The UK great bustard *Otis tarda* reintroduction trial

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Abstract

Great bustards became extinct in the UK during the 19th century due to a combination of factors including hunting, egg collection and changes in agriculture. In 2003, a 10 year licence was granted to begin a trial to reintroduce the species back to the UK. Here we report on the first five years of the trial and assess the progress made towards establishing a founder population. From April 2004 to September 2009 a total of 102 great bustard chicks were imported from Russia and 86 released on Salisbury Plain. Monitoring showed that post-release survival was 18% in the first year following release, and that mortality of released bustards was mainly attributable to predation and collisions. Estimated adult survival was 74%, although the sample size was small. All known surviving great bustards are site faithful to the surroundings of the release site returning throughout the year. A lek area has been established where males have been observed displaying to females. The first nesting attempt was in 2007, and in 2009, two females aged 3 and 4 successfully nested, fledging one chick each. Models incorporating the new demographic estimates suggest that at the end of the 10-year trial period the project can expect to have between 8 and 26 adults as a founder population.

Keywords: great bustard, *Otis tarda*, reintroduction, translocation, monitoring, Britain, Russia, UK

Introduction

Reintroduction has become an accepted intervention in conservation (Seddon et al., 2007; Armstrong & Seddon, 2008), and has been widely used for various organisms including birds and mammals. Due to the financial costs and low success rate, rigorous assessment of feasibility is essential prior to implementation as well as appropriately long post-release monitoring to assess success (IUCN, 1998). However, when gaps in knowledge exist about the ecology of a species in an area from where it was extirpated, it is often difficult to determine the ability of that species to survive and persist once the original causes of extinction are removed. Consequently, trial reintroduction provides an opportunity to fill in the gaps in understanding and to assess the feasibility of a full scale reintroduction project (Osborne, 2005).

Although the aim of a reintroduction is to establish a free-living, self-sustaining population, the progress of a reintroduction comprises a sequence of objectives, including the survival of released individuals, breeding by released individuals in the wild and then subsequent growth and persistence of the population (Seddon, 1999). Each of these stages must be assessed to identify the appropriate methodology and limitations (Seddon et al., 2007; Sutherland et al., 2010) and the importance of post-release monitoring has been increasingly emphasised in assessing progress with reintroduction projects. In many cases, even today, monitoring is found to be inadequate to appropriately assess success or failure (Fischer & Lindenmayer, 2000; Armstrong & Seddon, 2008). In order to assess the feasibility of reintroducing the great bustard *Otis tarda* to the UK, it was recognised that comprehensive post-release monitoring would be needed to assess progress and to inform future strategic decisions.

The great bustard has a fragmented distribution extending across the middle latitudes from Morocco to China (Morales & Martin, 2003). It is found on lowland grassland, steppe and arable land and often displays a preference for low intensity agriculture and crops over natural grasslands (Suarez-Seoane et al., 2002; Oparin et al., 2003; Morales et al., 2006; Magana et al., 2010). It is a polygamous ground nesting bird and exhibits the largest sexual size dimorphisms of mass (females 3.5-7.2kg, males 7-13kg) found in any bird species (Raihani et al., 2006; Székely et al., 2007; Alonso et al., 2009). The great bustard was a common breeding bird across large parts of Europe and Asia through the 18th century (Gewalt, 1959), but has experienced dramatic declines and local extinctions across its range during the 20th century (Palacin, 2008). It is currently classified as Globally Vulnerable (IUCN, 2010). The UK breeding population became extinct *circa* 1830 (Morales & Martin, 2003) and although the true cause of extinction is unknown (Collar, 1979) it was likely due to a combination of factors that included hunting, egg-collection and changes in agricultural practice (Osborne, 2005). Due to the geographical isolation of the UK from existing Central and Southern European populations and the high site fidelity of great bustards (Martin et al., 2008), natural recolonisation is unlikely to occur, even if conditions were suitable (Carter & Newbery, 2004). An attempt was made to re-establish the species in the UK at Porton Down in Wiltshire, between 1970 and 1998, but this was unsuccessful because the captive breeding approach failed to produce any chicks that survived to be released (Collar & Goriup, 1980). Further captive-breeding attempts have so far been unsuccessful at producing enough chicks to make a reintroduction attempt viable (Martin, 1996). Therefore, translocation of captive-reared birds from a wild donor population is the only realistic option for a reintroduction project. A donor population was identified in Russia where eggs from nests that would otherwise be lost to cultivation could be rescued and birds hatched and reared in captivity.

Following a rigorous feasibility study based on the IUCN reintroduction guidelines (Osborne, 2002), it was concluded that there would be no detrimental effects to the donor population and that the habitat and conditions on Salisbury Plain in Wiltshire could support this species. However, gaps exist in our knowledge of great bustard ecology and its ability to persist within the UK due to the long absence of the species. For that reason a 10 year licence allowing the release of birds on a trial basis was issued in 2003 by the UK Government's Department for Environment, Food and Rural Affairs (Defra). In accordance with the IUCN Guidelines on Reintroductions, the licence application had a number of success indicators to help steer the project through the initial stages of establishing a founder population.

