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Migration of wild and captive-bred Little Bustards *Tetrax tetrax*: releasing birds from Spain threatens attempts to conserve declining French populations

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Populations of the Little Bustard *Tetrax tetrax* in the farmlands of Europe have declined greatly over the last century. In Western Europe, France now holds the only remaining migratory population, which currently numbers fewer than 300 displaying males. However, the movements of these birds are virtually unknown, in spite of the important implications of this information for the conservation of this species. We identified migratory movements and overwintering areas of French migratory populations, using wild individuals fitted with satellite or radio-transmitters. Little Bustards completed their migration journey over a relatively short time period (2–5 days), with nocturnal migration flights of 400–600 km per night. All birds overwintered in Iberia. In addition, we tested the consequences of captive rearing on migratory movements. French wild adults and French captive-bred juveniles behaved similarly with regard to migration, suggesting that hand-raising does not alter migratory movements. However, birds originating from eggs collected in Spain and reared in western France did not migrate, suggesting a genetic component to migratory behaviour. These results therefore suggest that a conservation strategy involving the release in France of birds hatched from eggs collected in Spain may imperil the expression of migratory movements of the French population. More generally, to maintain the integrity of native populations, the introduced individuals should mimic their migratory movements and behaviour.

Keywords: Argos PTT, endangered species, satellite tracking, *Tetrax tetrax*, translocation.

In Europe, the Little Bustard *Tetrax tetrax* occurs in natural steppes and agricultural landscapes and is considered Near Threatened (IUCN 2008). Once continuously distributed from Iberia to Russia, this species experienced a drastic decline in its range during the 20th century (Cramp & Perrins 1994), and Western European populations (*T. tetrax*) are now restricted to Portugal, Spain, France and Italy, with an estimated 110 000–280 000 individuals, primarily in Iberia (Birdlife International 2000). Numbers are currently declining in all these countries (García de la Morena *et al.* 2006, 2007, Jolivet & Bretagnolle 2002, Cabral *et al.* 2005, Petretti 2006). France holds the last migratory population of the nominate subspecies, now restricted to the western part of the country, where they breed in an intensive farming landscape (Jolivet & Bretagnolle 2002). Although most of these birds leave their breeding grounds in October and return in March, a few overwinter on, or close to, their breeding grounds (authors' unpubl. data). A non-migratory population also exists in the south of France.

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The French migratory population has undergone one of the steepest declines documented for any bird species in Europe, falling from 6200 to 400 displaying males between 1980 and 2004, representing a 94% loss (Bretagnolle & Inchausti 2005), and the current extinction risk of this population has been estimated at 45% over the next 30 years (Inchausti & Bretagnolle 2005). To halt such a collapse, a conservation plan has been designed in France, including the reinforcement of populations implemented under a LIFE initiative since 2004 (Bretagnolle & Inchausti 2005). Reintroduction and population reinforcement have become a popular tool in conservation biology to rescue populations from the risk of extinction (Scott & Carpenter 1987, Griffith *et al.* 1989, Beck *et al.* 1994, Sarrazin & Barbault 1996). To maximize their efficiency, such conservation actions require an in-depth knowledge of the ecology and behaviour of the target species (Sarrazin & Barbault 1996), including information on wintering grounds and migration routes for migratory species. A careful search using the ISI Web of Knowledge indicated that very few conservation programmes had to deal with migratory species: between 1980 and 2009, just six of the 56 studies involving translocations or reintroductions of birds concerned migratory species, and only a single published study explicitly included migratory movements of released birds (Engelhardt *et al.* 2000).

