IBIS The International Journal of Avian Science

BOU

Ibis (2011), **153**, 4–13

Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme

VINCENT BRETAGNOLLE,* ALEXANDRE VILLERS, LEOPOLD DENONFOUX, THOMAS CORNULIER, PABLO INCHAUSTI & ISABELLE BADENHAUSSER

Centre d'Etudes Biologiques de Chizé, CNRS, 79360, Beauvoir sur Niort, France

The Little Bustard has undergone a steep reduction of its Western Palaearctic range over the last century. In the west of France, breeding populations declined by 96% from 1978 to 2008 in cultivated areas where grasslands have been converted into intensively managed annual crops. Little Bustard abundance and nest productivity have been monitored since 1995 in a 450-km^2 site in western France. We assessed the proximate causes of the decline of Little Bustards in French farming landscapes and quantified the effectiveness of conservation measures that aimed to reverse the decline. The decline of Little Bustard, from about 65 males in 1995 to just six males in 2003, could be related to a near absence of recruitment over this period. Since 2004, the establishment of more than 1300 ha of specifically targeted agri-environment schemes (AES) in the study site has led to a sharp increase in female productivity, mainly associated with nesting in AES fields. By imposing constraints on mowing dates, AES have prevented nest destruction and female mortality during mowing and, by increasing plant species diversity, provided chicks with a higher abundance of grasshoppers. This has contributed to reversing the trend, and increasing the population to around 30 males in 2009. Conservation strategies involving specifically targeted AES based on the identification of limiting factors can help to reverse the decline of threatened species.

Keywords: agriculture, conservation, farmland birds, grasshoppers, grassland, *Tetrax tetrax*.

Since 1994, agri-environment schemes (AES) have been widely used in Europe to counteract the general decline of farmland bird populations (Kleijn & Sutherland 2003). While some authors have shown positive effects (e.g. Berendse *et al.* 2004), evidence of the effectiveness of AES remains controversial due to the lack of quantitative assessment, inappropriate statistical tests or experimental designs (Kleijn & Sutherland 2003, Kleijn *et al.* 2004, 2006). AES specifically designed for threatened birds have yielded mixed and sometimes even negative results (e.g. Kleijn *et al.* 2001) that may pertain to a lack of precise understanding of the mechanisms of the decline prior to implementation.

*Corresponding author.
Email: breta@cebc.cnrs.fr

The Little Bustard *Tetrax tetrax* is a medium-sized Palaearctic steppe bird in the Otididae (Del Hoyo *et al.* 1996) that is considered near-threatened worldwide (IUCN 2008). In Europe, Little Bustards occur in natural steppes as well as in agricultural landscapes, though the species' range has greatly reduced over the 20th century (Goriup 1994), becoming extinct in at least 10 European countries (Cramp & Simmons 1980, Tucker & Heath 1994). Formerly continuously distributed from Iberia to Russia, western European populations (of the nominate subspecies *T. t. tetrax*) are now restricted to Portugal, Spain, France and Italy. Although these countries still harbour an estimated 110 000–280 000 individuals (Birdlife International 2004), populations have declined throughout the current range (Jolivet & Bretagnolle 2002, Cabral *et al.* 2005, Petretti 2006, García de la Morena *et al.* 2006). Western

France now holds the last migratory population of the nominate subspecies (Villers *et al.* 2010), although some populations breeding in northern Spain show partial migration towards southern and central Spain (García de la Morena *et al.* 2004, 2006). The estimated French population size was 8500 displaying males in 1978–79, falling to 1400 males in 1995 (Jolivet 1996) and to 1300 males in 2000 (Jolivet & Bretagnolle 2002). The decline has only affected the migratory population breeding in cultivated areas, whereas the non-migratory population breeding in the natural steppe area of La Crau, southern France, has recently increased (Wolff *et al.* 2002, Jolivet *et al.* 2007). The core population inhabiting western farmlands has undergone one of the steepest declines recently documented for a European bird: from 7800 males in 1978 to 390 in 1996 (95% decline over 18 years; Bretagnolle & Inchausti 2005), and to 300 in 2008, with an estimated extinction risk of 45% over the next 30 years (Inchausti & Bretagnolle 2005).

In 1996, a LIFE project started in France that aimed to collect data on Little Bustard breeding biology, which was largely unknown at that time (Cramp & Simmons 1980), to identify the causes of this decline and to propose conservation measures to reverse the trend. Here, we analyse the trends of a Little Bustard population from a large (450 km^2), intensively managed cereal agro-ecosystem of western France that has shown an 80% decline in just 8 years. We assess the causes of the decline, especially in relation to the loss of suitable breeding habitat and the decline in food availability (grasshoppers, Acrididae). We also show how the implementation of targeted AES aimed at mitigating the underlying causes of the Little Bustard decline has reversed the population trends in this population.