Here we report on progress with this project, and evaluate it using the success indicators. We then model population growth using revised parameter estimates based on data from the reintroduced population and compare the outcomes with those predicted in the original feasibility study. This review covers the period from 30 April 2004 (when the first eggs were collected) to 14 September 2009 (five years after the first release) by which time the first released birds were approximately 60 months old.

Study area

The release site is on Salisbury Plain, the largest continuous area of calcareous grassland in North-west Europe, which is mainly contained within the county of Wiltshire. It has a low density of settlements and roads, and land-use is split between low-intensity grazing, agriculture and an extensive military training area (380 km^2). The Salisbury Plain Site of Special Scientific Interest and Special Protection Area cover 197 km^2 and is protected under domestic legislation and the EU Birds Directive (Osborne 2005).

Methods

Donor population and egg collection

The donor population is located in the Saratov Oblast, Russian Federation (50°50’ N, 46 °12’ E). Eggs are rescued from nests that would otherwise be lost to cultivation and transported via a portable incubation unit to a rearing station. The nesting period is prolonged with a gap of 4 weeks between the hatching of the first and the last clutches. All eggs that fail to hatch are autopsied to check for infertility and other causes. After hatching all chicks are individually marked with coloured leg rings. Chicks are reared in cohorts of similar age and fed using a dehumanising suit and puppet to decrease the risk of imprinting on humans. Juvenile birds, between the ages of 30 and 70 days, are transported to the UK in animal crates in compliance with various national and international regulations, including CITES. Once in the UK, the birds are kept in quarantine for one month during which time they are screened for avian influenza and paramyxovirus. Chicks are sexed by body size from the sexual size dimorphism that becomes apparent from about 60 days.

Release and monitoring

Release into the wild takes place each year between September and October depending on the import date and weather conditions. The mean age at release is 100 days (range 58 -145), and birds are released into an open-topped fenced area (hereafter release pen) designed to exclude red foxes *Vulpes vulpes* and badgers *Meles meles*. The release pen was 3.5 hectares from 2004-2007 and then extended to 7 ha in 2008. The release pen is managed to contain a mosaic of arable crops, including oil seed rape, alfalfa and natural grassland. The release technique used during release has varied between years. In 2004, birds were kept in a netted enclosure within the release pen to allow them to become familiar with the environment prior to release but this method was discontinued due to two males being injured colliding with the pen during attempts at flight (Osborne & Fraser, 2005). In subsequent years, all birds were released directly into the release pen. Limited predator control against magpies *Pica pica*, carrion crows *Corvus corone* (potential nest predators) and red foxes was carried out in the immediate area around the release-pen. However, predator control does not occur in the adjacent military areas and there is therefore the potential for rapid replacement of removed predators.

Released bustards were individually marked with numbered wing-tags, colour-coded to identify release year. In addition, 55 individuals were fitted with back-pack, neck-collar or tail-mounted radio-transmitters (Biotrack TW-3), and ten individuals were fitted with Argos/GPS enabled Platform Transmitter Terminals (PTT) (PTT-100 105 gram LC4™ for males and PTT-100 40 gram LC4™ for females, Microwave Telemetry, Inc.) that provided daily information on location.

The release site and its surroundings are intensively monitored by GBG staff. In addition, with the aid of public relations work locally and nationally opportunistic sightings away from the release site were reported by the public approximately once a week on average. Sightings of birds reported by the public were only used in this analysis when individual identity was verified. Mortalities were recorded via wing-tag, transmitter and carcass recoveries. Dates of mortality were estimated and were usually thought to be accurate to within a few days of death. Post-mortems were carried out when possible to establish cause of death, including screening for disease. Released individuals that were injured after release and taken back into captivity were recorded as ‘dead’ for the purposes of analysis with date of injury taken as the date of mortality.

Estimating reproductive and survival parameters

Breeding attempts were assessed through intensive monitoring of the release area during the breeding period (March-June). Key signs indicative of breeding are displaying by males, signs of pecking on a female's head and females exhibiting nesting behaviour (Morales & Martin, 2003).

Due to the small sample sizes, data for males and females were pooled and only age-specific effects on survival were investigated. Pre-release survival is defined as the proportion of chicks surviving from import to release. Post-release mortality was defined as the period from release to 12 months after release. Daily survivorship for the first year post-release was estimated using Kaplan-Meier survival function. Individuals that were neither recovered nor resighted after 365 days were censored at their last resighting, whereas individuals that were known to survive for at least 365 days were censored at 365 days.

