Captive breeding and the conservation of the threatened houbara bustards

RUNNING TITLE: Captive breeding houbara bustards

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ABSTRACT: Translocation of captive-bred individuals to reinforce wild populations may be an important conservation approach for some species, but can be detrimental when employed to boost exploited wild populations, particularly where repeated long-term reinforcement aims to compensate for repeated unregulated offtake. We review evidence that captive breeding alters multiple physiological, life-history and temperamental traits through founder effects, genetic drift and unintended adaption to captivity, degrades learnt behaviours, and compromises biogeography, population structure and viability through introgression. We highlight these risks for the globally threatened African houbara *Chlamydotis undulata* and Asian houbara *Chlamydotis macqueenii,* two bustard species hunted throughout much of their ranges and now subject to multiple large-scale captive-breeding programmes and translocations. In eastern Morocco, annual releases of captive-bred African houbara are 2–3 times higher than original wild numbers, but no investigation of their potentially deleterious effects has, to our knowledge, been published although most wild populations may now have been replaced by captive-bred domestic stock, which are reportedly not self-sustaining. Despite multiple decades of reinforcement, we are not aware of any analysis of the contribution of captive breeding to African houbara population dynamics, or of the genomic consequences. Asian houbara release programmes may also be promoting rather than preventing declines, and need to contextualise themselves through rigorous analyses of wild population numbers, demographic rates and threats, maintenance of phylogeographic concordance of released with supplemented populations, profiling of traits crucial to survival, and the measurement and modelling of the impacts of reinforcement on physiological and behavioural fitness of wild populations.

KEY WORDS: captive-breeding · translocation · population reinforcement · sustainable hunting · supplementation · game management · restocking

1. INTRODUCTION

Captive breeding is an increasingly common component of wildlife conservation programmes worldwide (McGowan et al. 2017), helping prevent the extinction of many species (Bolam et al. 2020). Birds benefiting from *ex situ* programmes include the bearded vulture (*Gypaetus barbatus*) in Europe (Jenny et al. 2018), black stilt (*Himantopus novaezelandiae*) in New Zealand (Galla et al. 2020) and California condor (*Gymnogyps californianus*) in the USA (Walters et al. 2010) among many others. Indeed, more than 250 avian species may depend in varying degrees on *ex situ* management (Collar & Butchart 2014). Nevertheless, translocations of captive-bred individuals, aimed at reintroducing or reinforcing populations of threatened species, pose multiple risks (IUCN/SSC 2013) and often fail (Mathews et al. 2005, Converse et al. 2013, Berger-Tal et al. 2020).

Although commonly regarded as a species conservation endeavour, translocation of captive-bred individuals is frequently used to reinforce (i.e. supplement or restock) legally exploited populations (Griffith et al. 1989, Armstrong & Seddon 2008). IUCN guidelines stipulate that conservation releases should not take place until the cause of the original extinction or population decline has been addressed (IUCN/SSC 2013), and the success of such releases is commonly defined as the establishment of a population able to persist without further intervention (Griffith et al. 1989, IUCN/SSC 2013). The IUCN guidelines further advise that 'where populations are augmented for... recreational or commercial offtake… often conservation benefit… will either be non-existent or be secondary to other interests'. Indeed, if offtake is not regulated to sustainable levels, continuous captive-breeding reinforcement can itself become a conservation issue, particularly where it involves species of conservation concern.

We suggest this is the case with two threatened bustards, African houbara (*Chlamydotis undulata*) and Asian houbara (*C. macqueenii*). African houbara occupies semidesert lands from northernmost Mauritania to Egypt west of the Nile (BirdLife International 2020b), while Asian houbara is a resident breeder in semi-deserts from the Arabian Peninsula and Middle East to southern Iran and Pakistan and a migrant breeder from Central Asia to western China, wintering in the same general range as the resident populations (Combreau & Al Baidhani 2013, BirdLife International 2020a) (Fig. 1). For many centuries both species have been the prized avian quarry of Arab falconers, occupying a central place in the culture of the desert peoples of the Middle East (Bailey et al. 1998). However, over the past fifty years traditional falconry practices have been supplemented by increasingly technical and sophisticated methods (Bailey et al. 1998), with often large parties of falconers from the Gulf states hunting the species across almost all parts of their ranges (Stone 2008). Falconers' access to these ranges has been eased by economic influence and the disintegration of the Soviet Union, with their activities assisted by desert-adapted 4×4 vehicles, sophisticated communication systems and high numbers of pre-trained falcons, many of them hybridised for enhanced hunting performance (Bailey et al. 1998, Usman & Farooq 2016).