As migration behaviour is a unique trait of the focal population, preserving this trait has been considered a priority in the French Little Bustard conservation scheme, although very little was known about the migratory movements of wild individuals. We applied satellite telemetry (e.g. Green *et al.* 2002, Limiñana *et al.* 2007, Gschweng *et al.* 2008) to Little Bustards between 1997 and 2007 to study migration patterns and answer three related questions. Our first objective was to describe the migratory movements (flyways, stopover sites) and identify wintering areas of the French migratory population, this information being unavailable at the beginning of the conservation programme. Secondly, we compared migratory patterns between wild and captive-bred birds to verify that hand-reared chicks do not show altered migratory movement. Thirdly, many studies on bird migration have demonstrated a genetic component in shaping migration patterns, hence we predicted that hand-reared birds originating from the migratory population breeding in western France would show migratory movements similar to those of wild individuals, whereas hand-reared birds from a sedentary population would not. Given that the relatively healthy Spanish population could be a source of chicks for the reinforcement programme in France, although Spanish birds either show nomadic movements or are strictly sedentary, we tested whether translocated hand-reared Spanish chicks show migratory behaviour. The costs associated with satellite telemetry constrain sample size: to overcome this, we used additional data from radiotagged adults and fledglings to check the statistical robustness of our findings based on a limited number of satellite-tracked birds.

METHODS

Study area

The main release site was located in an intensive agricultural landscape in the southern part of the Département des Deux Sèvres, France (46°20′N, 0°37′W). It lies within a large study site (*c.* 450 km^2), which encompasses a Special Protection Area (SPA FR5412007) belonging to a broader network of conservation areas within the Poitou-Charentes region (four departments; Fig. 1a). An aim of management in this SPA is to improve the conservation of Little Bustards. The birds in this study, which came from breeding centres or were captured in the wild, were released in this area (Fig. 1a), with one exception. The birds were closely monitored after release during the post-nuptial season, which was especially crucial for hand-reared individuals. One wild individual was captured and released in the Centre region, 200 km from the main release point (Fig. 1a) after being equipped with an Argos transmitter.

Sample size and the origins of birds

To identify the wintering areas of French Little Bustards, four adult wild birds were fitted with Argos Platform Transmitter Terminals (hereafter PTTs). They were caught after the breeding season in the two study areas of central-western France (three birds in Deux-Sèvres and one in Indre; Fig. 1a, Table 1). In addition, as part of a long-term study on the breeding ecology of Little Bustards, 17 adults were also fitted with radio-transmitters during the spring of 1998 and 1999. During the winter of 1999–2000, these birds were radio-