To estimate annual age-specific survival probabilities, we used mark-resight data from all 89 released individuals and recoveries of dead birds. Date of marking was considered the day of the bustard's release, and intervals were set to one year from the date of first release on 15 September 2004 until 14 September 2009. Data used in the annual survival analysis were from resightings at the release site from September to December to meet the assumptions that resightings are obtained during a predefined sampling interval and within a defined sampling area. Dead recoveries from throughout the year were considered. Probabilities were estimated with program MARK (White & Burnham, 1999), using a Burnham Joint Live and Dead Encounters model that controls for study area effects (fidelity versus dispersal) that may influence detectability and probability of recovering dead individuals. The model was parameterised to explore differences between the year following release (juvenile 0-1 year) and adulthood (>1 years). The candidate models were ranked using Corrected Akaike's Information Criterion (AICc) and the top performing model chosen. The logit link function was used for all the models.

Success criteria

Success indicators (Table 1) were proposed in the original feasibility study to assess short-term progress and to identify limitations. They were based on the best data available at the time from comparable great bustard rear-and-release projects in Hungary and Germany, and from wild populations in Spain (Osborne, 2002).

Population modelling

We developed two demographic models to estimate the size of the founder population at time t (N_t) at the end of the trial period, and used these models to explore various scenarios. Firstly, we used the deterministic model (Eq. 1) to compare predicted population estimates before the trial (Osborne, 2002) with new estimates based on data presented in this paper. In the original model (Model 1a), the number of eggs collected, fertility rate and hatch rate were used to estimate the number of birds required to be imported into the UK. These three parameters were replaced by the mean number of chicks imported (I), a product of the three components. Mortality was applied instantaneously to reflect the number of birds surviving by May each year where S_a is adult survival and S_{pre} and S_{post} are pre and post-release survival respectively. We used the mean for each parameter estimate and did not incorporate measures of variation. Two scenarios were modelled; (Model 1b) using the actual mean number of chicks translocated each year, and (Model 1c) the desired number of chicks imported each year (40). These were compared with the pre-release survival model of Osborne (2002) and with the actual population growth.

Eq.1 $$N_{t+1} = N_t \times S_a + I \times S_{pre} \times S_{post}$$

Secondly, we incorporated demographic stochasticity in age-specific survival probabilities. To account for uncertainty with survival estimates, 1,000 iterations of the population model were simulated. Each iteration was randomly assigned a survival probability for each age class from a survival probability beta distribution using the mean survival probability and its variance. Using three post-release survival rates (13%, 18%, 23%) and four importation rates (10, 20, 30, 40), twelve scenarios were investigated. Simulations were performed in R (R Development Core Team 2008). Neither modelling approach incorporated breeding for two reasons. First, our aim was to understand how many captive-reared individuals will be established through release only; and secondly, there are still few data available on reproductive parameters of released birds or survival of wild-reared bustards.

Results

Number of released bustards

The number of eggs rescued varied between years influencing the number of imported and released bustards (Table. 2). Ultimately, 102 chicks were imported into the UK (at an average of approximately 20 birds per year). Pre-release survival from import to release (typically one month) was high at 88.0% (SE ± 6.3 %). A total of 86 birds were released, of which 45 were females (52.3%), 33 were males (38.3%), and 8 were unsexed (9.3%) (all birds of unknown sex died or were not re-sighted before any obvious sexual dimorphism was apparent). Of the birds released, 69.7% had known fates (7 alive, 46 dead and 7 disabled) whereas 30.3% had unknown fates by September 2009.

Survival and causes of mortality

Mortality was high for the first 150 days after release (Fig. 1a) with only 26.9% (95 % CI 17.7 - 41.1) of individuals surviving through this period. Subsequently survival from 150 to 365 days remained constant with no deaths reported, although, two individuals were not seen after 305 days. There was no significant difference between the survival rate of males and females (Cox regression: n = 78, z-value = 0.224, p-value = 0.82, Fig. 1b). Annual survival from the top-ranked model in the mark-recapture analysis (Table 3) for one year after release was estimated as 18.2 % (95 % CI 10.8 - 28.9). Annual survival for birds greater than one year was estimated at 74.6 % (95 % CI 51.4 - 89.2). There was a high probability of resighting newly released individuals at the release site (82.2%, 95% CI 50.2 - 95.4), and all surviving individuals greater than 1 year old returned to the release site. Using the joint live and dead encounters model the estimated probability of recovering dead individuals was 67.4% (95% CI. 55.7 -77.2).

Pre-release survival through transportation and quarantine was high but some individuals were injured as a result of collisions with the quarantine pens during attempts to fly. Post-release, there was no evidence in recovered carcasses of starvation or malnourishment. In many cases, it was difficult to determine the cause of death because carcasses had been scavenged. There were two isolated incidences of infection in 2005 with one instance of yersiniosis, probably from a wild rodent, and one unidentified infection. Predation accounted for death in most cases where the cause of death could be confirmed. Red foxes are thought to be responsible for the majority of predation, although the European badger may also have been responsible. Collision, with power-lines and agricultural fences, was the second most important cause of mortality identified (Fig. 2).

Breeding

The first great bustard clutch was laid in 2007 by a 2 year old female. She also nested in 2008, although, clutches in both years proved to be infertile. In 2009, two females nested (a 3 year old female and the 4 year old female that had nested the previous two years) with one clutch hatching one chick and the other hatching two chicks. Both females successfully fledged one chick.

