

Are farming and birds irreconcilable? A 21-year study of bustard nesting ecology in intensive agroecosystems



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ABSTRACT

Farmland landscapes in developed countries have undergone major habitat changes over the past 60 years leading to the decline of many species. Of these, the little bustard, a medium-sized, long-lived, ground nesting bird, has declined by 95% in France over the last 35 years. Here we present the results of a 21 year survey of the nesting ecology of this elusive species, analyzing 157 breeding attempts, the largest data set ever collated for this species. Females had a strong preference for meadows for breeding, yet this habitat only represented 14% overall habitat. Alfalfa alone accounted for 50% of nest locations. However, apart from vegetation type, females did not show any other pattern of habitat selection (vegetation height, nest position within field, field under agri-environmental contract-AES-). In addition, the laying period was extremely extended, spanning almost 3 months. We did not detect any strong effect of crop, date or whether the nesting field was in AES or not, on clutch size, egg size and egg-laying date. However, there were long-term changes in breeding phenology (females breed earlier than 20 years ago), and selection of vegetation between years and within years. Hatching success was very low (about half of the broods were destroyed by farm work), and both fecundity and productivity per female were found to be approximately one third of the values expected for a stable population. Overall, nesting females of Little Bustards select meadows in regard to their availability, but do not show any particular preference within meadows' vegetation structure or height. We show that in such system, meadows act as ecological traps, and furthermore, because females do not appear selective, it is impossible to manage meadows in order to limit this trap. We finally analyze whether the land-sharing AESs can conserve this species in intensive arable systems and conclude that the land sharing may not be sustainable. We discuss our results in light of the alternative of land sparing, and suggest that this is probably a better fit for the conservation of large-bodied bird species given their ecological constraints (large home ranges, presence of semi-natural landscape components and freedom from human interference).

1. Introduction

European farmed landscapes have traditionally consisted of complex mosaics of extensive crops: these diverse landscapes sustained high levels of biodiversity (Walk and Warner, 2000; O'Connor and Shrubbs, 1986). Over the past 50 years, however, farmed landscapes have dramatically changed with the intensification of farming techniques and simplification of land use patterns (Donald et al., 2006). These changes have resulted in a loss of biodiversity in Europe as well as North America, similar to the losses that may result from climate change (Herkert, 1997). Entire communities of plants, insects and birds have declined in response to agriculture intensification (Geiger et al., 2010). Farmland habitats host a high proportion of birds with threatened conservation status in Europe (Tucker and Heath, 1994) and farmland

birds are those declining most rapidly (Inger et al., 2015; PECBMS, 2017). Birds relying on extensive agriculture are threatened worldwide: bustards (*Otididae*) are a prime example, as a family of birds leaving in open, farmed or grazed, landscapes in Asia, Africa, Europe and Australia. Half of the 27 species are red-listed worldwide (BirdLife, 2017).

The little bustard *Tetrax tetrax* is a lekking grassland bird and is the smallest (body mass ~ 900 g) of the three western Palearctic bustards. Its range has shrunk during the last century (García de la Morena et al., 2006), disappearing from > 10 European countries (Collar et al., 2016). The French population has shown a particularly severe decline, especially the ecotype breeding in arable farmlands. The latter crashed from an estimated 7500 males in 1979 to 700 in 1995, 500 in 2000 (Jolivet and Bretagnolle, 2002) and just 330 in 2016, i.e. a 96% decrease in 35 years. Proactive conservation efforts in France started in

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1997 with the first LIFE project (1997–2001) which set up the first agri-environment schemes (AES) in collaboration with farmers and resulted in the designation of 8 Special Protection Areas in 2004 (Berthet et al., 2012). Such measures were effective with numbers declining more slowly since 2000 after the introduction of the Natura 2000 network and the designation of c.12,000 ha AESs targeting the little bustard (Bretagnolle et al., 2011). The decline was slowed, but continued and so a second LIFE project was undertaken to reinforce this unique migratory population (Villers et al., 2010) to avoid possible extinction (Bretagnolle and Inchausti, 2005; Morales et al., 2004). The project set up a conservation stock and a breeding center run by the local authority. But the abandonment of compulsory set-aside (2007), the decoupling of Common Agricultural Policy (CAP) aids, the high prices of cereals since 2009 and the most recent CAP reform (2015), annihilated the effectiveness of these measures and the Little Bustard in Centre-West France remains on the verge of extinction (Inchausti and Bretagnolle, 2005; unpubl. data).