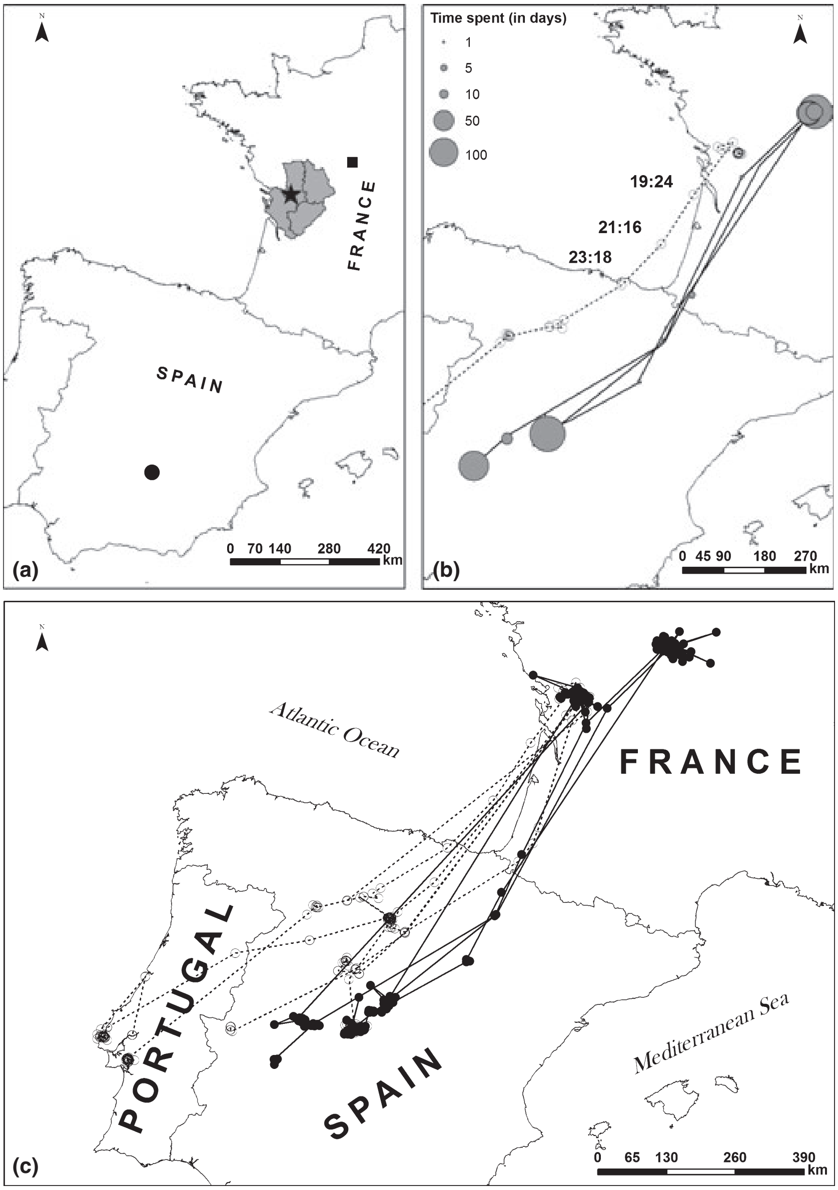

Figure 1. (a) Two release sites in France, in the Poitou-Charentes region (star) and in the Centre region (square), and egg collecting site in Ciudad Real region, Spain (circle). (b) Details of the flight path of one bird over the Bay of Biscay on 10 November 2005 and of the wild individual which was surveyed for two consecutive migrations. For this bird, circle size is proportional to the number of days spent at each location. (c) Migratory flyways and wintering locations for wild (plain lines, black dots) and hand-reared (dashed lines, empty dots) migrating birds.

tracked in the species' wintering areas in Spain using CESSNA 172 and 182 aircraft, at low speeds (*c.* 200 km/h). The planes were fitted with twin Yagi directional antennas. The planes flew at altitudes of *c.* 1500 m asl (range 900–3000 m), depending on weather, relief and Civil Aviation restrictions. The procedures used for scanning the frequencies and manoeuvring the aircraft to locate the transmitters followed those detailed in Kenward (2001) with adaptations proposed by Gilmer *et al.* (1981) and Alonso *et al.* (1996). The survey in our study covered the wintering areas where French PTT-fitted birds had been recorded in previous years and sites where Bustards were known to overwinter (García de la Morena *et al.* 2002, 2007).

To investigate migration of hand-reared birds, fledglings from breeding centres for the Little

Table 1. Characteristics of birds fitted with Argos PTTs.

Year	Ring	Origin	Country of origin	District/locality	Sex	Age	Migration (0 = no; 1 = yes; ?=unknown)	Migration distance (km)	Number of flights before reaching wintering grounds	Mean distance of long-flights (km)	Use of stopovers (number used)	No. of locations: Low class	No. of locations: High class	No. of locations: Tot.	No. of tracking days
1997	30 g power battery	W	FR	Deux Sèvres	?	Ad?	0	–	–	–	–	23	3	26	58
1999	30 g power battery	W	FR	Deux Sèvres	M	Ad	1	676	2	475	Yes (1)	144	22	166	163
1999	30 g power battery	W	FR	Deux Sèvres	M	Ad	1	807	2	528	Yes (1)	131	10	141	108
2003	20 g power battery	HR	SP	Migueltura	M	J	0	–	–	–	–	29	19	48	73
2003	18 g solar battery	W	FR	Indre	M	Ad	1	1003	?	?	Yes (2)	580	136	716	621
2003	20 g power battery	HR	SP	Migueltura	M	J	0	–	–	–	–	171	22	193	246
2005	20 g power battery	HR	FR	Charente	F	J	0	–	–	–	–	68	8	76	103
2005	18 g power battery	HR	FR	Deux Sèvres	F	J	0	–	–	–	–	75	26	101	147
2005	18 g power battery	HR	FR	Vienne	M	J	1	1125	1	375	Yes (3)	105	52	157	158
2006	20 g power battery	HR	FR	Indre	F	J	1	600	?	?	?	62	23	85	132
2006	20 g power battery	HR	FR	Charente	F	J	1	806	?	?	?	207	73	280	212
2007	20 g Argos GPS solar	HR	FR	Deux Sèvres	M	J	1	982	?	?	?	33	112	145	290
2007	20 g Argos GPS solar	HR	FR	Deux Sèvres	F	J	?	–	–	–	–	25	43	68	54
2007	20 g Argos GPS solar	HR	FR	Vienne	M	J	1	750	2	300	Yes (1)	30	119	119	81
2007	20 g Argos GPS solar	HR	FR	Deux Sèvres	F	J	1	1178	2?	300	Yes (3)	45	95	140	71