Resident populations of Asian houbara were almost entirely extirpated from the Arabian Peninsula in the 1970s and from Pakistan by the 1990s (Combreau et al. 2005) and have declined severely in Iran (Mansoori 2006), with hunting now dependent on its wintering migratory populations. However, by the year 2000 migratory Asian houbara were exploited repeatedly throughout their flyway, involving a combination of falconry, hunting with firearms, and trapping for illegal trade estimated in the 1990s at up to 7,000 per year from Pakistan alone (Goriup 1997, Bailey et al. 1998, Combreau & Al Baidhani 2013). Between 1994 and 2000, offtake was estimated to be three times the annual sustainable yield (Combreau et al. 2001); migratory Asian houbara declined by over 50 % in Kazakhstan and China between 1998 and 2002 (Tourenq et al. 2005), with further steep declines in parts of Kazakhstan between 2000 and 2009 (Riou et al. 2011). Recent demographic modelling of

Asian houbara breeding in Uzbekistan indicates an ongoing decline of over 9 % per year (Dolman et al. 2018), with at least 53 % of winter mortality attributable to hunting/trapping (Burnside et al. 2018). For African houbara no comparable quantitative data for anthropogenic mortality or population trends exist, but the contribution of overhunting to population declines, as documented in Goriup (1997) and Azafzaf et al. (2005), was further evident from reports of (e.g.) all populations in Morocco (except 'West Sahara') being 'severely reduced' by Middle Eastern falconers (Thévenot et al. 2003), 1,000 birds being killed annually by Arab falconers in Algeria's pre-desert zone (de Smet 1989) and a serious decline in Tunisia attributed to 'the abusive hunting of foreign falconers' (Chammem et al. 2003), with the low-density residual population still subject to illegal hunting by 'local poachers and Arab falconers' (Chammem et al. 2012). Consequently both species are now threatened, categorised as Vulnerable on the IUCN Red List (BirdLife International 2020a, b), with African houbara potentially at greater risk owing to its smaller total estimated population (e.g. ~9,800 individuals for African versus 39,000—52,000 individuals for Asian houbara, before the present era of reinforcements: Goriup 1997). More recently the global African houbara population has been put at 13,000–33,000 mature individuals, attributable to releases of captive-bred birds, although it is explicitly stated that 'a reliable estimate for the number of individuals in North Africa has not been considered achievable' (BirdLife International 2020b). Houbara are lekking species, and the consequent variance in reproductive success will further reduce contemporary effective population size (N_e) relative to apparent numbers (Hare et al. 2011).

To date, although there have been efforts to create protected areas and enforce legal protection, the primary conservation response to counter these declines has been captive breeding and release programmes (Fig. 1), which have been rolled out across the ranges of the two species (IFHC 2013, Dolman et al. 2018). However, the impact and conservation value of these programmes have received little independent scientific scrutiny. Here, we review the potential risks inherent in such programs, particularly when used for game reinforcement, and assess the degree to which this approach can be considered an appropriate response to the plight of the two species of houbara.

2. RISKS FROM CAPTIVE BREEDING

Releases and reinforcement involving captive-bred animals should respect biogeography and the genetic structure of source and recipient populations, to avoid homogenization and assimilation of previously differentiated gene pools, intraspecific hybridization and biotic impoverishment that can compromise fitness by disrupting local adaptations (Olden et al. 2004, IUCN/SSC 2013). Fisheries and gamebird reinforcement have frequently failed to allow for genetically distinct conspecific populations, leading to introgression (Petersson et al. 1996, Olden et al. 2004, Randi 2008, Barbanera et al. 2009, Forcina et al. 2018). However, the operational identification of evolutionarily significant units (ESUs) is contentious, particularly in terms of objective thresholds for isolation, the role of neutral genetic markers or nuclear loci, and behavioural or morphological proxies of heritable adaptive diversity (Fraser & Bernatchez 2001). Defining ESUs based on strict phylogenetic isolation assumes other fine-scale phenotypic divergence can be disregarded, as it is ultimately replaceable through future natural selection; but this may not sufficiently emphasize the ecological viability of populations through maintenance of adaptive diversity, leading to an emphasis on finer-scale (spatial and temporal) conservation units (Fraser & Bernatchez 2001).

Even where population structure is recognized appropriately in translocation and reinforcement strategies, supplementation of wild populations through captive breeding poses multiple additional risks. Captive breeding inevitably alters multiple heritable traits in species, through a combination of founder effects, genetic drift, relaxation of natural selection (because of plentiful food, no predation), and unintentional adaption to captivity, together producing changes in morphology, physiology, endocrine systems, metabolic rate, thermoregulation, innate behaviour and temperament (Snyder et al. 1996, Tieleman et al. 2002, Heath et al. 2003, Frankham 2008, Williams & Hoffman 2009, Champagnon et al. 2012, Lacy et al. 2013). These adaptations are 'overwhelmingly deleterious when populations are returned to wild environments' (Frankham 2008). Where trait optima differ between captivity and the wild then reinforcement of wild populations with captive-bred individuals will alter wild phenotypes; quantitative genetic modelling predicts this will occur even when selection differentials are weak, captive stock is continually refreshed by wild accessions, and captive-bred releases only comprise a small proportion of the free-living population (Ford 2002).

