Impacts of survival and reproductive success on long-term population viability of reintroduced great bustards

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Word count: 6,274

Reintroductions aim to re-establish species within their historical ranges through the release of wild- or captive-bred individuals following extirpation (or extinction) in the wild. While there is no general agreement on what constitutes a successful reintroduction, the probability of the population achieving long-term persistence should be addressed. Here, we review a 10-year trial reintroduction of the great bustard *Otis tarda*, a globally-threatened bird species, to the UK and assess long-term population viability. Despite changes in rearing and release strategy, initial post-release survival probability remained consistently low, with only 11.3% of bustards (n = 167) surviving from release to one year post-release. Nineteen breeding attempts were made by eight females; however, only one chick survived more than 100 days from hatching, and no wild juveniles have recruited into the population. Using demographic rates from the UK population and wild populations elsewhere and stochastic population modelling, we investigate the viability of this reintroduced population by predicting population size over the next ten years. Under current demographic rates the population was predicted to decline rapidly. Self-sufficiency was only predicted using the highest estimates from the UK population both for first-year and adult survival, and recruitment rates from wild populations elsewhere. Although changes have been made in rearing, release strategies, habitat management and release sites used, these changes appear to have modest impact on long-term viability. Substantial improvements in survival rates and productivity are required in order to establish a viable great bustard population in the UK, and we consider this unlikely.

Keywords: monitoring, conservation, habitat management, captive rearing, release strategy

Introduction

Reintroduction projects attempt to re-establish species within their historical ranges through the release of wild- or captive-bred individuals following extirpation or extinction in the wild (IUCN 1998; Ewen et al. 2012). They have become an important tool in conservation management; however, many reintroduced populations fail to establish, and it is often unclear whether these failures were due to *ad hoc* methodologies and management, or simply the limited success of released individuals (Wolf et al. 1996; Fischer and Lindenmayer 2000). The poor success of reintroductions worldwide has resulted in a drive towards the identification of rigorous research and monitoring targets identified *a priori* and the use of adaptive management to overcome uncertainty in the choice between different conservation management actions (Armstrong and Seddon 2008; Schaub et al. 2009; Ewen et al. 2012).

While there is no general agreement on what constitutes a successful reintroduction (Seddon 1999), reintroductions typically aim to establish a free-living, self-sustaining population through three main objectives: 1) survival of individuals after release; 2) settlement of individuals into the release area; and 3) successful reproduction and recruitment into the population (Griffith et al. 1989; Sarrazin and Barbault 1996; Teixeira et al. 2007). A key question that needs to be addressed by reintroduction projects is whether the population can achieve long-term persistence (Armstrong and Seddon 2008), where recruitment from breeding individuals compensates (or exceeds) adult death rate (Sarrazin and Barbault 1996). In the initial stages of a reintroduction there is much uncertainty concerning demographic rates and the suitability of habitat for supporting the reintroduced population, and population modelling typically focuses on predicting population growth and aims to highlight limiting factors (Armstrong and Reynolds 2012). Once reintroduced individuals survive the establishment phase and data on demographic rates from monitoring are more readily available, population modelling can be used to explore the effect of different management decisions and estimate how many more releases are required to ensure long-term viability of the population (Oro et al. 2008; Schaub et al. 2009; Armstrong and Reynolds 2012).

Here we assess the long-term persistence of a reintroduced population of great bustard *Otis tarda*, a globally-threatened bird species, in the UK. The great bustard was a common breeding bird across large parts of Europe and Asia during the 18th Century, and through a combination of hunting, egg collection and changes in agricultural practice, experienced dramatic declines and local extinctions across its range during the 20th Century (Palacín and Alonso 2008). It is currently categorised as Vulnerable on the IUCN Red List (IUCN 2014). Great bustards became extinct in the UK in the 1830s; attempts to rear this species for reintroduction began in the 1970s and following a rigorous feasibility study based on IUCN reintroduction guidelines, a 10-year trial reintroduction programme was initiated in 2004. The first five years of the reintroduction trial demonstrated that great bustards can be hatched in captivity from wild-collected eggs and that juveniles can be translocated from Russia and successfully released into the wild in the UK (Burnside et al. 2012). Although some released birds reached maturity, a major limitation on project success was the high mortality of juveniles in the first six months following release (Burnside et al. 2012).

Here we present results from the ten-year trial reintroduction of great bustards to the UK, and investigate the long-term viability of the reintroduced population. We have three objectives: 1) to determine survival rates from release to one year post-release and test whether different rearing or release strategies adopted during the project improved survival rates; 2) to calculate adult survival rates over the project period; and 3) to use these age-specific survival rates and data on the recruitment of individuals from breeding over the reintroduction period to investigate the long-term viability of the population. Using several population scenarios, incorporating current demographic rates and also demographic rates from wild populations elsewhere, we aim to provide evidence-based information on potential future population size and persistence to help inform management decisions.