METHODS

Study area

The study area (46°15′N, 0°30′W) covers 450 km^2 in western France, and contains over 18 000 fields of intensive agriculture, mostly dedicated to cereal crop production (41% of winter wheat in 2008) (Fig. 1). Land use on every field plot in the study site has been recorded twice a year since 1995 in a geographical information system (ARCVIEW 9.2, ESRI, Redlands, CA, USA) using 42 classes (including 38 crops) to accurately describe land use. The study area encompasses breeding and foraging habitats suitable for steppe land-birds, including three harriers *Circus* spp. and the Stone Curlew *Burhinus oedicnemus* (Salamolard & Moreau 1999). The presence of many Annex 1 species of the EU Bird Directive has led to the designation of half of the study site as a Special Protection

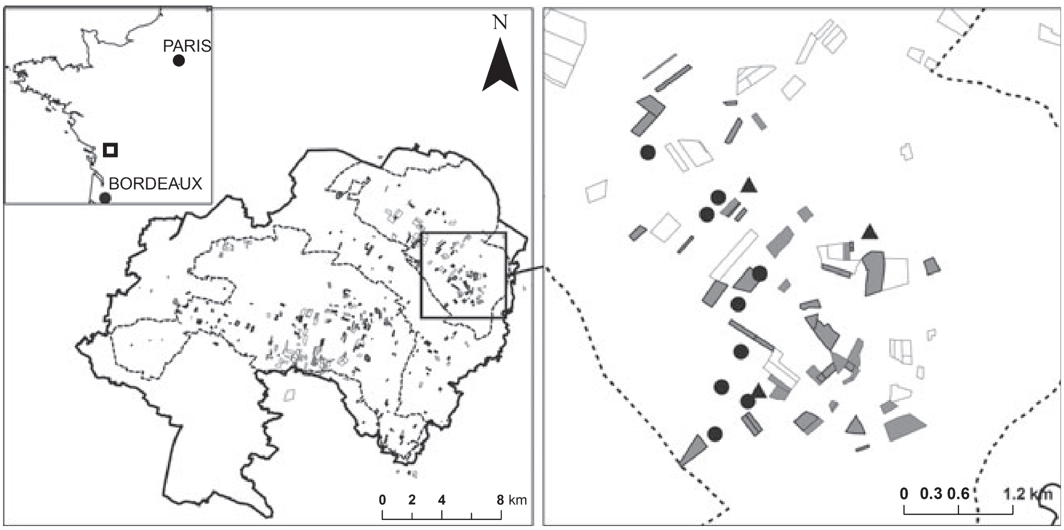

Figure 1. Location of the study area in western France. Left panel: study area and SPA 'Niort Sud-Est' in plain and dashed lines, respectively, with the different plots under AES. Right panel: close up with locations of males in 2003 (▲) and 2008 (●). Fields with AES specifically designed for Little Bustards in grey (mostly grasslands), other measures in open polygons.

Area (SPA; NATURA 2000 site) in 2004 (ZPS Niort Sud-Est, FR5412007).

A few experimental hectares of AES were implemented in the study site in 1999, and large-scale implementation started in 2004. AES had two main objectives: (1) to avoid the direct destruction of nests and/or incubating females by excluding any farming activities (especially mowing, but also grazing) in the target plot from mid-May to the end of July and (2) to increase habitat quality with regard to food availability for chicks (primarily large insects, especially grasshopper species; Jiguet 2002). Three main types of contracts were therefore designed within the AES on the study site. The first involved the conversion of annual crops into grassland and fodder crops (mainly alfalfa) for 5 years to increase the extent of perennial crops (Fig. 2c). The second type of contract prevented the mowing of alfalfa and set-aside fields, which may be used by females during the incubation period. The latter were typically plots that had already been used by Little Bustards prior to 2004 for nesting, or fields that were within or close to active leks. The third type of contract aimed at improving and restoring insect food webs to increase food abundance and availability to Little Bustard chicks by prohibiting the use of insecticides and herbicides in grasslands.

There are currently 11 specific AES contracts in this NATURA 2000 site, but those dedicated to Little Bustards mainly involve perennial crop management and restoration. In the most constraining AES contracts, farmers receive compensation for planting alfalfa that will not be harvested between 15 May and 31 July, when Bustards are nesting (see below). The compensation for losing on average two cuts, and planting alfalfa instead of a cereal crop, has varied over the years between 300 and 450 Euros/ha/year.