While wild traits such as clutch size optimize current and residual reproductive fitness (Charnov & Krebs 1974), captivity frequently selects for higher fecundity (Heath et al. 2003, Christie et al. 2012, Chargé et al. 2014a). Hatchery-rearing of Chinook salmon (*Oncorhynchus tshawytscha*) relaxes natural selection for large eggs; the rapid evolution of small eggs alters traits in reinforced natural populations (Heath et al. 2003). Increased fertility in game-farmed stock has been implicated in increasing rates of introgression into wild mallard (*Anas platyrhynchos*) populations (Čížková et al. 2012), of hybrid red-legged partridge × chukar (*Alectoris rufa* × *A. chukar*) into wild red-legged partridge (Casas et al. 2012), and of farmed hybrids of domestic Japanese quail × common quail (*Coturnix japonica* × *C. coturnix*) into wild common quail (through a sperm-competition advantage: Sanchez-Donoso et al. 2016). Captive populations may suffer important loss of immuno-competence from founder effects, inbreeding and genetic drift (Athrey et al. 2018). Captivity may also select for immuno-competence that is maladaptive in birds released into the wild, as breeding centres, concentrating individuals at high density, are prone to atypical pathogen outbreaks such as pox (Le Loc'h et al. 2016) that may alter the immunogenetic composition of survivors (Worley et al. 2010). Conversely, effective biosecurity may exclude natural pathogens from centres, resulting in released individuals with reduced resistance (Ewen et al. 2012).

Problematic changes to foraging, movement, territorial and anti-predator behaviours are commonly encountered in reintroduction attempts (Berger-Tal et al. 2020). Captive-bred animals may lose natural behaviours through genetic domestication (McPhee 2004, Houde et al. 2010, Moseby et al. 2016), habituation (Huber 2010) and lack of ontological development (Price 1999). Captivity may alter temperament (Snyder et al. 1996, McDougall et al. 2006, Frankham 2008), especially selecting against traits such as boldness or aggression (Belyaev 1979, Håkansson et al. 2007). In long-term captive stock the removal of the ‘wildest’ individuals through injury and mortality, combined with preferential retention of breeders amenable to artificial insemination, is expected to select for docility. This may have fitness consequences in the wild (Leopold 1944, McDougall et al. 2006); but ironically, in cases where released animals are hunted, it may also undermine their perceived worthiness as challenging quarry.

Learnt behaviours are also prone to loss in captivity (Snyder et al. 1996), particularly during chick-rearing (Collar 2020), with consequences for post-release survival. Loss of parental learnt behaviour may contribute to lower reproductive success in released head-started birds (e.g. Roche et al. 2008). Captive-bred released galliforms frequently have lower survival and breeding success than their wild counterparts, reflecting in particular their failure to acquire appropriate anti-predator behaviours (Rantanen et al. 2010, Rymešová et al. 2013, Collar 2020). Predator-aversion training improved post-release survival of farmed red-legged partridges (Gaudioso et al. 2011), but has generally produced mixed results (Berger-Tal et al. 2020), particularly for bird translocations (Tetzlaff et al. 2019), and is often labour-intensive, costly and potentially hazardous.

Captive breeding can alter phenotypes through ontogenetic effects arising from the environmental and physiological conditions experienced during foetal and early post-natal development (Reeves et al. 2020). Epigenetic modifications to gene activity and expression can be transmitted from parents to offspring, changing their phenotype or behaviour (Jablonka & Raz 2009, Jablonka & Lamb 2015). Epigenetic changes can be induced by stress, hormones, maternal neonatal care, nutrition, rearing conditions and other factors (Carere et al. 2005, Jablonka & Raz 2009, Sepers et al. 2021), particularly when recurrent or sustained (Jablonka & Lamb 2015), and they are therefore likely to be common in captive breeding systems. In great tit *Parus major*, changes in DNA methylation of a dopamine receptor gene have been implicated in epigenetic changes in exploratory behaviour over only four generations of captive selection (Verhulst et al. 2016), while experimental differences in early-life nutritional stress caused epigenetic changes to genes related to development, growth, metabolism, behaviour and cognition (Sepers et al. 2021). At least in theory, epigenetic variation could become widespread or fixed within a population even where it has no selective advantage, if unrelated individuals all encounter novel environments (Jablonka & Lamb 2015).