Methods

Release methodology

Between 2004 and 2012 chicks or eggs were imported from Russia and in 2014 eggs were imported from Spain (Table 1); all were reared in a purpose-built facility (for details see Burnside et al. (2012)). The number of eggs collected varied between years, ultimately influencing the number of eggs and chicks imported and released (Table 1). Whereas Russian chicks had been imported at 4 – 10 weeks of age in the first eight years of the reintroduction (Burnside et al. 2012), in the ninth year, 6 eggs were imported and reared in the UK, together with 9 chicks reared in Russia similar to previous years. Following a change in the regulations on exporting great bustard chicks from Russia in 2013, neither eggs nor chicks were imported or released in that year. In 2014 54 eggs and 2 chicks were imported from Spain (Table 1). Hatching success of artificially incubated eggs from 2004 - 2014 was 70.9% ± 5.7% (mean ± SE). Between 2004 and 2008, the total number of bustards released was 86, and despite problems with import regulations, an additional 114 bustards were released between 2009 and 2014.

All released individuals from 2004 – 2010 were released at the first release site (Site A) which was set up in 2004, with a second site (Site B) being set up in 2011; in 2011, the release cohort was split between the two sites (16 juveniles released at site A and 13 at site B). In 2012, we released 6 juveniles at site B, and five juveniles hatched from eggs and reared in the UK were released at site A. In 2014, we set up a third release site (site C) and the release cohort was split between site B and site C (17 juveniles at site B and 16 at site C). From 2004 – 2008 juveniles were released from a 30-day bio-secure quarantine unit into a 7ha open-topped release pen, from which they were free to leave (they were termed ‘hard release’). From 2009 the first trials of ‘soft release’ began, where individuals were held for c. 7 days after quarantine in a mesh pen within the larger release pen prior to release where they could habituate to their new environment. This release methodology was used in 2009 – 2011; in 2012 and 2014 this approach was combined with an extended period of rearing with dehumanisation suits; individuals were led into the release pen on a regular basis, allowing them to stretch, practice flying and develop foraging skills (termed ‘soft release with dehumanisation suits’).

Following monitoring methodology described in Burnside et al. (2012), we monitored released individuals regularly all year-round and intensively during the breeding season (March – June) and the first six months post-release around release areas. Furthermore, we followed up re-sightings from website and telephone reports and where individuals were recovered dead, post-mortems were performed by a vet. This review covers the period from 30 April 2004, when the first eggs were collected, to 30 November 2014, four months after the 2014 cohort of birds was released and by which time the oldest surviving bustard released was 10 years and 5 months old.

Released birds were individually marked with wing-tags from 2004 – 2011 (colour-coded according to the year of release), then BTO metal leg-rings and Darvic plastic colour-rings in 2012 and 2014. Microwave Telemetry Inc. (Columbia, USA) Argos/GPS enabled LC4 Platform Transmitter Terminals (PTTs) were fitted to 19 males (105g device) and 15 females (40g device) from 2007-2011 to provide daily information on location, which could be remotely accessed. In addition, BioTrack radio transmitters (Wareham, UK) were also fitted using a variety of different mount types: back-mounted (10 males and 10 females in 2004), necklace-mounted (17 females in 2005, 2006 and 2011) and tail-mounted (24 males and 14 females from 2005 – 2010).

Estimating reproductive and survival parameters

We investigated survival probabilities for first-years and adults by creating live re-sighting and dead recovery histories for 167 released birds from 2004 – 2012; we did not include individuals released in 2014 as they had only been released for four months at the time of writing the manuscript. Only juvenile bustards that were released and able to form part of the wild population were included in the analysis; individuals that became disabled during captive-rearing (e.g. damaged wings) and released into the project release pen were excluded as they were unable to leave the pen and therefore remained captive. Date of marking was considered to be the day of the bird's release and annual intervals set from the date of each individual's release for a maximum of 10 years. Release dates varied between years and ranged from 26th August to 17th October; one bird from 2011 and five from 2012 over-wintered in the main release pen and they were able to join the wild population outside the release pen from March onwards in the following year. For these latter birds the date where they were considered to be free-flying was taken as their release date.

First, we investigated the role of sex and different release methodologies on survival from release to 1 year post-release using Burnham live re-sighting and dead recovery data using MARK (v. 7.1) via the R package RMark (v 2.1.7) in R (v 3.0.2). Models were specified with survival probability dependent on sex, release year, release month (January, June, July, August, September, or October), release site (site A or B), release methodology (hard release, soft release, over-winter in release pen, or soft release with dehumanisation suits), and transmitter type fitted (satellite (PTT), tail-mounted (TMRT), necklace-mounted (NMRT), back-mounted radio transmitters (BMRT) or no transmitter). As re-sighting and recovery probability was likely to be dependent on whether an individual was fitted with a transmitter or not, and also whether the data from this transmitter were remotely accessible, we specified models with re-sighting and recovery probabilities to be dependent on transmitter type, sex (as females are much smaller and less conspicuous as males), both of these factors, or constant re-sighting and recovery probabilities. Second, following Doherty *et al.* (2010), we created all combinations of models, giving a candidate set of 56 models, and ranked models using corrected Akaike's Information Criterion (AICc; Burnham and Anderson 1998).