A number of possible causes of the decline have been identified: food deficit for chicks and fledglings (Jiguet, 2002), increasing application of agro-chemicals (Goriup, 1994) and destruction of clutches, broods or even incubating females during mowing (Bretagnolle et al., 2011; unpubl. data). However, their relative impacts on bustard population dynamics or persistence are unknown, because proxies have been the only tools used to assess both the causes of decline and the observed impacts of conservation measures, e.g. monitoring insect abundance (Guerrero et al., 2011), habitat quality (Delgado et al., 2009) or male numbers (Robleño et al., 2017). Information on basic population parameters such as fecundity, productivity and adult female turnover are completely lacking: the only two studies that investigated female breeding (Lapiedra et al., 2011; Morales et al., 2013) analyzed families. Here, we provide the first detailed description of female nesting ecology, nest habitat selection, egg and clutch sizes, and clutch and family fates, with a large sample size (over 100 nests). By describing the breeding biology of female little bustards in intensive arable land using data collected from 1997 onwards, we investigate the dependence of female nest habitat selection and breeding performance on current land use and farming practices. We question whether current public policies, such as AESs, provide enough incentives to avoid the extinction of these large-bodied farmland birds. These birds represent the most difficult conservation challenge in these habitats, given their large home ranges, avoidance of humans, and complex ecological requirements such as the presence of semi-natural habitats and crop mosaics. The AESs are based on land-sharing but we argue here that land-sparing may be the only strategy that matches the compromise required between allocating land for the conservation of large-bodied farmland birds and the tremendous challenge of feeding 9.6 billion people by 2050 (Godfray et al., 2010).

2. Methods

2.1. Study area

The study area was the Long Term Social-Ecological Research “Zone Atelier Plaine & Val de Sèvre” (46°15N, 0°30W), a site which covers 450 km² of intensive agriculture in Western France (about 13,000 fields), mostly dedicated to cereal production (Bretagnolle et al., 2018). Since 1995, the land use of every agricultural field has been recorded annually and mapped (ArcGIS 10.5; see Fig. 1). Large urban and wooded areas and river valleys have been excluded as they are unsuitable for grassland species, resulting in ~350 km² of habitats suitable for grassland birds (breeding and foraging habitat), including three harriers *Circus* spp. and Stone Curlews *Burhinus oediacnemus*. The presence of many species covered by the EU Bird Directive led to the designation of a NATURA 2000 site in 2004 (FR5412007).

2.2. Little bustard nest searching

The data used for the study were collected during intensive monitoring surveys performed over 13 breeding seasons from 1997 to 2009, and more occasional observations and nest searches since 2010 (94 nests were found and 28 families were observed in 1997–2009 vs 2 nests and 14 families since 2010). In 1997–2009, we systematically searched each year for nests over the study area. Nests of Little Bustard are exceedingly hard to find. Two methods were used to search for the nests: watching females walking between the nest area and foraging sites and active searches on foot through vegetation. We generally proceeded by detecting a field used by a female, by very intensive surveys and careful observations and, when a female was suspected, by walking through the field. Active searches consisted of walking in such field with three to five persons 10–20 m apart with a hose between observers in order to flush the female. Depending on the females' behavior (circular flights, type and frequency of alarm calls), a more intensive search would be carried out with observers only one to two meters apart (depending on the density of vegetation). About 90% active nests were found by using the latter method. Addition nests were found (and sometimes destroyed) by farmers during mowing. Nests were found on average 10 ± 7.84 days before hatching ($N = 72$). In order to limit the disturbance, a particular field was not searched more than twice in a week, except in the case of imminent mowing by farmers. It is therefore impossible to confirm whether all the nests in the prospected areas were found, and it is very unlikely to be so. Nest locations were recorded as precisely as possible (within 50 m) in the GIS, and from 2002 with GPS (5–10 m precision).