Success indicators

Four of the nine indicators were met (Table 1). In addition, three of the targets were potentially met given the large range of uncertainty in parameter estimates due to the small sample sizes. The following three targets were below adequate. First, the average number of birds imported has been half of the licence import quota of forty birds each year. Second, post-release survival was lower than the expected level, and third, adult survival failed to meet the adequate target for either sex although the confidence limits are large.

Population Modelling

Based on the parameters in Table 4, model 1a estimated 108 individuals after 10 years using 400 imported bustards (Fig. 3). However, it was apparent after the first year of release that this would be an overly optimistic prediction (Osborne & Fraser 2005). Model 1b predicts 12 individuals will be recruited into the breeding population from 200 imported birds during the trial period (Fig. 3), and is consistent with actual population growth (Fig. 3). Importing the originally estimated 40 birds per year would double the predicted founder population to 24 individuals.

Model 2 shows that there is uncertainty in how the population might develop due to large variation in the estimates of post-release and adult survival (Fig. 4). At the current rates of 20 birds imported per year and 18% post-release survival, the founder population has a 95 % probability of reaching 8 to 26 individuals at an equal sex ratio. Improving the post-release survival rate to 23 % and importing 40 chicks each year resulted in a predicted founding population of 32 to 56 individuals. The predictions are on average higher than estimated in Model 1. However, currently the population growth is at the lower end of the outcomes predicted by these models. The models suggest that if importation rates are maintained at less than twenty birds then the founder population after 10 years would be between 1 and 11 individuals.

Discussion

The first 5 years of the reintroduction trial have 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. Further, it has shown that released birds can survive in the wild over long periods and are generally faithful to the release area. In recent years, released birds have reached maturity and have reproduced successfully on Salisbury Plain.

The progress of the project has been assessed through intensive monitoring of individuals that were systematically marked from the beginning of the trial. Although post-release mortality has been high, individuals from every year of release have survived to adulthood, confirming that the habitat around Salisbury Plain can support individual great bustards. The reintroduced great bustards have not exhibited the long distance migratory behaviour known from the donor population in Russia (Watzke, 2007b), with the exception of three individuals that flew to France in 2005 shortly after their release. Ultimately two of these individuals died and one remains unaccounted for. All known surviving bustards have returned to the release site throughout the year but they are also known, based on reports of wing-tagged birds and data from birds fitted with satellite tags, to have explored more widely in south-west England (unpublished data).

The presence of conspecifics has been shown to influence the natal dispersal of great bustards in wild populations as well as the use of lek sites by males, with juvenile birds using the presence of other great bustards as indicators of habitat quality (Alonso et al., 2004; Martin et al., 2008). However, even in the absence of these cues, males in the UK have been observed displaying and returning to the release site to lek. This has management implications in relation to the potential benefits of establishing new release sites and leks in south-west England to start creating a meta-population structure.

Whilst released females have been able to locate suitable nesting habitat and have successfully reared chicks suggesting that arthropod abundance/biomass is sufficient in the breeding area. The number of breeding attempts is so far too small to be able to draw any empirical conclusions about nesting success or productivity rates. The level of breeding success was expected to be low at the beginning on the project as first time breeders tend to have a lower success rate than more mature and experienced birds (Ena et al., 1987; Morales et al., 2002; Watzke, 2007a; Martinez, 2008). As the population grows and the age structure develops, we would expect breeding success rates to improve as more females will be available to breed and older females have a higher probability of successfully rearing chicks (Morales et al., 2002). The social stimulation created by recruitment of breeding individuals will reduce potential Allee effects associated with small populations.

The low numbers of birds released together with low post-release survival rates have clearly limited the short-term success of the project. In extant populations, juvenile survival is estimated at 29.9% for the first year (Martin et al., 2007). Our results are comparable although the high mortality phase takes place post-release, when birds are 3-8 months old, rather than during the first 3 months as recorded by Martin et al. (2007). Low post-release survival is common in reintroductions across various taxa (Teixeira et al., 2007). This is potentially the result of captive-reared individuals lacking the appropriate behavioural responses to survive in the wild (Griffin & Blumstein, 2000). Maternally learned skills are likely to be important to juvenile great bustard survival because in the wild they stay with the mother for greater than six months (Martin et al., 2008). A number of studies have shown that wild-reared individuals in general have higher survival rates than captive-reared conspecifics (Griffith et al., 1989; Wolf et al., 1996). The Brandenburg (Germany) great bustard release project has experienced similar and variable post-release survival estimated between 15 % and 40% of released individuals from release to the following spring (Eisenberg, 2008). Fox predation had been the main cause of mortality in this project, which was mitigated to some extent by the use of predator-free fenced areas. Recently however, white-tailed eagles *Haliaeetus albicilla* are reported to have caused substantial mortality in juvenile birds (Eisenberg, 2008). Houbara bustard *Chlamydotis undulata* release projects have had similar difficulties with fox predation (Combreau & Smith, 1998). It has been demonstrated in a wide range of taxa that captive reared animals lack essential skills such as predator recognition (Griffin & Blumstein, 2000). Predator-awareness training with a live predator has been shown to improve post-release survival in houbara bustards (van Heezik et al., 1999), although, there are few empirical studies that confirm its effectiveness in other species of birds. In great bustards, the effort to elicit the correct flight response to a predator can lead to injuries when the birds are in confinement (D. Waters, pers. comm.) Collisions have also been an important cause of mortality post-release which may be due in part to behavioural naivety or perhaps to a reduction in feather quality due to time spent in captivity and the handling necessary during transport and veterinary checks. However, collisions are known to be an important cause of mortality in wild great bustard populations (Janss & Ferrer, 2000) and in other species of bustards in the wild; kori bustard *Ardeotis kori* (Martin & Shaw, 2010), Denham's bustard *Neotis denhami* (Shaw et al., 2010) and in little bustard *Tetrax tetrax* (Silva et al., 2010).