Only 17 free-ranging individuals out of 167 survived from release to one year post-release, and as their release times were staggered over eight years, individuals provided different amounts of data depending on their release year. Adults generally returned to their release area every spring and were re-sighted throughout the year typically at least once a month, but the longest period between re-sightings was 197 days. Therefore, we made the assumption that if an individual was not re-sighted within a year, then it was dead. We calculated age-specific annual survival (e.g. survival from 1 – 2 years post-release) for all ages as $Sa_{t+1} = N_{t+1} - N_t$, then averaged these vales to give mean annual adult survival ($\overline{Sa}$).

Population modelling

Based on Burnside at al. (2012), we developed new models using the demographic parameters from 2004 – 2012 to investigate population growth and persistence for the next ten years. To estimate the size of the founder population at time *t* (N_t), we used the deterministic model

$$N_{t+1} = N_t\overline{Sa} + I \times S_{post} + \frac{N_t}{2} \times r$$

where $\overline{Sa}$ is mean annual adult survival, I is number of individuals released, S_{post} is first-year survival, and r is recruitment into the population from breeding (survival of chicks from hatching to 1 year old). Sex ratio in wild populations elsewhere is variable (Oparin et al. 2003; Martín et al. 2007); in the UK population sex ratio is relatively equal, therefore we have assumed an equal sex ratio in the analysis. We modelled 10 scenarios (Table 4). First, we simulated population size over ten years if the reintroduction were to continue releasing 20 or 40 juveniles annually with the current demographic rates from the UK population (1 and 2, respectively). Second, to explore the conditions required to become self-sufficient without further releases, we modelled eight further scenarios: using recruitment rate (r = 0) from the UK population and either 3) average UK annual adult survival – the scenario most closely reflecting population dynamics if the reintroduction project is halted in 2015; or 4) high UK annual adult survival (upper 95% confidence limit (CI) of calculated $\overline{Sa}$); 5) recruitment rates from a wild great bustard population (r = 0.14 ± 0.09) from Morales, Alonso and Alonso (2002) with average UK adult survival rates; and 6) recruitment rates from a wild great bustard population (r = 0.14 ± 0.09) from Morales, Alonso and Alonso (2002) with high UK annual adult survival (upper 95% confidence limit of calculated $\overline{Sa}$. In models 3 – 6, we assigned average S_{post} to 33 individuals released in 2014; in addition, we created a third set of models with high S_{post} (upper 95% confidence limit of calculated S_{post}) for this 2014 cohort and Sa and r parameter value combinations as models 7 – 10.

Demographic stochasticity in average Sa, S_{post} and r was incorporated by creating 10,000 iterations of each model scenario, with each iteration and time period randomly sampling Sa, S_{post} and r values from distributions of 1,000 values each, generated using the mean and one standard deviation of estimates, and averaging across iterations to give estimated population size.

Results

Survival and causes of mortality

Survival probability from release to one year post-release was 11.3% (CI: 7.2 – 17.2%). Models investigating first-year survival showed that transmitter type was the most important factor affecting survival probability (Model 1, Table 2); however, the second most parsimonious model showed that survival was not related to any of the explanatory factors specified (Model 2, Table 2) and given that ΔAICc < 2 between these two models, we consider them to both to receive substantial empirical support. Model-averaged estimates showed that individuals fitted with back-mounted radio transmitters survived less well than individuals fitted with other types of transmitter (BMRT = 5.6% ± 5.9%; NMRT = 21.1% ± 12.6%; PTT = 12.5% ± 4.9%; TMRT = 9.5% ± 4.6%) or no transmitter fitted (11.1% ± 4.6%); however, these transmitters were fitted to bustards released in 2004 and as issues were identified in the harness design used, these results reflect initial problems in release methodology. When data from 2004 was excluded from the analysis, the most parsimonious model showed that survival was constant (AICc = 260.1). In subsequent years a different harness design was used for attaching back-mounted PTTs and these were also fitted by a more experienced researcher.

Model ranking showed that first-year survival probability did not differ between the sexes, between release methodologies, years, release sites or month of release (Table 2). Re-sighting probability in the best supported models was constant, whereas recovery probability was dependent on transmitter type (Table 2), with individuals fitted with satellite transmitters (100%) and back-mounted radio transmitters (80.0% ± 8.9%) more likely to be recovered than individuals fitted with tail-mounted (65.5% ± 7.2%) and necklace-mounted radio transmitters (36.3% ± 12.2%) and birds not fitted with a transmitter (45.8% ± 7.2%). After the first year, annual survival rate increased to 88.4% (± 5.19%: CI: 81.2 – 95.6%; n = 17).