2.3. Eggs, chicks and nesting success

Eggs and chicks were measured to the nearest 0.1 mm and weighed to the nearest 0.5 g using a spring scale. The egg volume was obtained using the formula $length \times width^2 \times 0.507$ (Hoyt, 1979). When possible, a nest found during the incubation period was visited again about the time the chicks should hatch. We used chick biometrics of known-aged individuals (from hand-raised captive chicks) to derive growth curves for the tarsus, as this parameter has proved the most reliable for ageing chicks (Appendix 1). In the field, chicks were visually aged by direct comparison with the female, since until 55 days old, chicks remain with their mother (Appendix 1). Laying date was either determined directly from nest visits or estimated by backdating from the hatching date assuming 21 days incubation for an egg (Cramp and Simmons, 1980; unpublished data). Since incubating nests were visited only once we could not use Mayfield method or its more recent developments (e.g., Shaffer, 2004) could not be applied to correct for nest failure rate. Nest success was therefore calculated as the fraction of hatching broods out of total broods, and is likely overestimated, while fledging success relied on opportunistic observations (see Bretagnolle et al., 2011 for details). Productivity is the number of fledglings (surviving to 45 days) per female.

2.4. Statistical analyses

For the analysis of nesting habitat selection, we first delineated the area in which all nests were discovered (Fig. 1), based on all nests found in all years combined, using a kernel method with an ad hoc smoothing parameter ($h = 1374$ m). We used compositional analysis of habitat (Aebischer et al., 1993) to compare the crops used to those available, at two scales (second-, and third-order habitat selection). Usually, this type of analysis uses individuals as statistical units, but, for our study, years were considered as the statistical units. At a large spatial scale (second order habitat selection), we compared the available crops in the nesting area (~7% of the study site, see Fig. 1) to the entire study site. Then, at a finer scale, we compared the crops actually used by breeding females to the available crops in the nesting area. As a first step, land