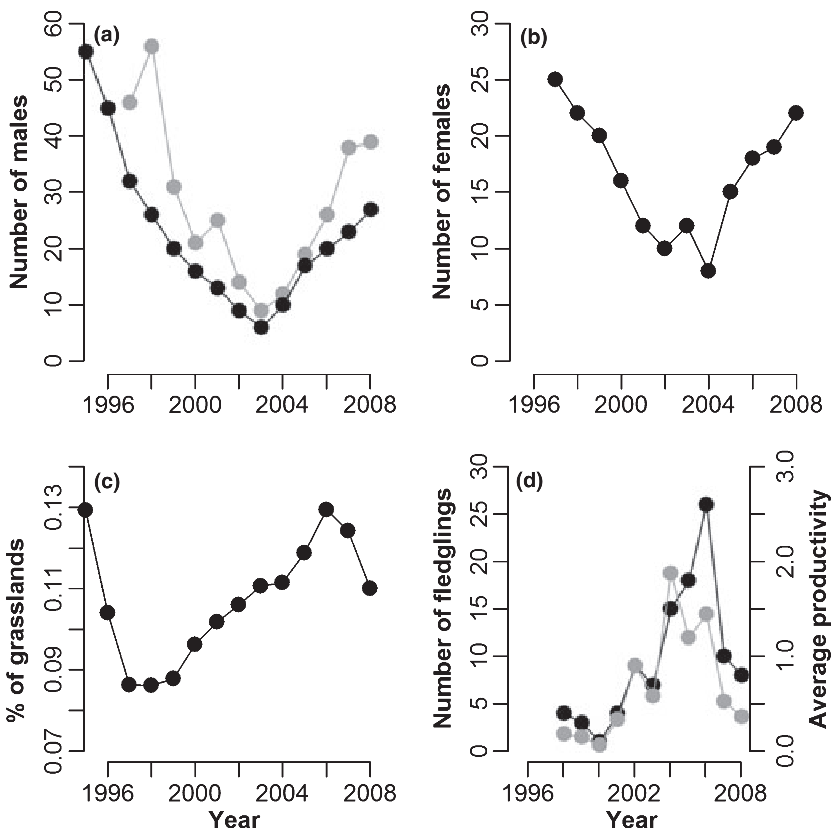

Figure 2. Population trends of Little Bustards and alfalfa cover in western France. (a) Number of male Little Bustards individually identified. In grey, all males irrespective of stay length; in black, males that stayed at least 30 days. (b) Minimum number of females sighted on the study site. (c) Percentage of grasslands on the study areas, including alfalfa. The proportion is the ratio of grassland surface over the entire study site (45 000 ha); see Methods for more details. (d) Total productivity, i.e. total number of fledglings aged more than 45 days in black; and average number of fledglings per female in grey.

Monitoring

The Little Bustard has an exploded lek mating system in which males display in aggregated sites that females attend only for mating (Jiguet *et al.* 2000). In our study site, Little Bustards are migratory (Villers *et al.* 2010). Males arrive on the breeding grounds from late March to early May, but new males continue to appear on the study site until late June, due to continuous movement between leks. Since 1995, Little Bustards have been intensively searched for on favourable plots throughout the study area during the breeding season, from late March to mid-July, by a team of three to five people, supported by other fieldworkers working on other species in the study site. The searches for Little Bustards were exclusively vehicle-based, using all roads and tracks of the study site. Sites known to have harboured Little Bustards in previous years were visited on a weekly basis, and historical sites (with no Little Bustards recorded for the last 5 years) were surveyed on a 2-weekly basis. Given the high detectability of displaying males, their clustered distribution and the coverage of the entire area by other fieldworkers, we are confident that the census was comprehensive for individuals making stays of at least 3 days. Throughout the breeding season, each male was checked at least twice a week, but in most cases, males were actually observed/located every day. Because of high individual variability in arrival and departure dates and in the length of stay in the study site, we used two population indices: (1) the number of males that stayed for at least 1 month, and usually defended a site wherein they actively displayed (the number of males staying at least 1 month was used as an index of Little Bustard population size in the study site) and (2) the number of males that were individually identified, irrespective of the length of their stay. Little Bustard males have been individually identified by breeding plumage (Arroyo & Bretagnolle 1999, Jiguet & Ollivier 2002), so that males that moved from one place to another could be monitored and were not counted as new males (repeated movements within the season have been recorded over distances of up to 8 km).

Females, despite their highly cryptic behaviour, were also intensively searched for throughout the breeding season to provide a minimal estimate of their number on the study site. This was especially true at the time of their arrival from migration, when they remain in groups for some time after the males establish their display territories. In addition, during the post-breeding period, Little Bustards gather in postnuptial groups, presumably to prepare for migration (Casas *et al.* 2009). In such groups, females and fledglings can be identified (Jiguet & Wolff 2000) and counted, thus providing an index of productivity for the population in a given year. These counts were only considered when they were carried out at the early stages of post-breeding to ensure that only local individuals were counted (Vincent Bretagnolle, unpubl. data based on marked individuals).

Nest searching

Despite the effort made to census and monitor declining Little Bustard populations, information on basic demographic parameters such as productivity has only recently been gathered (Jiguet 2001). Very few studies of breeding biology have dealt directly with females (but see Morales *et al.* 2008 and Delgado *et al.* 2009 for female density indices) because of the difficulty in making detailed observations, or of catching the birds to fit them with VHF transmitters (Ponjoan *et al.* 2008).

We systematically searched for nests in the study area over 11 breeding seasons from 1998 to 2008. Little Bustard nests are hard to find (Schulz 1985; H. Schulz pers. obs.), particularly in tall vegetation such as alfalfa fields. We used two methods to search for nests: watching females walking between nest areas and foraging sites, and active searches by foot in potentially favourable fields. The former method consisted first of detecting a field suspected to be used by a female (e.g. because a male was present nearby), usually through very careful observations, and walking systematically through the field to find the nest. The other method involved walking a potentially favourable field (e.g. with displaying males nearby, and/or a field previously used by a female) with two to six people 10–20 m apart carrying a rope to flush the female. Depending on the female behaviour (circle flights, alarm calls, etc.), a more intensive search was carried out with fieldworkers being only 1–2 m apart depending on vegetation density. To limit disturbance, fields were never searched more than once a week, except when there was a high risk of nest destruction due to mowing by farmers. Nest locations were plotted as precisely as possible (within 50 m) into the GIS and from 2002 onwards using GPS. A total of 141 nests or families were located in the 11-year survey. Since 2006, some clutches were artificially incubated (dummy eggs were placed within nests) to increase nest productivity, eggs being brought back at the nest just before hatching. Laying dates were back-calculated from an egg density regression curve obtained from captive breeding (Vincent Bretagnolle, unpubl. data), density being estimated as the ratio between egg mass and volume (length × width × width × 0.507). Although not all nests in the prospected areas were found, we assume that this large sample is representative of female breeding biology of the studied population.

