (a) the number of captive-bred birds that would need to be released to produce one captive-bred bird available to the hunt in October (CBR_{quarry}):

$$CBR_{quarry} = \frac{1}{S_{september}}$$

and (b) the number of captive-bred birds that would need to be released to provide one surviving adult returning 2 years after release, as compensation for a hunted wild adult (CBR_{comp}):

$$CBR_{comp} = \frac{1}{S_{september} \cdot S_{march} \cdot S_{adult}}$$

where S_{adult} is adult annual survival. Return in the first year after release was considered unlikely to result in successful breeding, although nesting attempts may occur (Bacon 2013). Because of the small sample of released birds remaining after their first return migration, a wild adult Asian Houbara annual survival of 72% (Combreau *et al.* 2001), similar to a provisional estimate from our study (76%; R. J. Burnside unpubl. data), was applied to captive-bred adults as it was the most robust available.

During a hunt, the bag composition of captive-bred and wild birds hunted will depend on their relative frequency in the landscape. We estimated the minimum release number required both to provide captive-bred quarry (mitigating impacts on wild birds) and to compensate for all wild adults hunted, with no subsequent deficit in breeding individuals. Within the modelled hunting concession (14 000 km^2) in Bukhara, Asian Houbara occurred at a mean density of 0.13 males/km^2 (Koshkin *et al.* 2016) and hence, assuming a balanced sex ratio (Combreau *et al.* 2002), 0.26 individuals/km^2. We assumed that the captive-bred quarry still alive by the end of September (CBQ) were evenly distributed relative to both wild birds and hunting effort, at mean density:

$$CBQ_{density} = \frac{CBQ}{14\,000\,\text{km}^2}$$

Based on indistinguishable flight and performance of captive-bred and wild birds when hunted (K. M. Scotland, pers. obs.), we assumed these to have an equal chance of escaping or succumbing once detected. Thus, relative densities of wild and captive-bred quarry determine encounter rates and the proportion of the hunting bag comprising captive-bred quarry ($CBQ_{\propto}$):

$$CBQ_{\propto} = \frac{CBQ_{density}}{Wild_{density} + CBQ_{density}}$$

where $Wild_{density}$ is the density of wild birds within the concession. The number of captive-bred birds that survived the hunt to return and subsequently recruit to the breeding population 2 years after release ($CB_{recruit}$) was estimated as:

$$CB_{recruit} = (CBQ - (HuntQuota \cdot (CBQ_{\propto})) \cdot S_{winter} \cdot S_{adult}$$

where HuntQuota is the quota to be hunted in the season. The number of wild adults hunted ($Wild_{hunted}$) was calculated as:

$$Wild_{hunted} = HuntQuota \cdot (1 - CBQ_{\propto})$$

Consequences for the exploited population were considered as the effective deficit or surplus in breeding individuals ($\Delta_{breeders}$) in the second breeding season after the hunt, when surviving released birds have reached breeding age, calculated as:

$$\Delta_{breeders} = CB_{recruit} - Wild_{hunted}$$

This model considered the numbers of hunted wild individuals that must be replaced under a quota that comprised only breeding-age adults. In reality, however, wild juveniles are also hunted and hence the number of breeding-age adults that must be replaced through surviving released birds is somewhat lower. Because the ratio of wild juveniles (young-of-the-year) to wild adults during the hunt is unknown, we initially considered all hunted birds to be adults, thus providing a precautionary upper estimate of release numbers required for compensation. We then extended this model, assuming that 19.5% of the wild October population consisted of juveniles ($Juv_{\propto}$), as predicted from preliminary modelling of age structure based on population productivity and survival (R. J. Burnside & P. M. Dolman unpubl. data). Assuming the probability of being targeted and successfully hunted was independent of age (Hardouin *et al.* 2015a), the proportion of juveniles in the hunt bag ($Wild_{juv}$) was then calculated as:

$$Wild_{juv} = Wild_{hunted} \cdot Juv_{\propto}$$

and the number of wild adults in the bag ($Wild_{adult}$) recalculated as:

$$Wild_{adult} = Wild_{hunted} - Wild_{juv}$$

The consequence of hunting wild juveniles, in terms of the subsequent loss of breeding adult recruits reaching age 2 years ($N_{juv.breeders}$), was estimated as:

$$N_{juv.breeders} = Wild_{juv} \cdot S_{juv.winter} \cdot S_{adult}$$

where $S_{juv.winter}$ is the survival rate of wild juveniles over their first winter. As there are no robust estimates of $S_{juv.winter}$ for wild migrants, we modelled it at a lower (equal to survival of captive-bred juveniles, S_{winter}) and an upper (equal to wild adult winter survival: 87.8%; R. J. Burnside unpubl. data) precautionary scenario limit. The resulting change in breeders (a modification of $\Delta_{breeders} = CB_{recruit} - Wild_{hunted}$) was then recalculated as:

$$\Delta_{breeders} = CB_{recruit} - (Wild_{adult} + N_{juv.breeders})$$

All analyses and calculations were performed in R (R Core Team 2013) and the model code is available in Appendix S1.