Origin: HR, hand-reared; W, wild. County of origin: FR, France; SP, Spain, Age: Ad, adult; J, juvenile.

Bustard were also fitted with PTTs. The eggs either were obtained from captive birds (a captive breeding stock is held at the Parc de la Haute Touche, Indre, by the Museum National d'Histoire Naturelle) or were collected in the wild from nests destroyed by farming activity. Hatchlings were reared in a rearing centre within the main study site, in the Département des Deux-Sèvres. The fledglings were released when 2 months old. Between 2003 and 2007, 93 chicks originating from France have been reared and released in the wild, of which nine were fitted with Argos PTTs (Table 1).

Along with these releases, a pilot trial was implemented in 2003, involving six eggs collected in the province of Ciudad Real (central Spain, Fig. 1a) that were incubated and reared in France (at the CNRS Chizé Lab); of these, two were fitted with PTTs, and the four others were tagged with radio-transmitters and were tracked throughout the winter in Spain and in the main French study area.

In total, 15 Little Bustards were fitted with satellite tags: four French adults, and nine French and two Spanish juveniles between 1997 and 2007 (Table 1). In addition, 17 French wild adults and four fledglings reared from Spanish eggs were fitted with radio-transmitters.

Fitting transmitters

Between 1997 and 2007, three different Argos PTT models were used (Microwave Telemetry Inc., Columbia, MD, USA), either battery or solar-powered, and weighing 20–30 g (Table 1). Another four PTTs deployed also recorded GPS locations twice a day. Radio-transmitters were purchased at Biotrack Ltd (Waerham, UK) within the same weight range. Both PTTs and radio-transmitters were attached with silk ribbon and a Teflon harness (Kenward 2001). The total equipment (transmitter + harness) weighed 22–32 g, representing 2.6–4.0% of the body mass (892 g ± 76, range: 750–1000 g). The birds were ringed, fitted and released within a 15-min period, as this species is very sensitive to stress. Ponjoan *et al.* (2008) showed that handling birds for >20 min resulted in a higher probability of mobility disorders. Hand-reared birds weighing over 600 g for females and 700 g for males were fitted, and kept at least 1 week in aviaries, allowing the position and adjustment of the harness to be checked before release.

Selection of Argos data for describing the patterns of migration

We used the method described in Judas *et al.* (2006) to exclude dubious Argos points. We excluded points for which the average speed calculated between two successive locations exceeded 80 km/h, a realistic maximum speed for Little Bustards. We used all seven classes of location quality provided by Argos (CLS 2007) for temporal issues related to migration starting and arrival dates, but only GPS locations and high-quality satellite locations (coded as 3, 2, 1 with a precision of respectively 150 m, 150–350 m, <1000 m; CLS 2007, Vincent *et al.* 2002) to estimate distances travelled and to display migration routes.

The statistical analyses were performed using R version 2.9.1 (R Development Core Team 2008). Given the small sample size available, we used Fisher's exact test to compare categories of birds (hand-reared and wild, males and females, French and Spanish) and assessed its statistical power (power was calculated using the 'statmod' package in R). If the statistical power was below 0.8, we estimated the theoretical sample size required to reach $\alpha = 0.05$, given the size of the effect, to judge the level of Type II error. Data are presented as mean ±1 sd.