Of 167 individuals released between 2004 and 2012, 5.4% have been re-sighted alive in November 2014, 65.3% were recovered dead and 29.3% have not been recovered nor re-sighted alive in the last year. The main probable cause of death for those individuals recovered was predation (45.0%), followed by collision with fences or power lines (28.4%), with a small proportion being related to other causes such as illness or conspecific attack (4.6%). In 22.0% of cases the cause of death was not known.

As of 30th November 2014, the reintroduced great bustard population consisted of 5 females and 4 males older than one year old. The adults range in age; up to 10 years old for females and up to 7 years old for males. Of the 33 juveniles released in 2014, three have been recovered dead. However, similar to Russian-originated juveniles released in previous years, these Spanish-originated juveniles also started to disperse away from their release sites at the end of October; no juveniles were recorded at release sites at the end of November. In the final two weeks of November 2014, ten juveniles were recorded; seven of these were in the Salisbury Plain area in groups of three and four juveniles, and three females were reported on the south coast and Channel Islands, mirroring the movement of previous Russian-originated cohorts.

Reproductive success and recruitment

From 2007, the year of the first nesting attempt, there has been at least one breeding attempt every year (Table 3). In wild populations, males usually breed from 5-6 years of age and females from two years of age (Morales & Martín 2003). In total 8 breeding females have been recorded during the reintroduction programme, with females breeding from two years old for up to five consecutive years. However, only 1 of 19 breeding attempts has produced a chick that has been re-sighted at more than 100 days after hatching, and no wild-reared chicks have recruited into the population (Table 3). Of the 19 breeding attempts 57.9% failed during incubation, due to egg infertility (27.3% of failures during incubation), egg predation (36.4%) and nest desertion (18.2%); 18.2% failed from unknown causes. During chick-rearing (n = 8 breeding attempts), 25% of all known losses were attributed to predation; 75% of these chicks failed from unknown causes.

In 57.9% of breeding attempts, females chose to nest within predator-exclusion fenced release areas. There was no apparent benefit to hatching success within fenced areas compared to outside (proportion of fertile nests hatched chicks ± 1SE: within: 0.62 ± 0.18, n = 16; Wilcoxon rank sum test: W = 40, p = 0.4). However, of the eight nests successfully hatching chicks, there was some indication that chicks from nests within fenced areas tended to live longer than chicks from nests outside (mean age of chick at failure ± 1SE: Within: 50.6 ± 23.9 days (n = 5); Outside: 18.7 ± 4.2 days (n = 3)), though this was not statistically significant (Wilcoxon rank sum test: W = 9; p = 0.8).

Population modelling

Population simulations suggest that with releases of 20 or 40 juveniles annually for the next ten years and with the current demographic rates, the population size would be less than 30 individuals (scenarios 1 & 2: Table 4; Figure 1a). If no further juveniles are released, with current demographic rates the population is predicted to decline to less than 4 individuals within 10 years (scenario 3; Table 4, Figure 1b). Decline occurs even using recruitment rates observed in wild populations since the high adult mortality of reintroduced birds would not be fully compensated by recruitment rates seen in wild breeding populations (scenario 5; Table 4, Figure 1b). Using high UK first-year survival or high UK adult survival and no recruitment from breeding (4, 7 and 8), the population declines more slowly (Table 4; Figure 1b). Only under the conditions of high survival rates across all ages and recruitment from released individuals equivalent to breeding individuals in wild populations was the current population predicted to increase in size without further import of eggs or juveniles (scenario 10; Table 4, Figure 1b).

Discussion

In the ten-year trial reintroduction of the great bustard to the UK, the project has achieved some key reintroduction targets including the hatching of eggs in captivity, the rearing and release of juveniles, lekking behaviour and breeding attempts of adults, and the long-term survival of some birds in the wild. However, despite some initial target criteria being met and refinements made in the pre-release rearing and release strategy, post-release survival has remained low and no wild-reared chicks have survived to recruit into the population. The initial feasibility study suggested that a viable population may only be achieved after ten releases of a minimum of 40 individuals (Osborne 2002); however, this target has not been met. The adult population size after ten years of trial releases is nine individuals and the current demographic rates are insufficient for population viability even with the release of further juveniles. We show that only under the very unlikely conditions of high first-year survival, high adult survival and recruitment equivalent to wild populations elsewhere will this population increase in size without further imports of eggs or chicks. However, in this scenario and others with high adult annual survival we used the upper confidence limit of the reintroduced population estimates (95.6%), whereas in wild well-studied populations elsewhere annual adult survival is estimated to be approximately 89.7% annually (J.C. Alonso et al, in Lane & Alonso (2001)). Furthermore, unpublished survival values obtained by J.C. Alonso and co-workers with a larger sample from various wild populations in Spain are even lower than these and previously published values (J.C. Alonso pers. com.), suggesting that our estimates are overly optimistic. Currently the outcome of 2014's release is unknown; however, even with substantial improvement in post-release survival of released individuals, unless there are also significant improvements in adult survival and recruitment rates, the population is unlikely to achieve long-term persistence.