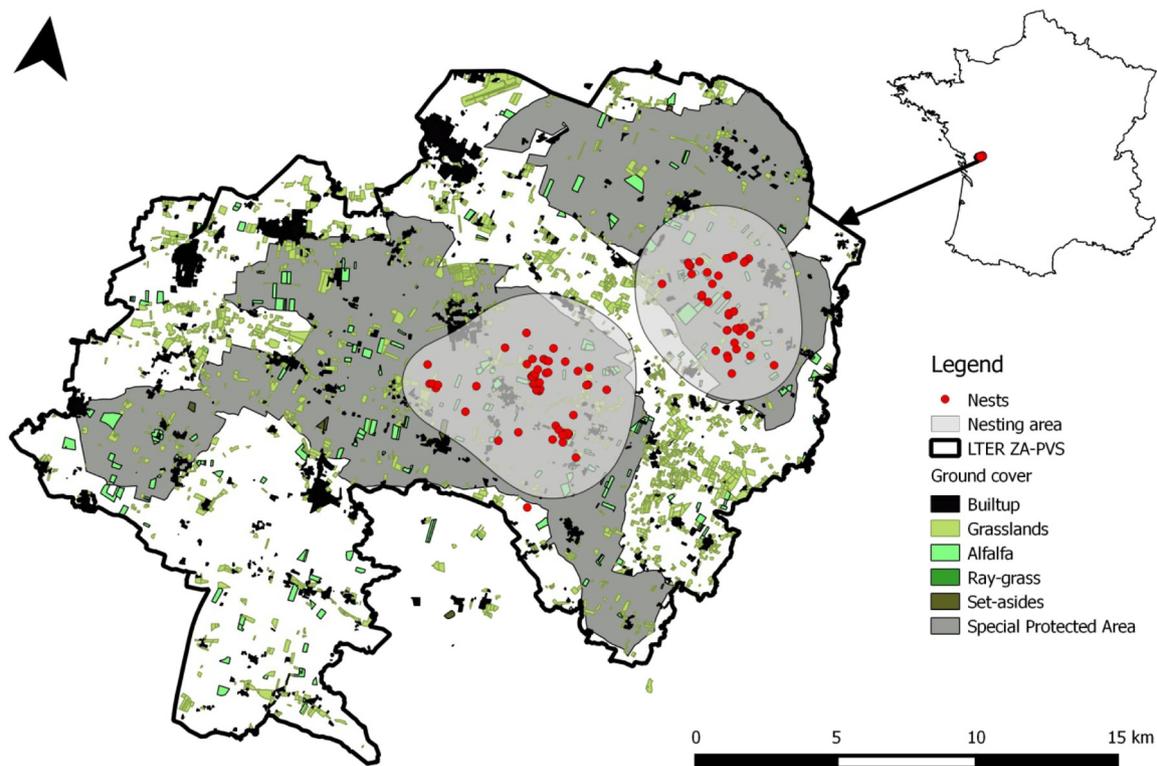


Fig. 1. The study area, the Long-Term Social-Ecological Research Site Zone Atelier Plaine & Val de Sèvre (450 km²; black line). The Natura 2000 area is shown in dark grey, with meadows (here shown for year 2010) in various green colours. Little bustard nests shown as red dots, and the “nesting area” (see [Methods](#) for delineation) in light grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

uses for all years (1997–2009) were aggregated and then the significance of habitat selection was tested globally using MANOVA multivariate linear models and pairwise Student's tests.

To detect possible non-random selection of field size or distance between nest and field border, we generated a set of random nests for each field (100 nests per field), then ranked the observed minimum distance to the field edge compared to the 100 generated distances (for each field). The distribution of the ranks was then compared to a uniform distribution assuming no selection of any distance classes with a Kolmogorov-Smirnov test. This analysis was limited to nests with GPS location data.

Clutch size, egg characteristics and breeding success were analyzed with Generalized Linear and Generalized Linear Mixed Models (GLM and GLMM respectively), with appropriate error distributions (Poisson for clutch size and productivity, Gaussian for egg size, and binomial for breeding success and the proportion of nests in alfalfa). We checked for normality of dependent variables when needed and log transformed them when necessary. All statistical analyses were performed using the R 3.3.0 statistical software (R Core Team, 2016), with packages *ade-habitatHR* (Calenge, 2006), *lme4* (Bates et al., 2015) and *mgcv* (Wood, 2017).

3. Results

3.1. Breeding habitat selection by nesting females

Among 119 nests in which habitat type was recorded in 1997–2009, 53.8% were found in alfalfa fields, 20.1% in set-aside fields, and 23.4% in other meadows including 12.6% artificial meadows (such as ray grass) and 10.1% permanent meadows (Fig. 2a). 70.5% of nests were in either pure or mixed leguminous fields, and only 27.7% were in pure graminaceous meadows (mostly set-asides). The habitat selected for breeding thus represented a mere 14% of the available habitat (Fig. 2a). At large scale, we found that the available habitat in the nesting area

differed slightly from the whole of the site in general (Fig. 1; $\lambda = 0.017$, $P = 0.004$). At a more local scale, breeding females were far more selective ($\lambda = 0.0007$, $P = 0.002$), preferentially selecting meadows in general, with a significant preference for alfalfa and set-aside, while there was no preference for ray grass or permanent meadows (see Fig. 2a). There was also a within-year trend, with an increase in the proportion of nests in alfalfa (GLM: $\beta = 0.49$, $n = 8$, $P = 0.0005$) through the season (Fig. 2b).

The field size did not have a significant effect on field selection when controlling for crop type (Appendix 2). The average size of fields selected by females was 3.56 ha, but there was a wide variation (range 0.47–26.6 ha). There was no selection of nest position within the field, with females laying eggs at random distance from edge of the field ($D(44) = 0.192$, $P = 0.07$) with the average distance from the nest to nearest edge being 26.1 m (range 0–100 m, Appendix 2). Finally, the vegetation height at the start of incubation, assuming a vegetation growth of 1.05 cm·day⁻¹ (unpubl. Authors' data on vegetation growth in alfalfa and meadows) was 38.7 ± 19.6 cm ($n = 62$, range 5–105.8 cm, Fig. 2c), varying significantly between years ($\chi^2_{(10)} = 45.9$, $P < 0.0001$) but not between types of vegetation ($\chi^2_{(2)} = 4.36$, $P = 0.11$).