RESULTS

Of the 65 released birds, 58 died, 27 in summer and 31 in winter, with 16 of the latter deaths occurring in Uzbekistan prior to migration, seven in Turkmenistan, four in Iran and four in Afghanistan (Table 2).

Neither release year, sex nor their additive interactions with release group significantly improved survival models (Table S1) and the null model was accepted as the most parsimonious. Spring release cohorts (comprising 1-year-old birds) experienced two periods of elevated summer mortality, in the first weeks post-release and during peak summer temperatures (July–August) (Fig. 1). Birds released in August (young-of-the-year) experienced both peaks simultaneously, and an apparently lower proportion of them survived to October (0.483 ± 0.09 se) than of birds released in spring (March: 0.600 ± 0.15 se; April/May: 0.692 ± 0.09 se). However, these differences were not significant across all the three periods (χ^2_2 = 2.514, P = 0.285) or contrasting all spring releases with August releases (χ^2_2 = 2.242, P = 0.13), with overall $S_{september}$ being 0.585 (se = ± 0.061). Of birds alive at the start of the migratory period, 60% began outward migration (Table 1). However, this should not be taken as the proportion of birds that expressed migratory behaviour, as all but one of those that did not

Table 2. Locations of mortalities pre- and post-migration of captive-bred Asian Houbara released in Bukhara, Uzbekistan, in the years 2012–2014.

	Country	Natural cause	Hunted within concession	Uncertain cause	Total mortalities
Summer (to end September)	Uzbekistan	21	1[a]	5	27
Winter (October–March)	Uzbekistan	8[b]	3	5	16
	Turkmenistan			7	7
	Iran			4	4
	Afghanistan			4	4
Total		29	4	25	58

[a]Hunted on 19 September. [b]Including one mortality from a powerline collision.

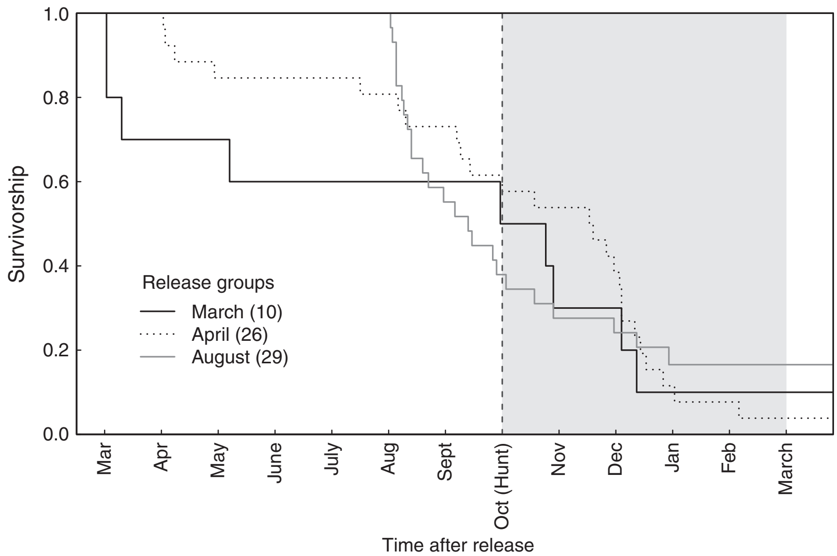

Figure 1. Survivorship of captive-bred Asian Houbara cohorts released in March (2013 only), April and August (in each of 2012–2014) with sample size in parentheses; the start of the hunting period is indicated with a vertical dashed line; the migration autumn/winter period is blocked in grey.

make a migratory movement before the end of December died in Uzbekistan before their sedentary or migratory behaviour could be established with certainty. Of the 21 birds that migrated, six survived and returned by the end of March (Table 1), while one individual did not migrate but survived the winter in Bukhara, giving an over-winter survival S_{march} of 0.184 (se = ± 0.061). Excluding individuals hunted in the concession, S_{winter} was 0.200 (se = ± 0.068). Overall, the proportion of birds surviving from release to the following spring was 0.108 (se = ± 0.039).

Of the 58 mortalities identified from location and engineering data, 33 could be investigated in the field (22 in summer and 11 in winter) and helped to validate the interpretation of those mortalities that could not be visited. Mortality in the summer period appeared to be mainly natural (21 individuals), but scavenging of carcasses by foxes made it impossible to determine the relative contributions of starvation, disease, injury and predation. Of the 11 traceable winter mortalities, all within Uzbekistan, seven were natural, three resulted from hunting and one involved a powerline collision in the Bukhara concession prior to migration (Table 2). Other winter mortalities could not be checked because of the inaccessibility of the wintering countries (Table 2). Of the total 25 mortalities that could not be checked or located in the field, 18 had unmistakable evidence of mortality, usually static GPS locations and activity sensor, while seven units suddenly ceased transmission.