Grasshopper abundance and arable weed diversity

Grasshopper surveys were carried out in AES fields (n = 10) and in non-AES fields (n = 18), sown with alfalfa in 2004 or 2005. Grasshopper abundance was estimated in each field by means of a cage sampler (1 × 1 m basis) at 15 random points in each field, and on two dates (11 July and 7 August) corresponding to the peak grasshopper densities for immatures and adults (see Badenhausser *et al.* 2007, 2008, 2009 for additional details on methodology). The total number of grasshoppers, either adults or nymphs, for each 1-m^2 plot was then averaged over the field and expressed as grasshopper density/m^2. In addition, since 1999, grasshopper abundance has been monitored every year in grasslands using a random sampling design that consists of selecting 30–221 fields among available grasslands (depending on years), including leguminous fields and herbaceous grasslands whatever their management (grazing, cutting or set-aside). For each field, 10 random 1-m^2 points were sampled.

Weed surveys were carried out from 10 April to 15 May 2006 in the same AES and non-AES alfalfa fields as for grasshoppers, using 30 randomly distributed 0.25-m^2 quadrats per field. In each quadrat, the presence of every species observed was recorded to obtain the total species richness for each field.

Statistical analyses

We used generalized linear effects models for statistical analyses, with error distribution and link function adapted to data distribution and characteristics, i.e. binomial, Poisson, quasi-Poisson or normal error terms. Although when performing statistical tests there may have been cases of non-independence in data (e.g. nests from the same female), we assumed that this was a minor problem as there were very unlikely to be repeated attempts from the same parents (i.e. male and female) in the same year. Mayfield or logistic exposure methods could not be used to examine nest survival due to the lack of repeated visits to nests.

RESULTS

Trends between 1995 and 2008

In our study site, the number of displaying males that stayed more than 1 month declined from more than 55 in 1995 to only six in 2003 (Fig. 2a). In 2003, six males were actually present throughout the breeding season, while three additional males arrived in June but stayed < 1 month. Thereafter, male numbers started to increase again, reaching 27 in 2008. Similar trends were found when using the number of males identified individually (although these data are available only from 1999 onwards, Fig. 2a) and for females, although surveys were less accurate than for males (Fig. 2b). Given the demographic parameters currently available for this species, i.e. adult survival of 75–80% and juvenile survival of *c.* 50% (Morales *et al.* 2004, Bretagnolle & Inchausti 2005), the decline of Little Bustards in the study site is compatible with a near absence of recruitment between 1996 and 2003. This would lead to a decrease of *c.* 15% per year compared with the observed decline of 18% per year. Based on post-breeding counts, female productivity was indeed almost zero in this period (Fig. 2d). After 2004, however, there was a sharp increase in the number of fledglings produced in the study site (Fig. 2d), from 2004 to 2006, exceeding the threshold value of one chick per female considered necessary for a sustainable Little Bustard population (Inchausti & Bretagnolle 2005). In 2007 and 2008, female productivity dropped as a likely consequence of very wet and cold springs that were detrimental to grasshopper abundance, a food resource necessary for Little Bustards to achieve a high reproductive success (Jiguet & Ollivier 2002).

Causes of decline in the Little Bustard: nest destruction and starvation

Between 1997 and 2008, 92 nests were found in the study site (at the incubation stage). Among 88 nests for which habitat type was recorded, 50% were found in alfalfa, 23% in set-aside and 24% in grasslands (either pure grass, or mixed with legumes). However, the percentage of nests in alfalfa varied strongly between years, from 14 to 100% (excluding years with fewer than seven nests found). In addition, there was strong seasonal variation, with early (first quartile) nests being found only in grasslands and mixed grasslands with legumes, whereas late nests were nearly always in alfalfa (last quartile). Little Bustards laid eggs over an extended period (81 days, laying dates available for 92 nests monitored between 1998 and 2008) ranging from 2 May to 22 July.

Overall, 36% of nests failed at the incubation stage, sometimes due to predation (7%), but mainly owing to destruction during mowing operations (70%) or abandonment by females after harvesting removed all vegetation, and thus camouflage (23%). Therefore, more than one-third of all nests failed at the incubation stage due to harvesting operations, a proportion that reached 50% (n = 45 nests) before AES were implemented in 2004 (see below). Productivity per female was obtained from the observation of 87 families (at all chick stages) and was very low, especially at the start of the study (Fig. 2d), with an average overall productivity of around 0.1 chicks per female. For 78 nests discovered at the egg stage and for which fledging status was known, productivity per breeding female was 0.26 chicks between 1997 and 2003 (n = 45 nests), but doubled (0.52 chicks per female) from 2004 on. There was strong evidence of brood reduction from hatching to fledging, with average family size (± sd) being respectively 1.32 ± 1.35, 0.77 ± 1.2, 0.51 ± 1.0, 0.49 ± 1.0 and 0.36 ± 0.97 for families at 7 days, at < 15 days, 15 –30 days, 30–45 days old and > 45 days, respectively (n = 78 nests). Despite a very high observation effort of Little Bustard families from hatching to fledging, no evidence of predation on chicks was found, and all of the dead chicks that were recovered showed signs of starvation. Anecdotal evidence based on radiotracked females in 1998 and 1999 indicated that females and their chicks as young as 10 days old could travel 1–2 km/day when grasshopper abundance was low and that, in such cases, females lost on average one chick every 2 days.