RESULTS

The proportion of migrants

PTTs provided high-quality locations (LC 3, 2 and 1) for an average of 76 ± 73 days (54–621 days) for the 15 individuals fitted with the Argos or Argos GPS system (Table 1). Of these, four did not migrate to Iberia, nine moved to Iberia and two PTTs stopped working before the latest observed departure date, precluding any conclusion about their migration status. Regarding radio-fitted birds, 10 of the 17 wild adults were found in Spain in winter aerial surveys.

Migration rate did not differ between wild adults (13/21 when four Argos and 17 radio-fitted individuals are pooled) and French-born fledglings raised in captivity (6/8, $P = 1.0$). Although sample sizes were limited, the proportions of migrating individuals in the two samples were so close (0.65 vs. 0.75) that power analysis indicated that this result was robust to Type II error (theoretical sample size required of 350 individuals). No significant difference was observed between males and females in the proportions of migrating birds (3/5 females and 6/6 males migrating; $P = 0.18$), although in the latter case the power of the test was very poor and only 10 additional individuals would have yielded a significant difference. In contrast, the geographical origin affected the pattern of migration. Of the six birds of Spanish origin, the two males fitted with a PTT did not migrate and wintered within the study site, a result further confirmed by the four other birds fitted with radio-transmitters, of which three wintered on the French release site, with no data available for the fourth. The difference in proportions (0 vs. 0.75 for Spanish and French birds, respectively) was significant ($P = 0.02$), even though the power of the test was only 0.64. However, a single additional individual would have been enough to reach a power of 0.8.

Migration routes, timing and distance

All the birds fitted with Argos PTTs which migrated ($n = 9$) left the study or release site between 4 October and 10 November. For five of the nine migratory birds, we could assess the precise journey duration: four of them crossed the Pyrenees (a journey of 450 km) in a one-night flight, while two nights were necessary for a fifth individual to reach its wintering area (two successive flights of 330 and 380 km). Two of these five birds were adults which had been caught in the wild, and the three others were captive-raised fledglings. The mean distance covered from breeding grounds (or release site for captive-bred birds) to winter quarters was 880 ± 201 km ($n = 9$; Table 1). Because of the short duration of their migration, detailed migration routes were available for only three birds (Fig. 1a,b). Two of them made stopovers just before or just after crossing the Pyrenees. The third individual crossed the Bay of Biscay (Fig. 1b). This path is based on three consecutive consistent locations (class 0 and 1); they suggest an approximate ground flight speed of 64 km/h (62 km/h when considering the two consecutive class 1 locations) and a maximum distance from land of 66 km. Only one bird (a male caught in the wild) provided data for two consecutive migrations. Interestingly, this bird crossed the Pyrenees in the same area in 2003 and 2004, the two flights being approximately 23 km apart.

Wintering areas in Spain

Three main areas of overwintering for migrating French Little Bustards were detected (Fig. 1a). One was located north and northeast of Valladolid (Iberian Northern Plateau) and was used both as a wintering area as well as a stopover for birds migrating southwards (used by six birds). The second area lay between Madrid and Toledo, Iberian Southern Plateau (six birds), and the third one was in Portugal, close to the Tagus estuary (two birds) and the Tagus valley in Extremadura (one bird; Fig. 1a). The single bird tracked over two successive migrations wintered in areas 150 km apart (Fig. 1c).

DISCUSSION

Our results indicate that the western French population of Little Bustards is mainly migratory, with most birds leaving for the Iberian Peninsula. This pattern is in sharp contrast to the population inhabiting the Mediterranean area in France, which is sedentary (Wolff *et al.* 2001). Some individuals in our main study site wintered locally (up to 13 birds in 1999 from a population of approximately 100 birds at the end of the breeding season; authors' unpubl. data) and others did not reach Spain but overwintered elsewhere in France. However, about 75% of birds did migrate, and there is some evidence that the decision to migrate or not may be specific to individuals: hand-reared birds which did not migrate in one year were also sedentary in following years. Thus, two colour-ringed birds have overwintered on the main study site, one for five consecutive years and the other for 3 years. Similarly, the only wild bird that was tracked for two consecutive seasons migrated twice.