With 58.5% of released birds surviving to October, approximately 1.7 birds (95% confidence interval (CI) 1.4–2.2) should be released to supply one captive-bred quarry for the hunting period. If it were possible only to hunt captive-bred quarry, a quota of 200 would require a release of only 342 (95% CI 280–440) captive-bred birds. By contrast, a compensation strategy (of releasing birds to replace hunted wild birds) yielded a recruitment rate from release to breeding 2 years later of only 7.8% (95% CI 2.3–13.3%), so that 12.9 birds (95% CI 8–44) would need to be released to replace each wild adult hunted. Compensation for hunting 200 wild breeders would, therefore, require an annual release of around 2579 birds (95% CI 1600–8800). Under the combined scenario of providing both quarry and compensation, large numbers have to be released to increase the hunters' chances of encountering captive-bred birds, with wild birds still contributing 50% of the bag even when 7000 captive-bred birds are released into the hunting concession (Fig. 2). A minimum release of around 1920 birds (95% CI 1580–5460) is required to allow a sustainable quota of 200 birds (of which 24% (95% CI 17–41%) would be captive-bred quarry and 76% wild), while having no effect (Δ_{breeders} = 0) on subsequent adult numbers (Fig. 2).

The inclusion of wild juveniles in the mitigation and compensation model did not change the finding that large numbers of birds need to be released to compensate fully for the loss of breeders. If juveniles formed 19.5% of the wild hunt bag with $S_{\text{juv.winter}}$ set to its precautionary upper limit (0.878, as for wild adults) the number required to be released for a sustainable quota of 200 birds was reduced by 6.3%, with 1800 fully compensating for all lost breeders and 22.4% of the bag consisting of captive-bred quarry (Fig. S1). Even when $S_{\text{juv.winter}}$ was modelled at the lower limit (0.200, as for captive-bred birds, S_{winter}), a sustainable quota of 200 still required 1640 to be released for compensation (with 20.9% of the bag consisting of captive-bred quarry), a reduction of 14.6% compared to the scenario of a wild bag comprising only adults.

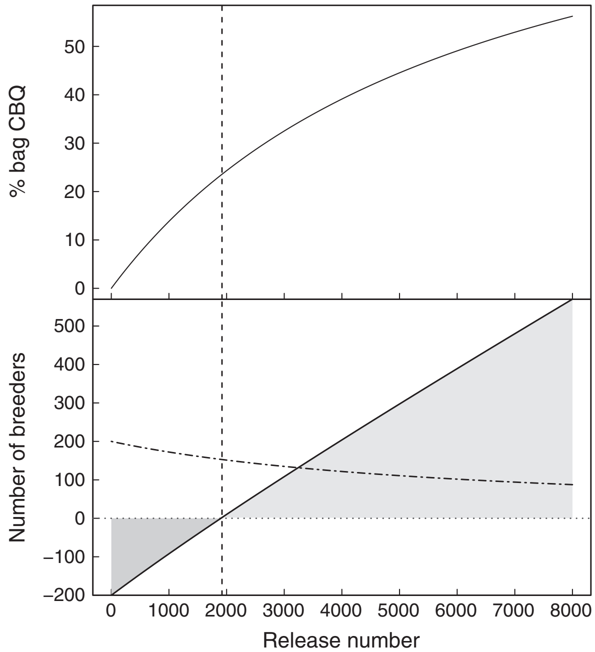

Figure 2. Deterministic model estimates of management outcomes in relation to numbers of captive-bred Asian Houbara released into a 14 000-km^2 hunting concession with an extant wild population density of 0.26 individuals/km^2 and a hunting quota of 200 individuals per year. The upper panel shows the percentage of the hunt bag comprising captive-bred released birds in October, after post-release mortality. The lower panel shows the number of wild breeders hunted (dot–dashed black line), and the net impact (solid black line) on numbers of 2-year-old breeding-age individuals, showing deficit (shaded, below zero) or surplus (shaded, above zero) and point of sustainability (vertical dashed line) at which numbers of surviving released replacements equal wild numbers hunted. CBQ, captive-bred quarry.

DISCUSSION

The mean survival of released birds to October was 58.5% and did not differ significantly between birds released in spring and August. Resident Asian Houbara released in Saudi Arabia had an initial 3-month survival of 47.5% (Judas 2000) with equivocal results for 'soft releases' (slow habituation to wild conditions) and predator-aversion training that attempted to address low post-release survival (Combreau & Smith 1998, van Heezik *et al.* 1999). Survival over the first 3 months of released captive-bred African Houbara *C. undulata* was 19–93% (Hardouin *et al.* 2014), but mean survival was not reported.