Genetic adaptation to captivity can be rapid (Snyder et al. 1996), occurring even under counteractive breeding protocols (Lacy et al. 2013, Chargé et al. 2014a). Selection for tameness changed silver fox (*Vulpes vulpes*) reproductive patterns within five generations (Belyaev 1979), and the expression of hundreds of genes in steelhead trout (*Oncorhynchus mykiss*) was altered in a single captive generation (Christie et al. 2016). Maladaptive changes in lamellar density of wild mallards were found after only 30 years of large-scale annual releases for hunting (Champagnon et al. 2010). Domestication risk is reduced by minimizing the number of captive generations (Snyder et al. 1996, Frankham 2008, Williams & Hoffman 2009); conversely, risks increase where long-term captive stock repeatedly reinforce free-living populations (Ford 2002, Araki et al. 2007, Willoughby & Christie 2019). Repeated accessions of wild individuals into captive populations is a common strategy used to reduce the rate of genetic adaptation to captivity (Frankham 2008, Witzenberger & Hochkirch 2011); however, this may not eliminate inadvertent domestication (Ford 2002) and is further confounded if the free-living source population already includes the progeny of large numbers of releasees with modified traits. By amplifying overall variance in reproductive success relative to the case in which there is no reinforcement, population supplementation typically lowers the effective size of the entire captive-wild system (N_{eT}) (Hare et al. 2011).

Where captive-bred individuals are released in numbers disproportionate to the size of the wild population, introgression can compromise biogeography, population structure and viability (Laikre et al. 2010, Champagnon et al. 2012, Thakur et al. 2018). IUCN translocation guidelines (IUCN/SSC 2013: p22) are explicit on this problem:

> “Where translocations involve reinforcement, … there is a risk of genetic swamping of the resident population(s) by the translocated individuals. This can potentially cause a reduction in vigour or reproductive success in a small, stable, resident population if a large proportion of the subsequent reproductive output is derived from the less well-adapted translocated stock.”

Semi-domestication of captive-bred individuals used for reinforcement would be less problematic if subsequent selection in the wild removed maladaptive traits, eventually restoring wild levels of fitness (Frankham 2008), although this purging process would still incur a demographic cost to the wild population (O'Sullivan et al. 2020). However, continued reinforcement changes wild phenotypes from their optima, even with moderate selection differentials, thereby reducing wild fitness (Ford 2002, Willoughby & Christie 2019). Despite generally lower survival and/or productivity, widespread introgression has resulted from large-volume releases of farmed wildfowl (Champagnon et al. 2013, Champagnon et al.

2016, Söderquist et al. 2017) and gamebirds (Parish & Sotherton 2007, Rymešová et al. 2013, Robertson et al. 2017, Madden et al. 2018), including hybrid chukar into modern red-legged partridge populations, genetically homogenised farmed red-legged partridge into local populations, and Japanese quail into common quail (Barilani et al. 2005, Barbanera et al. 2010, Casas et al. 2012, Forcina et al. 2021). Similarly, for migratory salmonids, reinforcement by captive-bred individuals results in introgression despite their much lower fitness (Araki et al. 2007, 2009, Satake & Araki 2012).

The limited evidence available suggests that the two species of houbara are particularly exposed to the dangers from captive-breeding reinforcement outlined here.

3. THE MULTIPLE UNKNOWNS OF LARGE-SCALE HOUBARA REINFORCEMENT

The Asian houbara was first bred in captivity in the 1970s by Mendelssohn et al. (1979), but it took two further decades of research before a model for their volume production was developed using artificial insemination, artificial incubation and the hand-rearing of chicks (Seddon et al. 1995). From this beginning, captive breeding programmes have been implemented across the ranges of both species (IFHC 2017), reinforcing houbara populations on a major scale. In 2004 a workshop comprising experts from all key North African range states concluded that the African houbara numbered 8,240–9,240 in total, principally in Algeria with smaller populations in Morocco, Tunisia and Libya (Azafzaf et al. 2005); yet between 1998 and 2016 one breeding centre released 116,500 captive-bred African houbara, 111,865 of them in Morocco (IFHC 2017), following this in 2017–2018 with a further c.17,000 birds in Morocco and c.7,000 in Algeria and Mauritania (IFHC 2018, 2019). Thus, reinforcement may have exceeded initial wild numbers more than ten-fold. For one concession covering 50,169 km^2 of eastern Morocco, area-weighted density estimates across hunting (64 % of area; 0.05 houbara km^{-2}) and non-hunting (36 %, and 0.1 km^{-2}) areas suggest initial (2001) numbers of approximately 3,400 houbara (Hardouin et al. 2015), with 2,838 estimated in 2001–2003 (Bacon 2017), into which 94,374 captive-bred birds were released between 1996 and 2016, averaging 10,000 annually from 2009 (Bacon 2017); thus every year releases now exceed initial numbers at least three-fold.

Arab falconers take approximately 2,000 African houbara annually in eastern Morocco, of which 85 % are captive-bred (Bacon 2017), while the wild-born birds include hybrids between truly wild individuals and releasees or their progeny (Bacon et al. 2018); captive-bred released birds also contribute the majority of nests found (Bacon 2013). Such a high proportion of released captive-bred birds suggests a ‘put-and-take’ game management strategy (Goriup 1997) rather than genuine conservation reinforcement.