Reintroduction and reinforcement programmes aim at restoring wild populations at sustainable levels with identical biological characteristics to the original population (Armstrong & Seddon 2008). In the case of migratory populations, once the migratory behaviour has been identified, it is necessary to assess whether released individuals will present the same behaviour. We provide here the first comparison, albeit based upon a small sample size, of wild, local hand-reared and translocated hand-reared migration patterns for a threatened bird species. Captive-raised and wild birds migrated to Iberia in similar proportions, indicating that captive breeding did not alter migration movements. This result, although based on a fairly small sample size, was robust as indicated by power analysis. The birds used similar flyways, possibly because young released birds benefitted from the guidance of experienced adults on migration. We know from observations that captive-bred birds joined flocks of wild individuals and that mass departure does occur in the Little Bustard populations, with sometimes half of the post-nuptial groups disappearing from the study area from one day to the next, indicating that Bustards migrate in flocks. However, areas in which captive and wild birds overwintered differed to some extent: only one captive-raised bird overwintered in an area used by wild tracked birds. As the wild adults were monitored from 1997 to 2003, whereas hand-reared birds were studied from 2003 to 2007, we were unable to distinguish between the effect of captive rearing and a change in wintering areas (perhaps due to anthropogenic or climatic factors).

Although data on the return journey from Iberia were available for only one wild adult fitted with a PTT, between one-third and half (according to cohorts) of the captive-bred birds returned in spring to the Poitou-Charentes region 1 or 2 years following their release. Moreover, both male and female captive-bred birds behaved normally, as males displayed and held territories and females bred repeatedly. These observations combined with the telemetry results allow us to suggest that captive-bred birds behave similarly to wild Little Bustards not only in their migratory movements, but also during the subsequent breeding seasons. Interestingly, the experiment consisting of the release of captive-bred birds originating from eggs collected in Spain (in an area where the local population of Little Bustard is sedentary, sited in the Iberian Southern Plateau) revealed that these birds did not subsequently migrate but joined the flock of sedentary birds instead. Despite the small overall sample size, three-quarters of French-bred Bustards migrated, whereas none of the Spanish ones did. In addition, the behaviour of the latter is consistent with known movements of Spanish birds, where Bustards are sedentary or perform short-distance seasonal movements (Morales *et al.* 2002) as in southern France (Wolff *et al.* 2001). This suggests that the migrating phenotype of the Little Bustard has a genetic basis, as has been demonstrated in other bird species, and is assumed to be widespread across taxa (Berthold *et al.* 1992, Berthold & Pulido 1994). As the propensity to migrate or to remain sedentary can evolve over a relatively short period (Berthold *et al.* 1992, Berthold 2001), it has been suggested that genetic variations in the propensity to migrate should exist, even within sedentary populations (Pulido 2007). This is as yet unknown for resident Little Bustards.

The conservation scheme currently taking place in western France considers the migratory trait of Little Bustards to be of prime importance. Our results indicate that if captive breeding appears not to alter this behaviour, birds need to be collected within areas where the species is known to migrate and overwinter in Spain. Our results suggest that birds from Spain do not produce migrant offspring, although the migratory behaviour of hybrids is unknown. This therefore calls into question a strategy of collecting eggs in Spain to enhance French populations, and thus we cautiously suggest that only fledglings of migratory populations should be released in the future. In more general terms, successful translocation programmes need not only to ensure population recovery, but also the expression of migratory behaviour (i.e. flyways, wintering areas) and therefore the origin of released birds. In the specific case of the Little Bustard in western France, the settlement of a captive breeding centre with sufficient number of birds originated from the local migratory population has allowed the release of approximately 350 juveniles over the last 5 years, thus boosting local productivity while preserving biological characteristics of the target population. Parallel to this action, agricultural schemes are being undertaken to restore agricultural habitats that are suitable not only for the Little Bustard, but also for many other farmland bird species.

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