Of 21 released birds that migrated, only six survived to return the following spring, indicating considerable overwinter mortality. The only previous study of the performance of captive-reared migratory Asian Houbara found that, of seven birds released in September in Kazakhstan, five completed the outward migration but only two survived the winter (Riou *et al.* 2011b). Our estimate of overwinter survival (18.4%) seems rather low, but survival rates have been shown to be lower for captive-bred released individuals compared with wild counterparts in a range of bird species (Parish & Sotherton 2007, Evans *et al.* 2009, Burnside *et al.* 2012). However, comparable rates for wild juvenile Asian Houbara are not yet known and could be similar to those of released individuals, as observed in some raptor species (Nicoll *et al.* 2004, Mihoub *et al.* 2014), particularly given the challenges of locating suitable safe passage and wintering grounds.

Modelling indicated that even a mixed mitigation and compensation strategy required the release of an order of magnitude more birds than the modest hunting quota, as a result of low initial return rates and subsequent adult mortality prior to recruitment. An additional consideration under this scenario is that, as some of the wild birds hunted in Uzbekistan during October are migrants from beyond the Kyzylkum (Combreau *et al.* 2011) and surviving captive-bred birds show release site fidelity, releases achieving zero net deficit may enhance local breeding numbers in compensation for the depletion of other flyway populations.

Allowance for the possibility that the hunted wild birds may include juveniles, some of which will not survive to enter the breeding population and therefore do not need to be compensated for, slightly reduced (by 6.3–14.6%) the numbers of individuals that needed to be released, depending on the level of wild juvenile survival. However, our estimate of age structure is derived from measures of breeding productivity from years with consistently low predator numbers following a rodent crash (R. J. Burnside unpubl. data) and good nest success (Koshkin 2015) that may not represent the long-term mean. In China, Asian Houbara nest success varied strongly with varying predator abundance (Combreau *et al.* 2002). If the mean proportion of juveniles in the wild hunt bag across a full inter-annual predator cycle is lower than 19.5%, then the number required for compensation will lie between those reported here for the combined adult and juvenile hunt bag scenario and the adult-only scenario.

Under the alternative mitigation scenario, with the number of releases needed to hunt one captive-bred individual an order of magnitude lower than those needed for compensation, one possibility would be to seek to manage captive-bred Houbara to substitute for wild birds as quarry. If achieved, this would mitigate the pressure on the wild population while reducing the need for (and the risks associated with) release of large numbers of captive-bred birds into extant populations. *Ex situ* captive-bred populations frequently experience trait domestication, loss of genetic variation and outbreaks of epizootic disease (Snyder *et al.* 1996, Frankham 2008). As it is unclear whether post-release mortality effectively filters deleterious traits, a precautionary approach would avoid repeated industrial-scale releases that can eventually form a substantial proportion of the extant population, as reported for African Houbara (Bacon 2013). *Ex situ* measures may also divert focus from *in situ* conservation (Dolman *et al.* 2015) while creating the impression that large hunt bags are viable. Making such a mitigation strategy practicable would require locally increasing the relative density of captive-bred quarry to wild birds, potentially through one or more of:

(1) concentrated releases, contingent on density dependence in both survival and dispersal (Hardouin *et al.* 2012, 2015b);
(2) later releases, to reduce dispersal distance;
(3) releases into apparently suitable areas with lower density as a result of population depletion.

The last option is not available where releases occur in breeding areas distant from winter hunting grounds.

Although supplementation of captive-bred birds has been used for 20 years implicitly as the means to conserve the Asian Houbara, its potential effectiveness in terms of mitigating or compensating for hunting has hitherto remained unexplored. However, the high numbers of releases needed to achieve a plausible conservation result represent substantial drawbacks in terms of both cost and risk, because captive breeding must maintain the highest genetic quality, avoid domestication and minimize the negative fitness consequences in the wild of traits selected over generations of *ex situ* management. Until it is possible to control anthropogenic winter mortality (e.g. by stronger enforcement by range states, effective implementation of protected areas and engagement with local communities), it seems that captive breeding can only support, and not substitute for, biologically determined sustainable hunting quotas scrupulously observed on well-managed concessions.

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SUPPORTING INFORMATION

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

Appendix S1. R code for modelling the captive-bred release numbers and its influence on the percentage of the hunt bag consisting of captive-bred quarry. In R script format.

Table S1. Model selection table for the proportion of captive-reared Asian Houbara surviving from their release (spring vs late summer; $n = 65$) to the end of September incorporating sex, year of release and release group (three levels).

Figure S1. Deterministic model estimates of management outcomes in relation to numbers of captive-bred Asian Houbara released incorporating wild juvenile density.