3.2. Phenology of breeding

Laying dates were available for 105 nests (1997–2009; 79 nests and 26 families with chicks < 5 days old) on a weekly basis and 103 nests on a daily basis. The laying period was very long, with the earliest date being May 2nd and the latest being July 22nd, covering almost three months. The median laying date was June 11th. The egg-laying showed a very clear bi-modal pattern (Fig. 3a), with 42% of the nest laying dates in the first mode (i.e., May 1st to June 15th) and 58% in the second mode (June 15th to July 22nd). As the sample size per year was fairly small, we used a five year sliding window to examine variations in the distribution (Fig. 3b). Successive windows all showed a bimodal

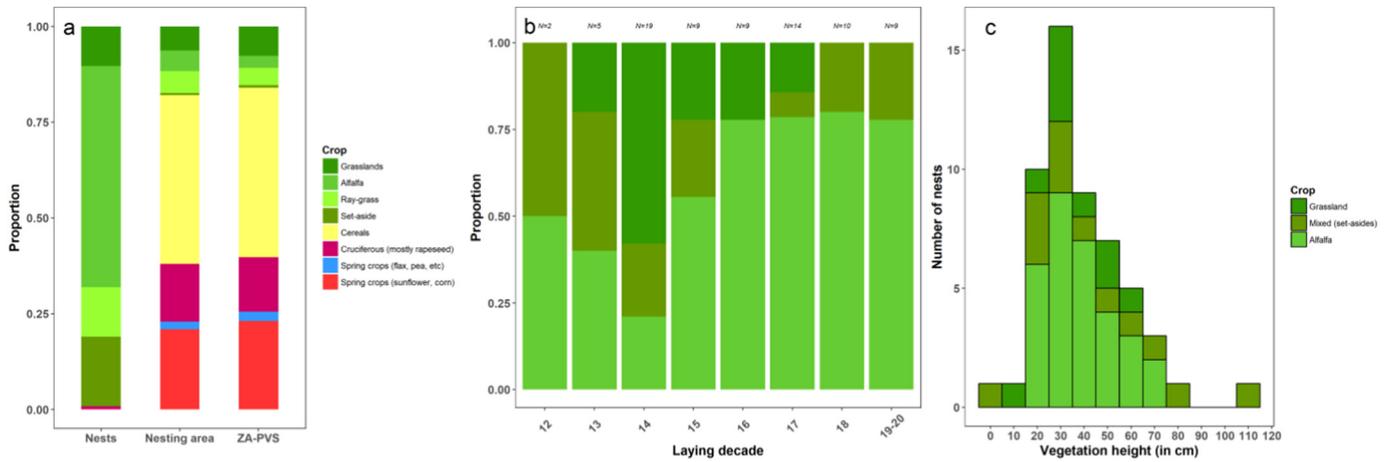


Fig. 2. Female little bustard habitat selection as a function of crop types, laying date and vegetation height. a) Proportions of crop types for the nests (left), in the nesting area (middle) and the whole of the LTSER (right). b) Proportions of meadow types for nests as a function of the laying date. The date is defined in “decades” (10 day weeks with decade 1 = first ten days of March). c) Histogram of vegetation height at onset of laying for different meadow types.

distribution but in the early years, the second mode was higher while, more recently, the first mode was higher. The median laying date (June 11th) was between the modes, at the peak time for alfalfa harvesting. There was no difference in laying dates between AES fields and non-AES fields ($\chi^2_{(1)} = 2.42, P = 0.12$).

3.3. Clutch and egg sizes, and female productivity

76 complete clutches were assessed for the period 1997–2009. The average clutch size was 3.09 ± 0.78 eggs (range 2–5, Fig. 4a). Clutch size did not vary significantly with the type of vegetation ($\chi^2_{(2)} = 0.637,$

$P = 0.73$) or laying date ($\chi^2_{(1),74} = 0.16, P = 0.68$; Fig. 4b). Similar results were found for clutch volume as none of the models tested performed better than the null model ($\Delta AIC > 2$). 186 eggs were measured (Fig. 4c). The egg volume (nested within nest, treated as a random factor) was unaffected by clutch size, laying date or vegetation type. Egg volume did not vary within a season ($\chi^2_{(1)} = 0.7, P = 0.4$; Fig. 4d) or between years ($\chi^2_{(10)} = 10, P = 0.39$). There was no difference in clutch size ($\chi^2_{(1)} = 1.02, P = 0.31$) or egg volume ($\chi^2_{(1)} = 0.13, P = 0.71$) between AES fields and non-AES fields (Fig. 4f).