3.1. Population management strategy

One possible rationale for such extraordinarily high reinforcement levels as those outlined above is that the majority of birds are expected to die through post-release mortality, or to be hunted out (as a ‘put-and-take’ strategy would intend), but there is no published policy to place this practice in context. Under the Convention on the Conservation of Migratory Species of Wild Animals (CMS), a draft action plan for the Asian houbara (CMS 2005) proposed limiting offtake to a sustainable level informed by the best available knowledge of population dynamics. Captive-bred releases were to be permitted to increase or supplement houbara numbers for lawful sustainable falconry, but only if (a) following IUCN re-introduction guidelines, (b) subject to CMS approval and (c) with public reporting of strategies, captive-breeding inventories and results of releases. Current large-scale captive-bred releases and translocations operate with apparent autonomy, lacking such wider accountability, as part of a general strategy of replenishing and reinforcing wild populations

(IFHC 2011, 2017). Despite multiple decades of reinforcement, we are not aware of any published science to justify the numbers involved and no analysis of the contribution that captive breeding makes to African houbara population dynamics, although such assessments are necessary to determine the success of any conservation translocation strategy (Hardouin et al. 2015, Bacon et al. 2017).

3.2. Phylogeography

Analysis of mitochondrial DNA shows the two houbara species to be significantly differentiated (Idaghdour et al. 2004, Pitra et al. 2004, Korrida & Schweizer 2014), having diverged during the Lower Pleistocene (between 0.77 and 0.94 Mya: Korrida & Schweizer 2014). For African houbara, no phylogenetic structure was found across Tunisia, Morocco and Algeria (both mtDNA and microsatellite analysis: Lesobre et al. 2010, Korrida et al. 2012, Korrida & Schweizer 2014), consistent with long-distance female breeding dispersal (e.g. of 200 km); these have therefore been managed as a single population unit for reinforcement (Lesobre et al. 2010) (see Fig. 1). In contrast, Asian houbara populations are phylogenetically structured, with individuals from the Middle East (Jordan, Negev-Sinai) differentiated from migratory Central Asian populations (mtDNA analysis: Pitra et al. 2004, Korrida & Schweizer 2014) while resident populations in the south-eastern Arabian Peninsula (Yemen) are even more strongly differentiated from both the Middle East and Central Asian populations (microsatellite analysis: Riou et al. 2012). Moreover, further subtle differentiation exists within migratory Central Asian populations between West Kazakh birds and the remainder (Riou et al. 2012).

The apparent lack of genetic structure of most migratory Central Asian houbara populations is consistent with recent expansion (18-98 kya: Korrida & Schweizer 2014) during the last glacial period. However, a lack of structure in neutral genetic markers—as frequently found following post-glacial range expansion—can mask important differences in adaptive phenotypic traits that have diverged through selection (Fraser & Bernatchez 2001, Meyer-Lucht et al. 2016). The morphology of Asian houbara differs between resident southern and migrant Central Asian populations, among which weight then varies along a west–east cline, being lowest for the longest-distance migrants from easterly populations (Combreau & Al Baidhani 2013). Important aspects of their migration strategies are probably under genetic control (Burnside et al. 2017), with individuals showing unnatural migration behaviour when translocated into other populations (Burnside et al. 2020), consistent with the subtle phylogenetic and morphological differences between birds in western and eastern Kazakhstan (Riou et al. 2012, Combreau & Al Baidhani 2013). It is therefore disconcerting that current release strategies for Asian houbara appear to consider neither phylogenetic origin nor migratory population structure, as demonstrated by the following reports:

(a) non-migratory birds of contrasting Asian phylogenetic stock (Combreau et al. 2011a) released into the Arabian Peninsula (Islam et al. 2012, Azar et al. 2016);

(b) birds derived from (one or more) non-migratory populations released in eastern Pakistan, outside the natural breeding range of the species (Daily Times 2015), also noting that the release of non-migratory stock on wintering grounds in Pakistan cannot in any case compensate for the continued over-exploitation there of migratory populations from distant breeding regions including China;

(c) captive-bred 'resident' stock of unspecified and potentially mixed geographic origin released into the Central Asian flyway (IFHC 2011) (Fig. 1); and

(d) birds captive-bred in southern Kazakhstan in a facility originally established with accessions from central Kazakhstan (IFHC 2011) released into the western (Caspian) flyway (Combreau et al. 2011b), resulting in atypical occurrences of (ringed) captive-bred birds from this breeding facility far outside the usual wintering range, including

Azerbaijan (Xəbər 2020), the Gilan province of Iran (R. D. Sheldon *in litt.*) and Turkey (G. M. Kirwan *in litt.*).