We found that first-year survival rates were lower in individuals fitted with back-mounted transmitters than individuals fitted with other transmitter types or no transmitter. However, this relationship was largely due to inappropriate mounting methods used in the first year of release (2004). Devices were fitted with straps were passed over the front of the bird and elastic braided along the length, which is likely to have significantly reduced elasticity. Many of these individuals were harmed or fatally injured as a result of collisions (44%) and it was considered that the strapping material may have restricted movement; therefore, in subsequent years, back-mounted devices were fitted using a wide elastic band with appropriate tension by more experienced individuals (Alonso 2008). There are many studies showing the negative effects of transmitter attachment on energy expenditure, reproduction and survival (Barron, Brawn, and Weatherhead 2010); however, in general (excluding the 2004 released birds) we did not find that individuals without a transmitter had a higher first-year survival rate compared to those with transmitters. We do not rule out that transmitter attachments may have a negative effect on the survival and behaviour of released birds, but suggest that a combination of behavioural and release condition factors played a greater role in mortality. Also, individuals fitted with satellite transmitters were more likely to be recovered dead than those fitted with radio-transmitters or not fitted with transmitters. Given that many individuals over the last ten years have dispersed away from their release sites, monitoring devices, in particular satellite transmitters, have played a key role in allowing us to monitor individuals. For many released individuals not fitted with transmitters, once they leave the release area we have relied heavily on re-sightings reported by the general public, which are often of only a small number of individuals each year. Therefore, many individuals are not re-sighted again after they left the release area, resulting in loss of information from a significant proportion of released individuals on survival, dispersal and cause of death, which is essential for any reintroduction project.

Great bustard juveniles remain with their mother for at least the first six months after hatching in the wild (Alonso et al. 1998; Martín et al. 2008). In long-lived species with extended periods of parental care, maternally-learned skills (e.g. learning to recognise prey and predators, using habitat or responding to changes in environment, appropriate interactions with conspecifics etc.) are likely to be essential for survival and reproduction (Bennett and Laland 2005). For example, captive-rearing has been shown in other species to produce individuals lacking in appropriate anti-predation behaviour (Griffin, Blumstein, and Evans 2000), and individuals experienced with predators show greater survival than those without experience or experience only with model predators (Heezik, Seddon, and Maloney 1999; Frair et al. 2007). Although informal predator training was trialled with model foxes in 2010 and with dogs in 2012 during this project, it is difficult to quantify the effects, if any, of this training as it was not carried out in a standardised manner. However, released juveniles associating with older individuals, either single females or small female or mixed groups, shortly after release or in the spring following release have generally been more long-lived than those dispersing individually or associating more closely with other released juveniles; therefore social learning from older individuals is likely to be critical to improving post-release survival. In wild populations in Spain, male chicks that were better fed by their mothers were more readily integrated into adult male groups (Alonso et al. 1998). However, in the UK population it is unclear what determines whether a juvenile will be accepted into an adult group, or whether some juveniles simply choose to remain with the other juveniles, but the ratio of juveniles accepted to adults within the group is generally around 1 – 2 juveniles per adult. Therefore, with low numbers of adults surviving, it is very unlikely that large numbers of released juveniles in the future will benefit from social learning.

Collisions are a major cause of mortality in wild bustard populations (Janss 2000; Martin and Shaw 2010); however, captive-reared individuals may be particularly vulnerable due to differences in musculature, feather condition, and flight performance (Robertson, Wise, and Blake 1993; Liukkonen-Anttila, Saartoala, and Hissa 2000; Hess et al. 2005). Take-off ability may affect success in escaping predators, and this may differ between individuals depending on their energy resources and body condition (Putaala et al. 1997). Biometric information has been collected from individuals at release each year; however, following concerns over the impact of pre-release condition on post-release survival we began collecting systematic data on flight feather condition at release from 2011. It is likely that feather condition played a significant role in mortality from predation and collision (Ashbrook, pers. comm.). Importing juveniles from Russia to the UK may have affected the condition of birds due to a combination of a 48-hour journey in crates, a 30-day quarantine period with restrictive facilities prohibiting practice flights and an unnatural diet, together with the stress of regular human disturbance and handling. In 2012, eggs were imported, limiting the quarantine period to the first weeks following hatching, and the use of dehumanisation suits and larger pen areas enabled the chicks to be exercised and allowed them to feed in specially managed habitat. Unfortunately, problems with feather condition, likely due to a diet containing too little protein and possibly vitamin D deficiencies, meant that these chicks were held back and released the following spring. However, given greater freedom for juveniles to exercise flight musculature and forage naturally, and also reductions in handling, the project team considered importing eggs to be an improvement over importing chicks.