Overall, 40 clutches (41.6%) failed during incubation, due to predation (7.5%), destruction during harvesting (55%) or abandonment

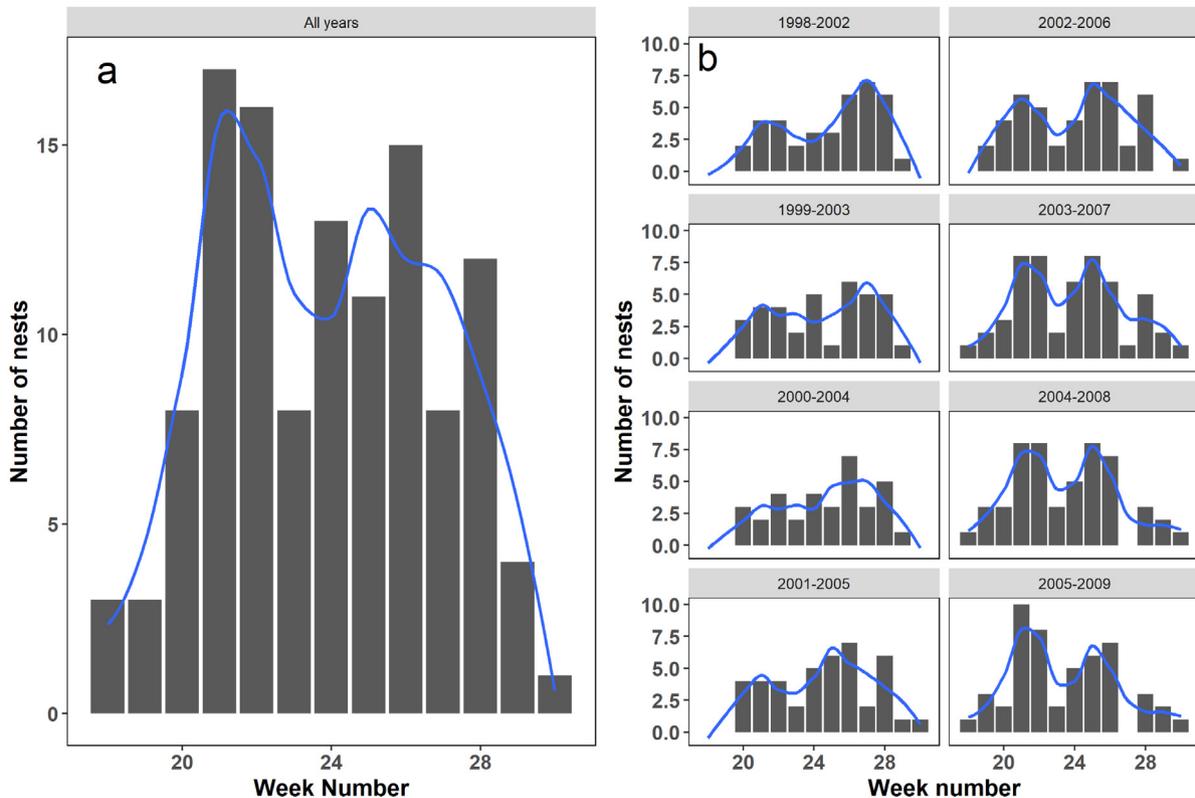


Fig. 3. Egg-laying dates (onset of laying) (week 1 = January 1st). a) Overall distribution (all nests combined). b) Distribution in 5 year sliding windows.