3.3. Consequences of captive breeding reinforcement

Whether large-scale reinforcement potentially risks semi-domestication of wild houbara populations depends on the degree of modification in captivity, and the relative fitness on release, of captive-bred birds. Long-term captive-bred stock of African houbara shows genetic changes across multiple life-history traits (ejaculate size, male display rate and female egg production) due to unintended selection (Chargé et al. 2014a), despite genetic management that avoided inbreeding and maintained genetic diversity (Rabier et al. 2020). Genetic covariance among pre- and post-copulatory traits (Chargé et al. 2013) can accelerate these responses to unintended selection. Bustards, being hyper-vigilant and stress-prone, are also at particular risk of trauma injury and hence of selection for docility (Dolman et al. 2015), and this risk must be intensified by artificial insemination, making temperamental domestication adaptive. Captive-bred Asian houbara (in Saudi Arabia, of Pakistan stock) had 17 % lower resting metabolic rate and 28 % lower evaporative water loss than wild birds transported from Afghanistan (Tieleman et al. 2002), which may in turn reduce maximum oxygen consumption and thus predator responses (Nespolo et al. 2017). However, the full extent of genetic adaptation to domesticity remains unassessed.

Also uninvestigated are the consequences of houbara captive management for immune genetics and gut biomes. This omission is serious: until biosecurity protocols were fully developed, flocks were exposed to novel pathogens not commonly encountered in the wild, including Newcastle disease and chlamydiosis (Lacroix et al. 2003), while canary and fowl genotypes of poxvirus became endemic in African houbara breeding flocks in Morocco, and Asian houbara flocks in the Arabian Peninsula, respectively (Le Loc'h et al. 2016). Such novel pathogens can impose direct selection; this may be further amplified in African houbara, as immune-challenge reduces male courtship display and ejaculate quality, egg fertilization and embryo viability (Chargé et al. 2010) as well as chick survival (Chargé et al. 2011), thus potentially increasing selection differentials favouring atypical genotypes. Moreover, captive management has involved ‘genetic dumping’, whereby offspring from the most represented (and most closely related) breeders are preferentially released to reinforce wild populations (Chargé et al. 2014a); this promotes genetic diversity in the captive stock, but reduces it in reintroduced cohorts (Chargé et al. 2014b); again the consequences for free-living populations have not been assessed.

Hunters speaking off the record report that captive-bred African houbara in Morocco generally underperform as falcon quarry. Accumulating evidence from correspondence and social media posts in both Asia and the Middle East has shown released captive-bred Asian houbara exhibiting maladaptive levels of tameness, tolerating or even approaching humans, vehicles and buildings, although the relative strength of genetic domestication and behavioural acculturation cannot be gauged. Importantly, while wild young houbaras spend c.50 days with their mothers after hatching (PMD, RJB unpubl. data) and are assumed then to acquire a repertoire of vigilance and anti-predator behaviours that promote their post-independence survival (Combreau & Smith 1998), captive-bred birds cannot experience this vital parental relationship. Anti-predator training has been attempted with Asian houbara (van Heezik et al. 1999), but is clearly impracticable for large-scale releases.

Wild life-history traits and demographic parameters prior to releases in Morocco are unreported, and unbiased comparisons of captive-bred houbara to wild phenotypes are now problematic as ‘a substantial proportion of wild-born individuals may be offspring from translocated birds’ (Bacon et al. 2018). However, the evidence is unpromising. Annual survival rate of captive-bred African houbaras released into non-hunting areas was 67 %

(Hardouin et al. 2015), while that of wild-born birds from approximately 8 months (6 months post-independence) was broadly similar (females ≈ 48 % yr^{-1}; males ≈ 72 % yr^{-1}) (Hardouin et al. 2012). In Asian houbara such low adult annual survival rates would be insufficient to sustain a population (Dolman et al. 2018). Moreover, released captive-bred African houbara show contrasting patterns of condition-dependent dispersal compared to wild birds (Hardouin et al. 2014). Controlling for age-related effects, the former exhibit substantially lower nesting propensity, while those released in spring lay smaller eggs and have 40 % lower brood survival than wild-born birds; that these effects remain undiminished with age, indicates a persistent difference in breeding performance (Bacon et al. 2018). Preliminary demographic modelling indicates that the African houbara population in eastern Morocco is unviable and would decline without continued reinforcement, even in the absence of hunting, primarily due to low juvenile and subadult survival (Bacon 2017). Indeed, if this introgressed population is currently not self-sustaining without further reinforcement, it would no longer constitute a wild population (IUCN 2019).

Non-migratory Asian houbaras released from stock deriving from Balochistan, Pakistan, have bred in Saudi Arabia (Islam et al. 2012), but with apparently low success (Maloney 2003); long-term viability of these populations is unknown. Captive-bred non-migratory birds released in the United Arab Emirates (UAE) (of stock deriving from Iran, Pakistan and the Arabian Peninsula; Azar et al. 2016) also have low nesting probability (Azar et al. 2018), with a mean annual survival for the first year after release of 48 %, rising only to 54 % in subsequent years (Azar et al. 2016). For locally sourced captive-bred migratory Asian houbara released in Uzbekistan, post-release survival to the autumn is sufficient (56 %) to provide alternative quarry for hunters, and approaches that of wild-born juveniles (61 %) (Burnside et al. 2016, Dolman et al. 2018), but survival over their first migration is considerably lower than that of wild juveniles (23 % versus 37 %) (Dolman et al. 2018).