Poor survival of individuals from release to one year post-release was highlighted as a major factor limiting success in the first years of the project, with predation and collision being the major causes of mortality (Burnside et al. 2012). Attempts were made to address predation risk by establishing new release sites which were considered to have lower or controllable predator populations. As released individuals frequently dispersed away from release sites, showing similar behaviour to individuals from their source population (Watzke 2007), the rearing programme was extended beyond release with dehumanisation suits in an attempt to improve group cohesion around release sites and assist with the learning of foraging activities. In addition, supplemental food was provided at release sites in an attempt to reduce dispersal (Williams et al. 2013), assisting establishment. However, none of these changes in later years of the project were found to significantly improve post-release survival, with individuals continuing to disperse away from release sites in their first winter. In 2014, attempts were made to reduce dispersal behaviour by collecting eggs from populations in Spain, where individuals do not tend to disperse as far as individuals from Russian populations (Martín et al. 2008; Palacín et al. 2011); however, as of the end of November 2014, no individuals from this cohort remain at release sites and at least four of these individuals have been re-sighted on the south coast and on the Channel Islands, near to locations of re-sightings from previous years. The evolution of dispersal in animal populations has been associated with changes in environmental conditions, with greater seasonality tending to result in increased dispersal behaviour (Johnson and Gaines 1990). Given that individuals released from both Russian and Spanish populations have dispersed south in autumn, it is possible that these dispersal movements are in response to unfavourable winter conditions such as low temperature and high rainfall, which may negatively impact on energy expenditure, and poor food availability, for example through winter senescence in many plant species. If this is the case, and further released individuals disperse away from the release area, it will limit the reintroduction project’s ability to improve post-release survival rates and achieve population viability; however, at this time the effect of the change in donor population on post-release survival is unknown.

Although surviving individuals have made breeding attempts in all years from 2007, no chicks have been recruited into the population due to failures during incubation and chick-rearing, and in one case, during the first winter. In two cases, females were also predated during chick-rearing, highlighting the vulnerability of breeding females and the importance of protecting them during this period. Given our small dataset on reproductive rates it is difficult to draw solid conclusions on future management to improve reproductive output, but we did find some indication that chicks from nests within fenced areas survived slightly longer than chicks from nests outside fenced areas, probably due to reduced predation pressure and creation of suitable nesting habitat. However, temporarily fencing areas to provide protection from mammalian predators involves human disturbance around the nesting area, for example, regular changes in power supplies (for an electric fence), which may increase the likelihood of nest desertion. Improving reproductive rates is one of the largest obstacles to the success of the reintroduction project and needs further investigation into the causes of nest failure during incubation, careful consideration of fencing nests found outside specially fenced areas and further investment in nesting habitat creation through agri-environment schemes or land acquisition, including large permanently fenced areas. Furthermore, a detailed assessment of whether invertebrate populations in southern England are sufficient to support the required level of productivity in great bustards is required. Adult survival may increase naturally if wild-born juveniles are recruited into the population, as such birds are likely to benefit from maternally-learned skills, and if larger group sizes develop.

Reintroduction programs should always include a significant monitoring component (Seddon et al. 2007; Ewen et al. 2012); without monitoring the results or failure of the project may not be clear. In addition, reintroductions should regularly evaluate the progress towards specific targets (Armstrong & Seddon 2008). Here, we assessed project results annually and performed larger reviews every five years; however, recommendations from these reviews were not always acted upon by conservation practitioners, possibly limiting the success of the project. Launching or continuing a reintroduction of a long-lived species with a complex biology needs. additional scrutiny, as reintroducing these species may be more prone to failures than r-selected species. Nonetheless, reintroductions can generate a wealth of data that can reveal much about underlying ecology, behaviour and life history, so that they will input into future conservation programmes. This monitoring work presented here was undertaken as part of a LIFE-funded project which came to an end in 2014. It can be used to help inform future decision making by those seeking to take the project forward in 2015 and beyond, though as the authors are no longer directly involved we are unable to comment further on future plans.

The great bustard has declined across large parts of its world range and recent intensive conservation efforts have managed to achieve population increases in only very small parts of that range. It is a long-lived species with complex social behaviour that finds it hard to survive in a human-dominated agricultural landscape, meaning that a reintroduction to southern England was always going to be an ambitious project. Over ten years of the trial reintroduction some significant milestones have been achieved and the rearing and release methodologies have been improved and refined. Despite this progress, current demographic rates remain too low for establishment and long-term persistence of a wild population. At the end of the ten year trial period it is clear that without substantial improvements in key demographic parameters, the successful re-establishment of this species in southern England is unlikely.