AES and Little Bustard productivity

The number of hectares within AES in the study site grew rapidly from 2004 to 2008, with nearly 1200 ha under contract in 2008, though only approximately 20% of these AES were actually sown with alfalfa (Table 1). In addition, we tried to aggregate fields under contract spatially to achieve locally stronger effects both in attracting Little Bustards to favourable habitat and in increasing grasshopper abundance (Fig. 1).

We did not find any effect of AES on either clutch or egg size (Gaussian generalized linear models (GLM); $F_{3,101} = 0.915$ for egg size, $P = 0.44$; Poisson GLM for clutch size, $P > 0.5$). Clutches were laid in AES fields slightly later than in non-AES fields (average difference ± se = 4.1 ± 0.79 days). Nevertheless, the proportion of Little Bustard nests found in AES fields increased from 0 to nearly 70% after 2004 (Table 1). Only two nests out of 37 (5.4%) were destroyed in AES fields. There was no evidence that male Little Bustards settled preferentially in the AES fields (Fig. 1). However, this is difficult to test satisfactorily because the scheme for contracting with farmers took into account the presence of males, by implementing AES close to sites with displaying Little Bustards.

Alfalfa, grasshoppers and Little Bustard productivity

The area of alfalfa in the study site shows two periods with opposing trends: a strong decline from 1995 until about 2000, followed by a stabilization and an increase from 2003 to 2004 (Fig. 2c). Only

Table 1. Number of hectares under contract with farmers in the study site between 2005 and 2008 (contracts were established with farmers the previous year) for each type of AES. The last two rows show the number of Little Bustard nests found in the study site and the proportion in AES fields.

AES	2005	2006	2007	2008	Total ha in AES
Set-aside	115	52	17	18	202
Alfalfa (un-mowed during spring)	23	20	10	1	54
Alfalfa (in replacement of annual)[1]	20	–	90	50	160
Other[2]	350	96	270	–	716
Total	508	168	387	69	1132
% nests found in AES	15	50	62.5	58.5	
Number of nests found	7	9	13	8	

[1]In some contracts, this also includes no mowing during spring (with additional payment).
[2]Includes mainly 'drilling' and herbicide reduction.

part of the increase in alfalfa area since 2004 was attributable to AES because it involved approximately 600 ha of alfalfa overall, only 200 ha of which was in the AES (Table 1).

Plant species richness was significantly higher in alfalfa fields with AES (mean ± se = 31.8 ± 4.2) than without (16.5 ± 2.1; $F_{1,17} = 12.8$, $P = 0.002$). AES also had a positive effect on the abundance of the main grasshopper taxa encountered in the study site (Gomphocerinae, *Pezotettix giornae* Rossi and *Calliptamus italicus* L.) irrespective of the sampling date (Fig. 3): 121.4 ± 28.4 ind/15 m^2 in AES fields and 14.6 ± 3.6 ind/15 m^2 in the non-AES fields (quasi-Poisson GLM, $P < 0.001$, dispersion parameter = 1.02) on the first sampling date, and 38.3 ± 9.1 ind/15 m^2 in AES fields and 12.8 ± 3.2 ind/15 m^2 in the non-AES fields (quasi-Poisson GLM, $P < 0.001$, dispersion parameter = 16.6) on the second sampling date. Grasshopper abundance and plant species richness in alfalfa fields were positively related in AES fields, although this relationship was possibly masked by insecticide treatments in non-AES fields (Badenhausser *et al.* 2008). In other words, the herbicide and insecticide ban in AES alfalfa increased weed diversity and grasshopper abundance, although a causal link could not be established.

There was a clear positive relationship between grasshopper abundance (calculated as the mean abundance over the surveyed fields for a given year) and Little Bustard productivity (number of fledglings counted in post-nuptial groups) ($F_{1,8} = 11.05$, $P = 0.01$; Fig. 4).

DISCUSSION

European farmed landscapes have traditionally consisted of complex mosaics of extensive crops that sustained high levels of biodiversity (Potter 1997, Walk & Warner 2000). Over the last 50 years, however, farmlands of western European countries have experienced dramatic changes, mainly through the intensification of farming techniques (Fuller *et al.* 1995, Siriwardena *et al.* 2000, Robinson & Sutherland 2002). Plants, insects and birds have declined at the community level (Tucker & Heath 1994, Pain & Dixon 1997, Bouma *et al.* 1998, Söderström & Part 2000, Chamberlain *et al.* 2000).

In the case of the Little Bustard, habitat loss and degradation, a result of agricultural intensification and increasing application of agro-chemicals that reduce food availability, were suspected to be responsible for the species decline (Goriup 1994). Our 15-year study has largely confirmed those threats and quantified their effects on Little Bustard productivity. Food reduction, mostly in arthropods, which are an essential resource for fledging success (Jiguet 2002), may be a limiting factor for Little Bustard productivity in agricultural habitats (Traba *et al.* 2008). Indeed, grasshoppers

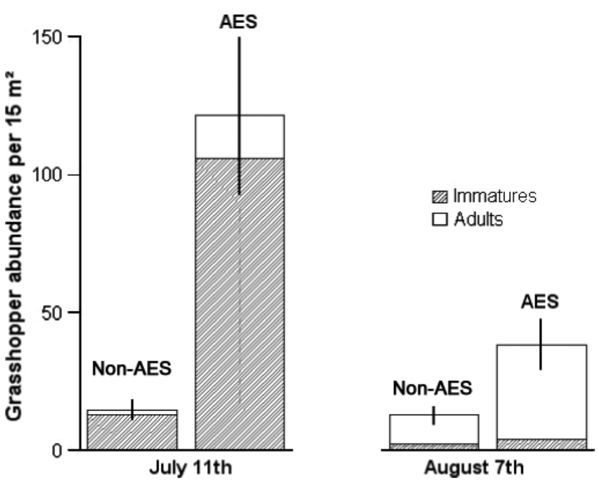

Figure 3. Total number of grasshoppers (immatures and adults) over 15 m^2, in AES and in non-AES alfalfa fields at two sampling dates (total ± se).