Moreover, first-winter captive-bred birds initiate migration later and winter farther north than wild juveniles (Burnside et al. 2017), the long-term consequences of which are unknown. Relative breeding productivity of surviving captive-bred releasees is also unknown, as low return rates have to date precluded measuring the productivity of older, experienced females (Dolman et al. 2018). The performance of other reinforced populations in Central Asia (including Navoi district in Uzbekistan, and different regions of Kazakhstan, see Fig. 1) are unreported.

For Asian houbara, levels of reinforcement are increasing through releases of captive-bred birds both translocated from the Arabian Peninsula and produced in facilities within Central Asia (Fig. 1), with further breeding centres planned (TACC 2021) and a declared ambition to release 35,000 birds a year into the flyway (Allinson 2014). Indeed, at current levels of unregulated offtake, the levels of reinforcement required to stabilise populations are, alarmingly, ≈1.5 times total wild numbers annually (Dolman et al. 2018). High mortality during first-winter migration may remove many less fit captive-bred individuals, but even so the small numbers that survive (Burnside et al. 2016) may then breed, resulting in introgression.

4. A WAY FORWARD FOR CAPTIVE BREEDING OF HOUBARA

The number of houbara breeding centres that have been built in the past 30 years is not easy to establish (we identify 19 in Fig. 1, of which 16 are currently active). The evidence reviewed above suggests that these programmes risk and might indeed be contributing to the declines in wild populations that they are intended, ultimately, to prevent. In the light of this concern, there are questions that dedicated research can and must answer in order to establish the scientific basis by which houbara hunting and any reinforcement strategy can become truly sustainable (IUCN 2000). The most fundamental of these concern the numbers, densities and trends in regional populations, the ecological and anthropogenic causes of variation in these values, the natural demographic rates in the absence of reinforcement, and the demographic consequences of any supplementations. For the Asian houbara captive-breeding schemes, information on important aspects of their genetic management should be made publicly available, particularly regarding: numbers of founders and their current representation in captive populations; long-term effective size of captive populations (which will be influenced by any loss of genetic diversity through historic bottlenecks and founder effects, inbreeding and genetic drift: Hare et al. 2011, Athrey et al. 2018); and the maintenance or merging of phylogeographic lines derived from diverse accessions. Such information is needed on, for example, (a) stock in the Arabian Peninsula derived from Pakistan, Kazakhstan, Iran and Afghanistan (IFHC 2013) managed as a captive-bred non-migratory 'resident population' used for releases (IFHC 2011); (b) the number and geographic origin of founders of a breeding flock of 5,270 Asian houbara transferred from Morocco to establish a breeding centre in UAE (IFHC 2012); and (c) whether accessions from separate flyways in western and central Kazakhstan are managed separately within Central Asia (IFHC 2017). Demographic and genetic profiling (including whole genome sequencing and genome-scale comparison) of wild populations, and of the captive populations derived from them, is essential in order to allow the closest possible alignment of the two. Such profiling is required to determine the extent of heritable domestication in captive populations (including immuno-competence and temperament), the relative importance of learning and genetics to predator awareness, and the extent of introgression into wild populations. Appropriate levels of reinforcement, the various impacts (ecological, behavioural, genetic) of released captive-bred birds on wild populations, the physiological and behavioural fitness of the two groups, and their relative productivity and survival all need measuring and modelling. While it is possible that such investigations have been undertaken, we are not aware that the resulting information has been made publicly available. Ultimately such information would contribute to the development of broader conservation programmes for the two species. For wild populations to remain wild, a package of measures is needed involving non-hunting areas and scientifically established quotas on numbers of birds both released and hunted (Dolman et al. 2021), along with media outreach campaigns to sensitize hunters to the unsustainability of the status quo. Existing houbara breeding and conservation programmes have mobilised considerable resources and overcome technical challenges to achieve remarkable volumes of production of birds for release. If such resources and expertise could be directed to a more holistic conservation programme for these species, it would be hugely beneficial both for the species and for the long-term future of sustainable hunting. Depending on the evidence, captive breeding might play a diminished or at least geographically restricted role, e.g. ‘put-and-take’ birds inside concessions, separated from networks of non-hunting areas where wild populations can recover without reinforcement. Elsewhere, we outline what would be required to achieve sustainable hunting and a long-term future for Arab falconry (Dolman et al. 2021). Such measures are the only reliable way in which the long tradition of Arab falconry and indeed the two species of houbara will themselves ultimately survive.

*Acknowledgements***.** RJB was funded by the Ahmed bin Zayed Charitable Foundation, Daniel Salliss drew Fig. 1, and AE Kessler, Stuart Butchart, Richard Grimmett and three anonymous reviewers provided very helpful comments on an earlier draft.