Acknowledgments

The Great Bustard Reintroduction was started by the Great Bustard Group in 2004 and the University of Bath joined the project in 2005. The LIFE+ partnership of the Great Bustard Group, Royal Society for the Protection of Birds, University of Bath and Natural England was established in 2010, ending in 2014. We thank Leigh Lock for his guidance on the project and for comments on the manuscript. We thank Leigh Lock for his input and management of the project and also for his comments on drafts of the manuscript. We thank the Great Bustard Group for their efforts in importing, rearing and releasing individuals for the reintroduction project and wish them every success in the future. We thank Paul Goriup for his helpful comments and suggestions on drafts. We gratefully acknowledge Dr Anatoli Khrustov, Director of the A.N. Severtsov Institute of Evolution and Ecological Problems (Saratov

Branch), Russian National Academy of Science for his role in making the reintroduction possible. We thank the project staff, volunteers and general public for collecting data on Great Bustards in southern England. We thank Professor Juan Carlos Alonso and an anonymous reviewer for their valuable comments on a previous version of this work. This work was funded by LIFE+ consortium grant LIFE09/NAT/UK/000020.

Biographical sketches

Kate Ashbrook is interested in biodiversity conservation and specialises in using modelling to inform evidence-based conservation management. Andrew Taylor and Louise Jane worked for the RSPB on monitoring and designing agri-environment schemes for bird populations across the UK and were part of the reintroduction project from 2011 - 2014. Ian Carter has worked as an ornithologist with Natural England (and predecessors) for over 20 years and has a particular interest in bird reintroductions.

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Table 1. The number of eggs collected, hatched and transported from source population and released in the UK great bustard reintroduction trial from 2004 to 2014. In 2012, 6 eggs and 9 chicks were imported from Russia (Ru); in 2014 54 eggs and 2 chicks were imported from Spain (Sp).

	2004 – 2008	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**Total**
Source population	Ru	Ru	Ru	Ru	Ru	-	Sp	
Number of eggs collected	232	48	46	60	42	0	56	484
Number of eggs hatched	154	38	32	49	35	0	44	352
Number of chicks transported to the UK	102	26	25	35	9	0	2	199
Number of juveniles released in the UK	86	18	23	29	11	0	33	200

Table 2. Summary of model selection from first-year survival models for great bustards in the UK reintroduction trial. Survival probability (S_i) was specified as dependent on year of release, release site, release methodology (method), month of release (month), sex, transmitter type fitted (attachment) or constant (.). The probability of re-sighting a live individual (p_i) and recovering a dead individual (r_i) was specified as dependent on transmitter type (mark), sex, an interaction between attachment type and sex (mark × sex) or as constant (.). The probability that individuals remained in the sampling area (F_i) was held constant.

	Model	**df**	**AICc**	**ΔAICc**	**Weight**
1	S(attachment); p(.); r(attachment); F(.)	12	296.63	0.00	0.44
2	S(.); p(.); r(attachment); F(.)	8	297.85	1.22	0.24
3	S(site); p(.); r(attachment); F(.)	9	300.07	3.44	0.08
4	S(sex); p(.); r(attachment); F(.)	10	300.32	3.69	0.07
5	S(method); p(.); r(attachment); F(.)	11	300.64	4.01	0.06
6	S(attachment); p(sex); r(attachment); F(.)	14	301.30	4.67	0.04
7	S(.); p(sex); r(attachment); F(.)	10	302.31	5.68	0.03
8	S(site); p(sex); r(attachment); F(.)	11	304.57	7.94	0.01
9	S(sex); p(sex); r(attachment); F(.)	12	304.87	8.24	0.01
10	S(method); p(sex); r(attachment); F(.)	13	305.25	8.62	0.01

Table 3. Reproductive success of great bustards released in the UK.

	2004 - 2008	2009	2010	2011	2012	2013	2014	Total
Number of nesting attempts	2	2	4	2	2	2	5	19
Number of nests hatched	0	2	2	2	0	0	2	8
Number of chicks re-sighted at >100 days old	0	1	0	0	0	0	0	1
Number of chicks recruited into population	0	0	0	0	0	0	0	0

Table 4. Demographic parameters used in population simulations and estimated population size after ten years (N_{t10}). Parameters shown are the numbers of imported chicks released (I), survival probability from release to first year post-release (S_{post}; n = 167), annual adult survival (Sa; n = 17), and recruitment of individuals into the population from breeding of released individuals (r). Errors shown are ±1 standard errors. Asterisks denote parameters from wild populations from Morales, Alonso and Alonso (2002) and crosses denote parameters from the reintroduced UK population.