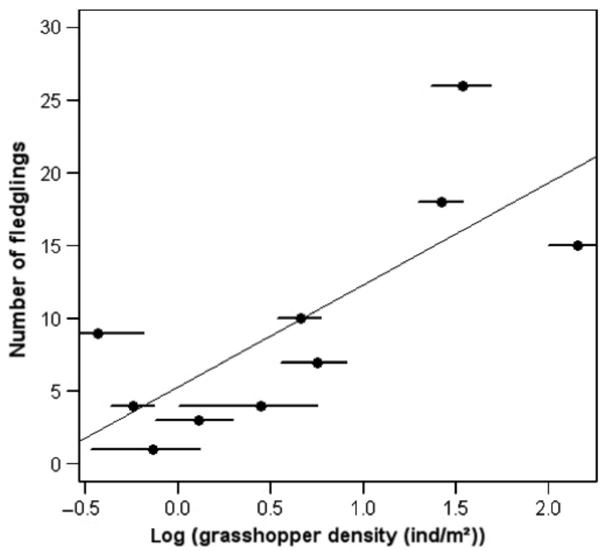

Figure 4. Little Bustard productivity (total number of fledglings aged more than 45 days) and grasshopper density (ind/m^2 ± se) in grassland fields over the study area.

constitute the bulk of Little Bustard chick diet (Jiguet 2002). Data obtained in captivity have revealed that Little Bustard chicks require around 200 grasshoppers per day (Vincent Bretagnolle, unpubl. data). With an average grasshopper density of $< 1/m^2$ (in non-AES fields), female Little Bustards must forage either in the richest plots or over large areas. Little Bustards rarely nested in crops other than alfalfa in our study site. Over half of Little Bustard nests were destroyed during the mowing of alfalfa, at least until AES were implemented. Before AES, there was a strong implication that a significant proportion of females did not breed, and for those that laid eggs, half of the nests were destroyed by alfalfa harvesting during incubation. For the remaining clutches that hatched, brood reduction, probably due to food shortage, resulted in almost complete chick loss. Consequently, between zero and two fledglings joined the post-breeding gatherings each year, resulting in almost no recruitment into the breeding stock between 1995 and 2001.

A first phase of the conservation strategy (1995–2000) consisted of gaining an understanding of Little Bustard breeding biology in agricultural landscapes and the consequences of farming activities on productivity and survival. Only thereafter could conservation measures start to be formalized and implemented on our study site. Little Bustard conservation efforts in France have been targeted at increasing insect availability (Jolivet & Bretagnolle 2002) and decreasing nest destruction through agri-environmental measures and, to a lesser extent, preventing female mortality during the mowing of grasslands. The main result of the conservation actions undertaken on our study site has been a complete reversal of the population trend, with male population size in 2008 being similar to that in 1998. It is not known whether the population increased due to local recruitment or immigration, as the ringing of a large number of wild chicks is technically difficult and questionable given the conservation status of the species. Large-scale monitoring of the entire western French population of male Little Bustards every 4 years since 1996 (Jolivet *et al.* 2007) has revealed a strong decline in non-SPA zones and, at the same time, either stable or increasing Little Bustard populations in SPAs. Thus in 2009, 85% of males were in SPAs in the region Poitou Charentes (compared with only 50% in 2000). This suggests that immigration might have contributed to the observed population increase (associated with the attractiveness of the SPA relative to surrounding areas), in addition to local improvements in productivity. Unfortunately, data on male dispersal are scarce and we can only propose a scenario that would need to be verified through data analysis on factors affecting male movement at a local scale, such as habitat quality and the presence of conspecifics. On the other hand, the observed rate of population increase (20% between 2003 and 2008) is still compatible with the recruitment of fledglings produced locally, with no need for immigration. In other words, the sharp increase in local productivity could be a direct consequence of a beneficial effect of AES on Little Bustard dynamics, as nests were increasingly located in fields under AES after 2004, the latter allowing higher survival for both females and chicks compared with years before the settlement of AES. However, it was not technically possible to quantify those effects directly on female or chick survival. In summary, even if the relationship between the increase in the number of chicks fledged and the settlement pattern in AES fields is largely correlative, the improvement in local resource abundance (see below) is very likely to have contributed to the increase in local Little Bustard productivity.