In the wild, adult survival is thought to be high, being estimated at 92% in Iberian populations (Martin et al., 2007). The reintroduced UK population has a similarly high rate although the estimate is based on only a very small sample. Estimates and the resulting reliability of model predictions should improve in future when more data become available. On current estimates we predict that the growth of the founder population through continued supplementation will be slower than originally thought (Osborne, 2002). This is primarily due to the small numbers recruiting into the population which is a product of low import numbers and post-release survival. Assuming these parameters do not improve, a longer period of time will be required to establish a founder population sufficiently large to have a high chance of persisting in the wild in the long term. Whilst the population is still small it remains prone to stochastic events such as a period of high mortality due to extreme weather and a reduction in the potential benefits of social stimuli from con-specifics.

Small population size also increases the challenge of assessing the project quantitatively rather than qualitatively, making it harder to plan for the future (Seddon et al., 2007; Armstrong & Seddon, 2008). There is limited value in measuring progress of a reintroduced population using data from existing wild populations, as there will be considerable variation in factors such as anthropogenic disturbance, infrastructure, predator types, climate, attitudes to conservation, and availability/access to other sub-populations in different areas. The values for demographic parameters required to ensure a self-sustaining population are thus likely to be different in southern England from those of other populations. For this reason, modelling is the appropriate approach to investigate the rates of recruitment needed for sustainable growth and to set success indicators accordingly (Seddon, 1999; Seddon et al., 2007; Armstrong & Seddon, 2008). The reliability of these models should improve as more data become available in future from monitoring of the expanding population.

Reintroduction projects involving red kite *Milvus milvus*, white-tailed eagle and, to a lesser extent, osprey *Pandion haliaetus* in Britain have already achieved considerable success (Green et al., 1996; Evans et al., 2009). Although, Cade (2000) pointed out the success rates tend to be higher in birds of prey than in other birds. The great bustard is one of a number of bird reintroductions that are currently in progress in Britain, with other projects involving the corncrake *Crex crex*, cirl bunting *Emberiza cirlus* and common crane *Grus grus*. The results of these projects may have considerable influence on the extent to which this sometimes contentious approach to conservation is utilised in future.

Recommendations

Although this experimental reintroduction has shown some encouraging signs of success, it is still at an early stage and further work will be required in order to establish a self-sustaining population. The numbers of birds released annually are, on average, about half of that planned. While this may not undermine the project in the long term, it does increase the likely timescale for success. Accordingly, it is recommended that priority should be given to increasing the number of birds released each year. Continued supplementation will provide a valuable buffer against stochastic effects that could result in the population being reduced to dangerously low levels or even extinction. Current rates of post-release survival are limiting the growth of the population. Experimentally investigating ways to improve survival may offset low import numbers and will be of potential benefit to global bustard conservation as a whole. The importance of accumulating improved demographic data for the newly established population for modelling purposes cannot be overstated. Long-term post-release monitoring will be essential to inform a strategy for taking this reintroduction project forward, through improving our understanding of habitat use, breeding productivity, survival of wild-reared chicks and likely rates of population growth.

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Biographical sketches

ROBERT JOHN BURNSIDE is interested in the use of reintroduction as a conservation tool and the design of monitoring techniques for assessing success. IAN CARTER has worked as an ornithologist with Natural England (and predecessors) for over 20 years and has a particular interest in bird reintroductions. ALASDAIR DAWES has worked in conservation for over 10 years, with a particular interest in birds. DAVID WATERS is the Director of the GBG, an organisation he founded in 1998. LEIGH LOCK works for the RSPB on various species recovery projects across the UK. PAUL GORIUP has worked with great bustards for 30 years. TAMAS SZEKELY is interested in biodiversity conservation and specialises in wader breeding systems.

Table 1. Targets and success indicators for the first five years of the great bustard reintroduction and estimates of demographic rates achieved. Success indicators are derived from release projects in Hungary and Germany, and from wild birds in Spain (Osborne, 2002).