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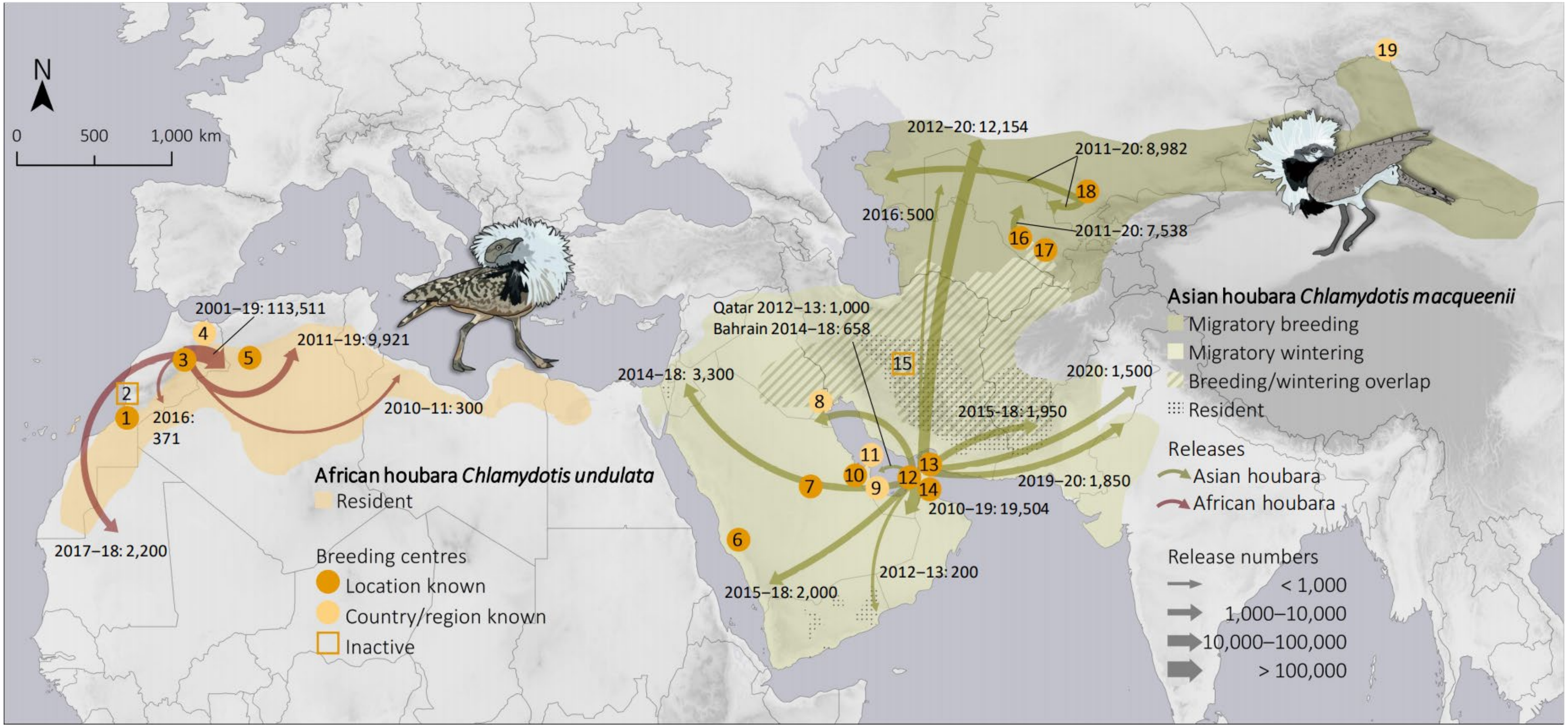

Fig. 1. Global distribution of two threatened bustard species (African houbara *Chlamydotis undulata* and Asian houbara *C. macqueenii*) showing the international network of captive breeding centres and (where known) the scale of translocation and releases. 1: International Foundation for Natural & Wildlife Preserves, Morocco; 2: International Foundation for the Conservation & Development of Wildlife, Morocco; 3: Emirates Centre for Wildlife Propagation, Morocco; 4: Errachidia Wildlife Breeding Centre, Morocco; 5: Emirates Bird Breeding Centre for Conservation, Algeria; 6: National

Wildlife Research Centre, Saudi Arabia; 7: King Abdulaziz City of Science & Technology, Saudi Arabia; 8: Kuwait Houbara Breeding Centre; 9: International Foundation for Ecological Research, Qatar; 10: The Rawdat Al Faras Houbara Breeding Centre, Qatar; 11: Centre for Breeding & Reproduction of Falcons & Houbara, Qatar; 12: National Avian Research Centre, UAE; 13: Sheikh Khalifa Houbara Breeding Centre, UAE; 14: Central Veterinary Research Laboratory, UAE; 15: planned centre, Iran; 16: Emirates Bird Breeding Centre for Conservation, Uzbekistan; 17: The Emirates Centre for Houbara Conservation, Uzbekistan; 18: Sheikh Khalifa Houbara Breeding Centre, Kazakhstan; 19: planned centre, Tuva, Russia.