AES, at least for those cropped with alfalfa, also benefited other components of biodiversity. This perennial cover allowed higher diversity of arable weeds and grasshopper biomass compared with other annual crops where grasshoppers are almost absent. In addition, AES alfalfa showed higher diversity of weeds, and high abundance of grasshoppers, compared with non-AES alfalfa, suggesting that herbicide and insecticide bans are important practical measures to restore functional biodiversity in intensively managed agro-ecosystems. Although the AES involving alfalfa and its associated management practices were specifically designed for the protection of an endangered species, alfalfa seems to play a key role in intensive agricultural landscapes, at least at the regional level. We believe that alfalfa constitutes a semi-permanent habitat with relatively few impacts from management operations, resulting in higher associated biodiversity than in surrounding annual crops and helping to maintain the functioning of trophic chains in intensive agroecosystems. The implementation of AES and their costs have recently been the focus of much criticism (Kleijn & Sutherland 2003, Kleijn *et al.* 2006). Overall, it has been found that the results of AES in terms of their effect on farmland biodiversity were at best equivocal, and at worse negative. Based on our data on the population dynamics of Little Bustards as well as on more general benefits of AES in our study site, we argue that AES relying on ecological studies and therefore using ecological processes as proximate mechanisms for targeting measures can be implemented at reasonable costs with major benefits for farmland biodiversity.

We would like to thank the many fieldworkers who helped with searching for Little Bustard nests and monitor males over the years, too many to name individually. This study was partially financially supported by the European Union (LIFE FR000091). We also thank Ludovic Renaudet, Victor Turpaud-Fizzala and Carole Attié for their help. V.B. expresses his gratitude to the BOU and especially to Will Peach for inviting him to the Farmland Bird Conference held in 2009. The manuscript has been very much improved by comments from J. Vickery and D. Chamberlain.

REFERENCES

Arroyo, B.E. & Bretagnolle, V. 1999. Field identification of individual Little Bustard *Tetrax tetrax* males using plumage patterns. *Ardeola* **46**: 53–60.

Badenhausser, I., Amouroux, P. & Bretagnolle, V. 2007. Estimating acridid densities in grassland habitats: a comparison between presence-absence and abundance sampling designs. *Environ. Entomol.* **36**: 1494–1503.

Badenhausser, I., Mediene, S., Paris Le Clerc, N. & Bretagnolle, V. 2008. Effects of agri-environnemental agreements on acridids and plant species richness in alfalfa crops. In Hopkins, A. *et al.* (eds) *22st International Symposium of the European Grassland Federation*: 54–56. Uppsala, Sweden: Swedish University of Agricultural Sciences (SLU).

Badenhausser, I., Amouroux, P., Lerin, J. & Bretagnolle, V. 2009. Acridid (Orthoptera: Acrididae) abundance in Western European Grasslands: sampling methodology and temporal fluctuations. *J. Appl. Entomol.* **133**: 720–732.

Berendse, F., Chamberlain, D., Kleijn, D., Schekkerman, H. 2004. Declining biodiversity in agricultural landscapes and the effectiveness of agri-environmental schemes. *Ambio* **33**: 500–505.

Birdlife International. 2004. *Birds in Europe II: Population Estimates, Trends and Conservation Status*. Cambridge: BirdLife International.

Bouma, J., Varralyay, G. & Batjes, N. 1998. Principal land use changes anticipated in Europe. *Agric. Ecosyst. Environ.* **67**: 103–119.

Bretagnolle, V. & Inchausti, P. 2005. Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining Little Bustard (*Tetrax tetrax*) in agricultural habitats. *Anim. Conserv.* **8**: 59–68.

Cabral, M., Almeida, J., Almeida, P., Dellinger, T., Ferrand de Almeida, N., Oliveira, M., Palmeirim, J., Queiroz, A., Rogado, L. & Santos-Reis, M. 2005. *Livro Vermelho dos Vertebrados de Portugal*. Lisbon: Instituto de Conservaçao da Natureza.

Casas, F., Mougeot, F., Viñuela, J. & Bretagnolle, V. 2009. Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. *Anim. Conserv.* **12**: 346–354.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**: 771–788.

Cramp, S. & Simmons, K. 1980. *The Birds of the Western Palearctic*, Vol. **2**. Oxford: Oxford University Press.

Del Hoyo, J., Elliott, A. & Sargatal, J. 1996. *Handbook of the Birds of the World*, **Vol. 3**. Hoatzin to Auks. Barcelona: Lynx Edicions.

Delgado, M.P., Morales, M.B., Traba, J. & Garcia De La Morena, E.L. 2009. Determining the effects of habitat management and climate on the population trends of a declining steppe bird. *Ibis* **151**: 440–451.

Fuller, R.J., Gregory, R., Gibbons, D., Marchant, J., Wilson, J., Baillie, S. & Carter, N. 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* **9**: 1425–1441.

Garcéa de la Morena, E. L., De Juana, E., Martínez, C., Morales, M. B. & Suárez, F. 2004. Sisòn Común (*Tetrax tetrax*). In Madroño, A. (Ed.) *Libro Rojo de las Aves de España*: 202–207. Madrid: SEO-Birdlife-Ministerio de Medio Ambiente.

García de la Morena, E., Bota, G., Ponjoan, A. & Morales, M.B. 2006. *El sisón común en España. I censo Nacional*. Madrid: in SEO/BirdLife.

Goriup, P. 1994. Little Bustard *Tetrax tetrax*. In Tucker, G. & Heath, M. (eds) *Birds in Europe: Their Conservation Status*: 236–237. Cambridge: Birdlife International.

Inchausti, P. & Bretagnolle, V. 2005. Predicting short-term extinction risk for the declining Little Bustard (*Tetrax tetrax*) in intensive agricultural habitats. *Biol. Conserv.* **122**: 375–384.

IUCN. 2008. *IUCN Red List of Threatened Species*. Gland, Switzerland: IUCN.