Measure	**Adequate**	**Excellent**	**Reintroduction project 2004-2009** mean ± Standard Error (n)	**Target met?**
1. Hatching success of artificially incubated eggs	54%	75%	66.4 (232)	YES
2. Number of chicks moved from Russia each year	30	40	20.4 ± 5.9 (5)	NO
3. Pre-release survival (males)	53%	75%	88.0 ± 6.3 % (102)*	YES
4. Pre-release survival (females)	45%	75%		YES
5. Post-release survival to end of year one (males)	25%	28%	18.2 ± 4.6% (86)* 95%CI 10.8% - 28.9%	NO

6. Post-release survival to end of year one (females)	38%	42%		NO
7. Post-release survival from year one per annum (males)	78%	87%	74.6 ± 10% (10)* 95%CI 51.4% - 89.2%	NO
8. Post-release survival from year one per annum (females)	83%	92%		NO
9. Year in which first evidence of breeding is recorded	5	4	4	YES

* Male & female data are pooled

Table 2. The number of eggs collected and hatched in Russia and chicks transported and released in the UK great bustard reintroduction trial from 2004 to 2008.

Year	2004	2005	2006	2007	2008	Total
Number of eggs collected	61	61	25	32	53	232
Number of eggs hatched	48	47	14	6	39	154
Number of chicks transported to UK	28	38	9	6	21	102
Number of chicks released in the UK	22	32	9	6	17	86

Table 3. Summary of model selection from annual survival of great bustards from the UK reintroduction trial as calculated from a Burnham Live and Dead Encounters. Age specific mortality (S_i), probability of resighting a live individual (p_i), probability of recovering a dead individual (r_i) and probability an individual will remain in the sampling area (F_i) were considered. Age structure (i) was defined as 1, where the estimate is constant across age groups and, 2 for two age groups split into first year and adult (2-5 years). All models were fitted with a logit link function and ranked according Corrected Akaike Information Criteria (AICc).

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Number of Parameters**	**Deviance**
$\mathbf{S_2\ p_2\ r_1\ F_1}$	209.89	0	0.475	1	4	34.79
$\mathbf{S_2\ p_2\ r_2\ F_2}$	211.09	1.20	0.260	0.54	5	33.80
$\mathbf{S_2\ p_2\ r_1\ F_2}$	211.78	1.89	0.184	0.38	5	34.49
$\mathbf{S_2\ p_0\ r_2\ F_2}$	213.73	3.83	0.069	0.14	5	36.44
$\mathbf{S_2\ p_2\ r_2\ F_2}$	217.94	8.05	0.008	0.017	8	33.80
$\mathbf{S_2\ p_0\ r_1\ F_1}$	224.84	14.9	0.00027	0.0006	7	43.03
$\mathbf{S_0\ p_2\ r_1\ F_1}$	227.89	18.00	0.00006	0.0001	3	54.95

Table 4. Model parameters for the reintroduced great bustard population

Parameter	**Parameters of model (Osborne 2002)**	**Achieved parameters (2004 – 2009)**
Eggs collected each year	75	46.4*
Fertile Eggs	75 %	84.3 %*
Eggs Hatch	72 %	66 %*
Number of chicks imported	40.5	20.4
Conservative survival until release (male)	53 %	88 %
Conservative survival until release (female)	43 %	88 %
Post-release survival to end of year one (females)	88 %	18.2 %
Post-release survival to end of year one (males)	88 %	18.2 %
Survival > 1yr old female	87 %	74.6 %

Survival > 1yr old male	92 %	74.6 %

*Parameters were not used in the model

Figure legends

Figure 1. Estimated survival of reintroduced great bustards. a) solid line represents all 86 individuals released between September 2004 - September 2009, and dashed lines are 95% confidence intervals. b) Survivorship separated by sex for 78 individuals (45 females, 33 males). Cross-hair ticks indicate censored individuals that were not recovered or resighted after the indicated date during the 365 days.

Figure 2. Fates of captive-reared great bustard juveniles reintroduced to the UK between 2004 and 2009. Sample sizes are on the right hand axis.

Figure 3. Predicted population size of UK great bustard reintroduced population through rear-and-release and assuming there is no breeding occurring; 1a- (+) original projected growth before the start of the project (Osborne 2002); 1b- (●) revised model importing 20 chicks a year; 1c- (○) revised model importing 40 chicks a year; and (▲) actual population growth from 2004.

Figure 4. Estimated founder population sizes for great bustards reintroduced to the UK at the end of the 10 year trial period using 12 scenarios of post-release survival and number of birds imported to the UK (see Methods for details). Lines are two standard deviations above and below the estimated mean after 1,000 runs and represent the 95 % probability of attaining a population this size.