	Scenario	$\boldsymbol{I}$	$\boldsymbol{S_{post}}$	$\boldsymbol{Sa}$	$\boldsymbol{r}$	$\boldsymbol{N_{t10}}$
1	Reintroduction continued	20	11.3% ± 0.025†	88.4% ± 0.052†	0†	16.9 ± 0.02
2		40	11.3% ± 0.025†	88.4% ± 0.052†	0†	29.9 ± 0.03
3	Reintroduction abandoned (average S_{post})	0	11.3% ± 0.025†	88.4% ± 0.052†	0†	3.9 ± 0.007
4		0	11.3% ± 0.025†	95.6%†	0†	8.2 ± 0.006
5		0	11.3% ± 0.025†	88.4% ± 0.052†	0.14 ± 0.09*	3.9 ± .007
6		0	11.3% ± 0.025†	95.6%†	0.14 ± 0.09*	8.8 ± 0.02
7	Reintroduction abandoned (high S_{post})	0	17.5%†	88.4% ± 0.052†	0†	4.6 ± 0.009
8		0	17.5%†	95.6%†	0†	9.6 ± 0
9		0	17.5%†	88.4% ± 0.052†	0.14 ± 0.09*	10.3 ± 0.02
10		0	17.5%†	95.6%†	0.14 ± 0.09*	20.4 ± 0.02

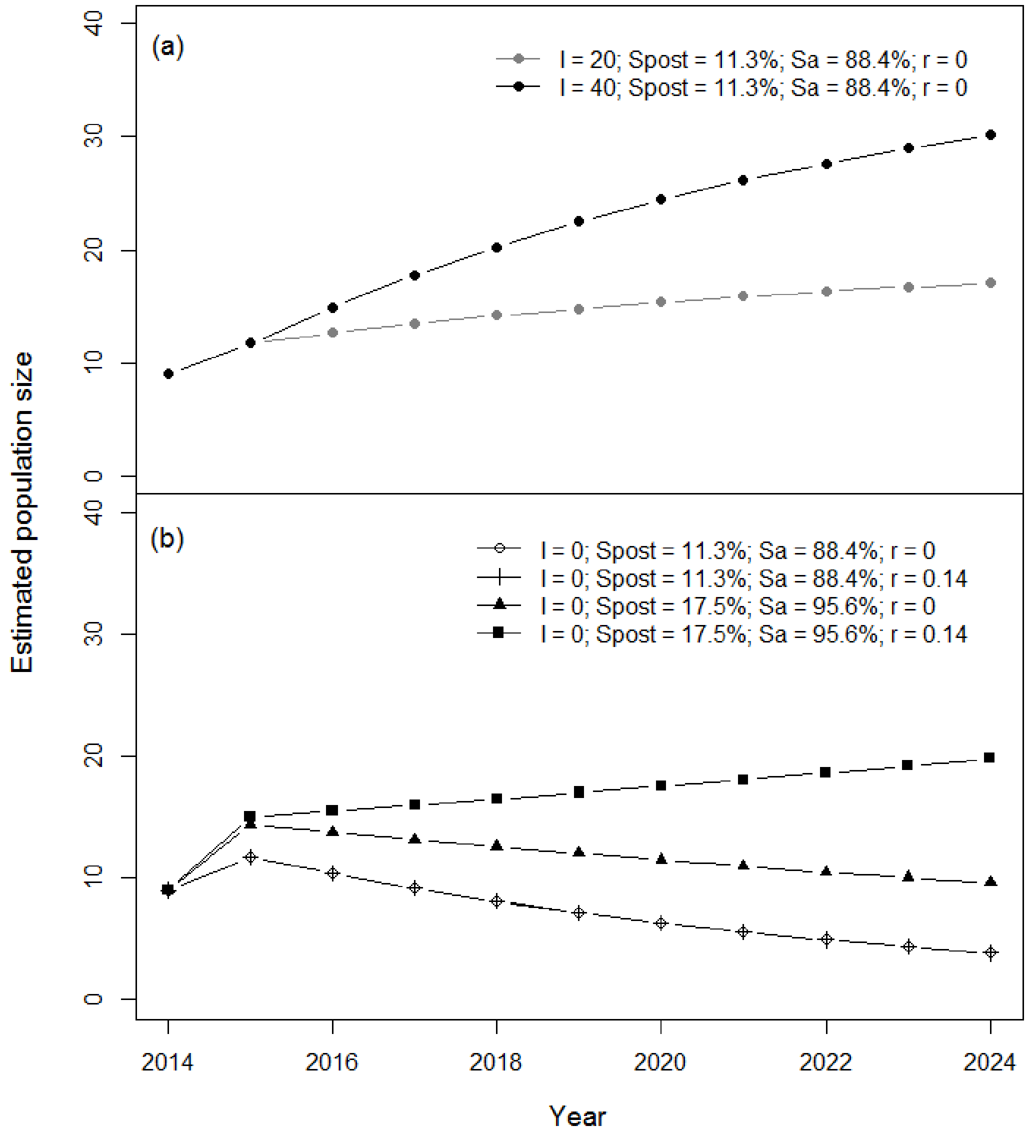

Figure 1. Estimated great bustard population size from 2014 – 2024 under different survival and recruitment scenarios (see table 4 for parameter values). Panel (a) shows population size where the reintroduction is continued and 20 (in grey) or 40 chicks (black) are released annually. Panel (b) shows population size if no further chicks are released with average post-release survival with (circles) and without recruitment (crosses) and with high post-release survival with (squares) and without (triangles) recruitment.