Jiguet, F. 2001. *Défense des Ressources, Choix du Partenaire et Mécanismes de Formation des Leks chez l'Outarde Canepetière*. PhD thesis, Université Paris 6.

Jiguet, F. 2002. Arthropods in diet of Little Bustards *Tetrax tetrax* during the breeding season in western France. *Bird Study* **49**: 105–109.

Jiguet, F. & Ollivier, D. 2002. Male phenotypic repeatability in the threatened Little Bustard *Tetrax tetrax*: a tool to estimate turnover and dispersal. *Ardea* **90**: 43–50.

Jiguet, F. & Wolff, A. 2000. Déterminer l'âge et le sexe des Outardes canepetières *Tetrax tetrax* à l'automne. *Ornithos* **7**: 30–35.

Jiguet, F., Arroyo, B. & Bretagnolle, V. 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. *Behav. Process.* **51**: 63–82.

Jolivet, C. 1996. L'Outarde canepetière, *Tetrax tetrax*, en déclin en France-situation en 1995. *Ornithos* **3**: 73–77.

Jolivet, C. & Bretagnolle, V. 2002. L'Outarde canepetière en France: évolution récente des populations, bilan des mesures de sauvegarde et perspectives d'avenir. *Alauda* **70**: 93–96.

Jolivet, C., Bizet, D., Wolff, A. & Bretagnolle, V. 2007. Statut de l'outarde canepetière en France en 2004 et mesures de conservation. *Ornithos* **14**: 80–94.
Kleijn, D. & Sutherland, W. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* **40**: 947–969.
Kleijn, D., Berendse, F., Smit, R. & Gillissen, N. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* **413**: 723–725.
Kleijn, D., Berendse, F., Smit, R., Gilissen, N., Smit, J., Brak, B. & Groeneveld, R. 2004. Ecological effectiveness of agri-environment schemes in different agricultural landscapes in The Netherlands. *Conserv. Biol.* **18**: 775–786.
Kleijn, D., Baquero, R., Clough, Y., Diaz, M., Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R. *et al.* 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* **9**: 243–254.
Morales, M.B., Bretagnolle, V. & Arroyo, B.E. 2004. Viability of the endangered Little Bustard *Tetrax tetrax* population of western France. *Biodivers. Conserv.* **14**: 3135–3150.
Morales, M., Traba, J., Carriles, E., Delgado, M. & de la Morena, E.G. 2008. Sexual differences in microhabitat selection of breeding Little Bustards *Tetrax tetrax*: ecological segregation based on vegetation structure. *Acta Oecol.* **34**: 345–353.
Pain, D. & Dixon, J. 1997. Why farming and birds in Europe? In Pain, D. & Pienkowski, M.W. (eds) *Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation*: 1–24. London: Academic Press.
Petretti, F. 2006. Conservation of Steppe Birdlife in Italy. In Gafta, D. & Akeroyd, J. (eds) *Nature Conservation*: 235–239. Berlin: Springer.
Ponjoan, A., Bota, G., Garcia De La Morena, E.L., Morales, M.B., Wolff, A., Marco, I. & Manosa, S. 2008. Adverse effects of capture and handling Little Bustard. *J. Wildl. Manage.* **72**: 315–320.
Potter, C. 1997. Europe's changing farmed landscapes. In Pain, D. & Pienkowski, M. (eds) *Farming Birds in Europe*: 25–42. London: Academic Press.
Robinson, R. & Sutherland, W. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* **39**: 157–176.
Salamolard, M. & Moreau, C. 1999. Habitat selection by Little Bustard *Tetrax tetrax* in a cultivated area of France. *Bird Study.* **46**: 25–33.
Schulz, H. 1985. *Grundlagenforschung zur Biologie der Zwergtrappe Tetrax tetrax*. PhD thesis, EG-Forschungsvorhaben, Abschlußbericht. Staatl. Naturhistorisches Museum, Braunschweig.
Siriwardena, G., Crick, H., Baillic, S. & Wilson, J. 2000. Agricultural land-use and the spatial distribution of granivorous lowland farmland birds. *Ecography* **23**: 702–719.
Söderström, B. & Part, T. 2000. Influence of landscape scale on farmland birds breeding in semi-natural pastures. *Conserv. Biol.* **14**: 522.
Traba, J., Morales, M., Garcá de la Morena, E., Delgado, M. & Krištn, A. 2008. Selection of breeding territory by Little Bustard (*Tetrax tetrax*) males in Central Spain: the role of arthropod availability. *Ecol. Res.* **23**: 615–622.
Tucker, G. & Heath, M. (eds) 1994. *Birds in Europe. Their Conservation Status*. Cambridge: Birdlife International.
Villers, A., Millon, A., Jiguet, F., Lett, J.-M., Attie, C., Morales, M.B. & Bretagnolle, V. 2010. Migration of wild and captive-bred Little Bustards *Tetrax tetrax*: releasing birds from Spain threatens attempts to conserve declining French populations. *Ibis* **152**: 254–261.
Walk, J. & Warner, R. 2000. Grassland management for the conservation of songbirds in the Midwestern USA. *Biol. Conserv.* **94**: 165–172.
Wolff, A., Dieuleveut, T., Martin, J.-L. & Bretagnolle, V. 2002. Landscape context and Little Bustard abundance in a fragmented steppe: implications for reserve management in mosaic landscapes. *Biol. Conserv.* **106**: 211–220.

Received 17 July 2009;
revision accepted 27 October 2010.
Associate Editor: Juliet Vickery.