Fig. 1

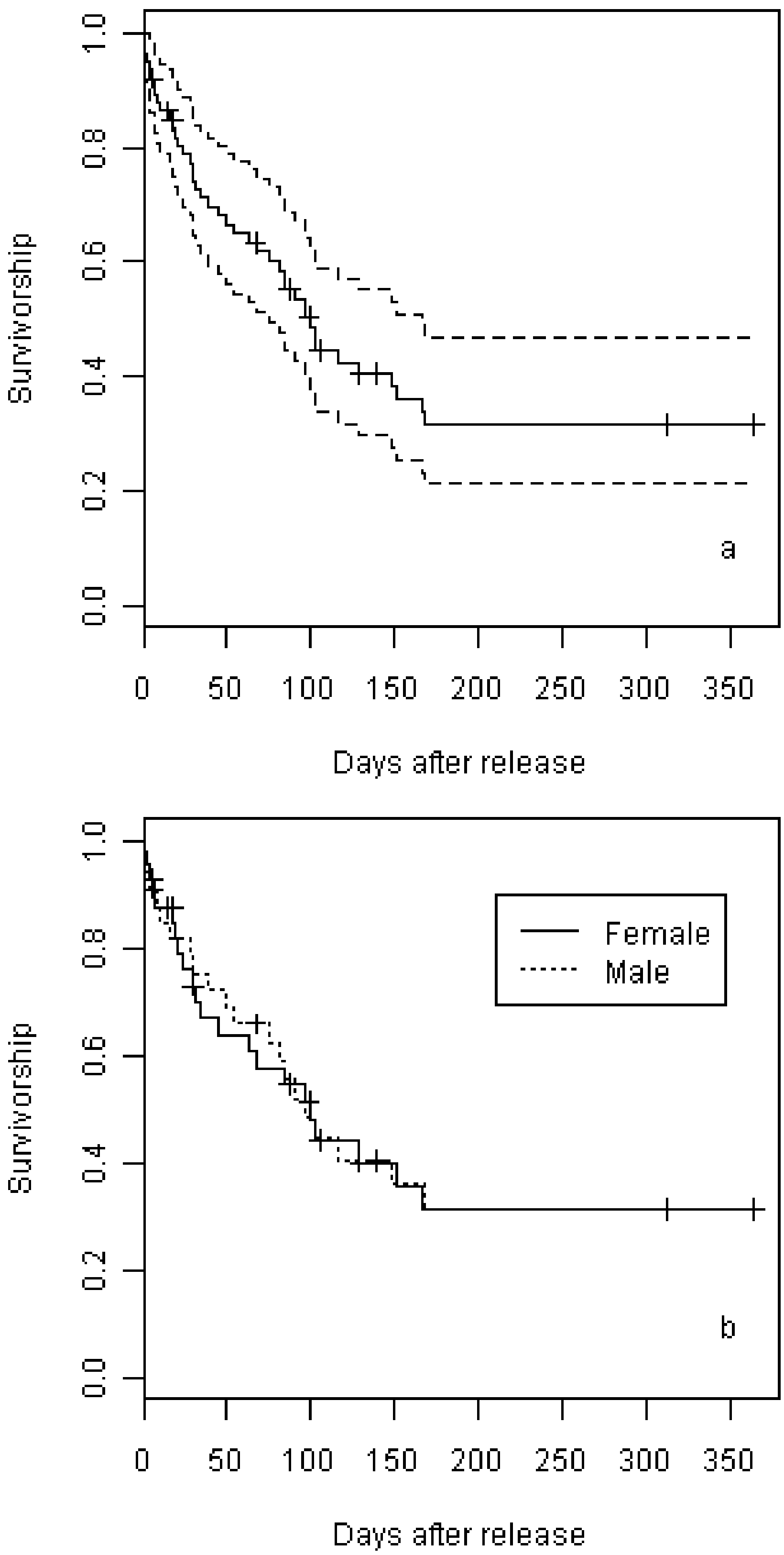

Survivorship
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
200
250
300
350
Days after release
a
b
Female
Male

Fig 2.

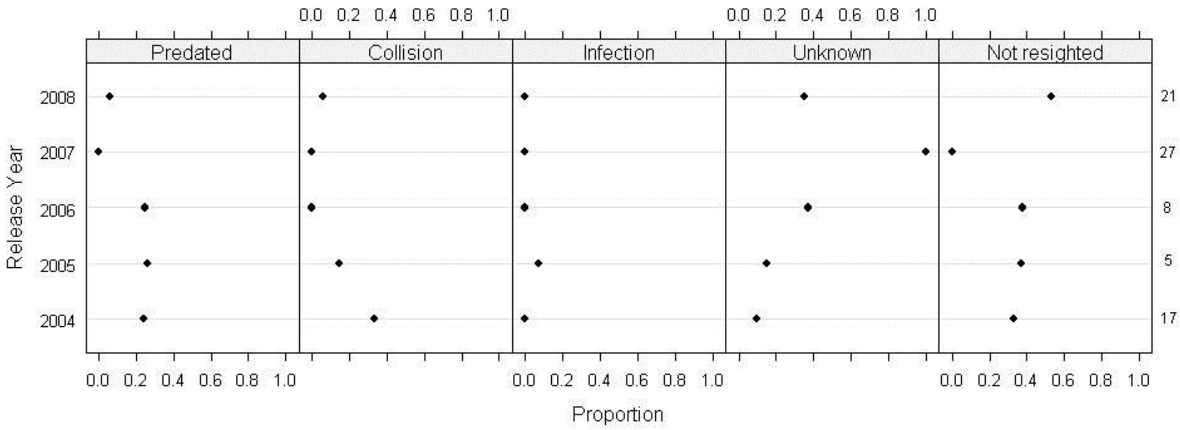

Predated
Collision
Infection
Unknown
Not resighted
Release Year
2008
2007
2006
2005
2004
21
27
8
5
17
0.0 0.2 0.4 0.6 0.8 1.0
Proportion

Fig. 3

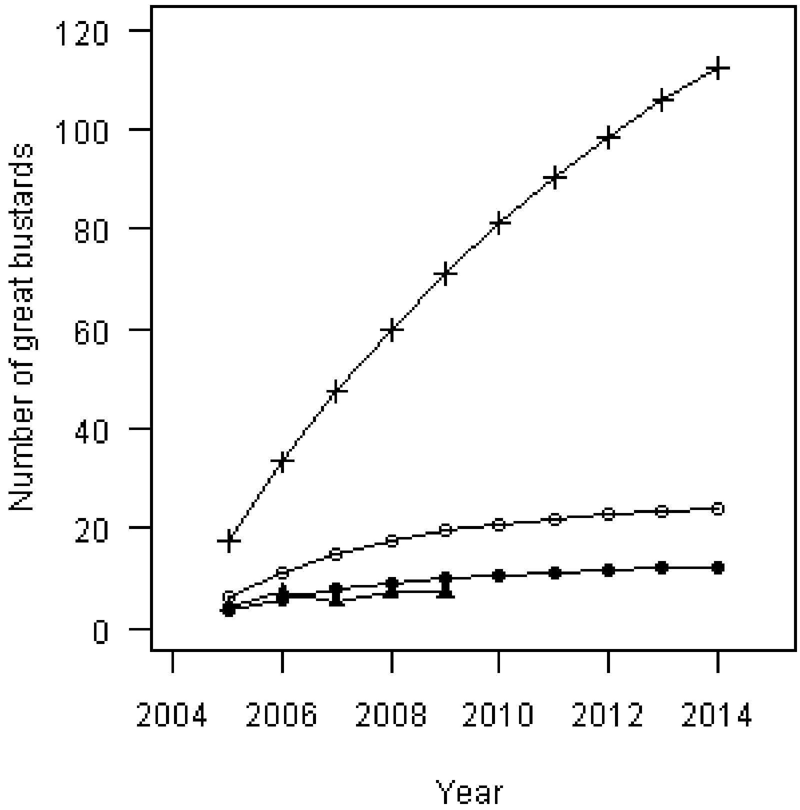
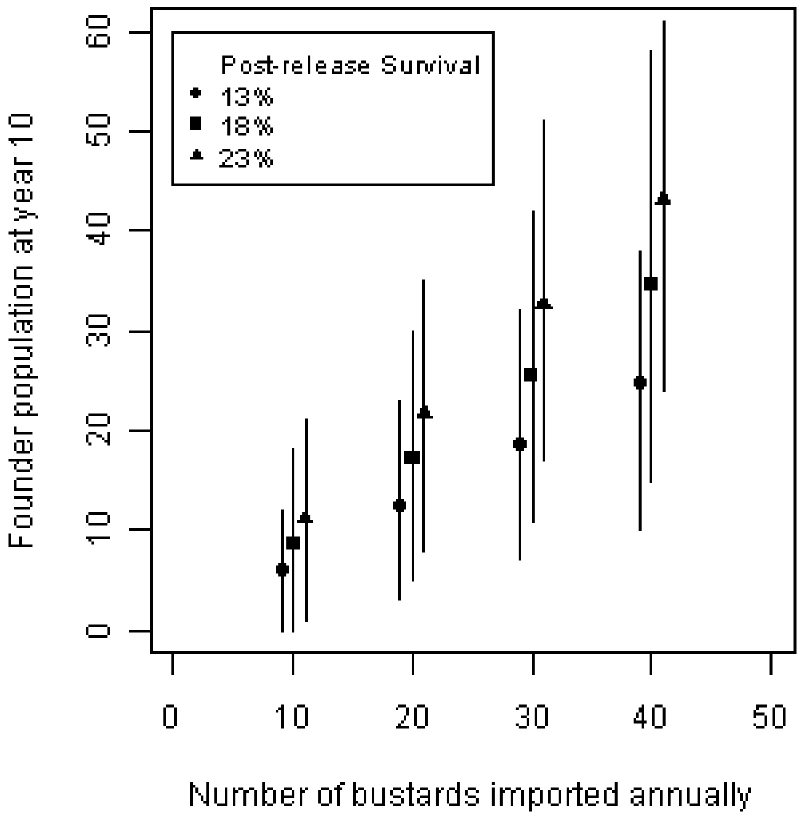

120
100
80
60
40
20
0
Number of great bustards
2004
2006
2008
2010
2012
2014
Year

Fig. 4


Post-release Survival
13%
18%
23%
Founder population at year 10
0
10
20
30
40
50
60
Number of bustards imported annually