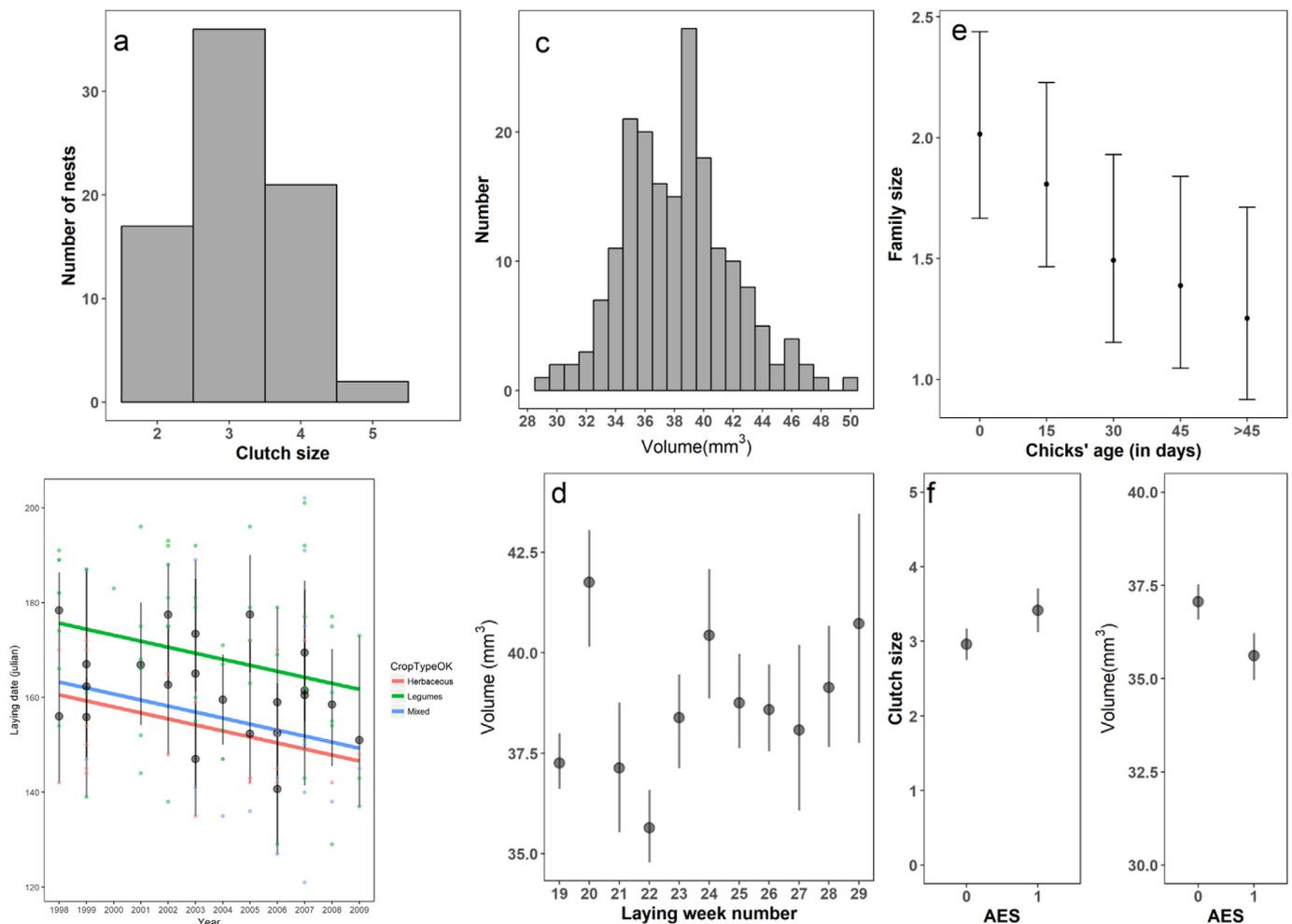


Fig. 4. Little bustard clutch, egg and chick family sizes.

- a) Histogram of clutch size (1997–2009).
 b) Average egg laying date for each meadow type as a function of the year. The regression lines are significant (see text).
 c) Histogram of egg volume.
 d) Egg volume as a function of laying date (mean \pm 1SD).
 e) Brood size (mean \pm 1SD) as a function of chick age.
 f) Clutch size and egg volume depending on whether the nest was in an AES (1) or in a non-AES field (0).

following nest damage (37.5%). For the 67 nests discovered before hatching (1997–2009) for which fledging success was known, female productivity was 0.62 ± 1.12 chicks. Counting only the 33 females who hatched at least one chick, the productivity was 1.27 ± 1.32 . The size of brood reduced from hatching to fledging, with average brood size ranging from 2.11 ± 0.85 chicks at hatching (for nests with at least one hatchling) to 1.29 ± 1.17 chicks after 45 days (84 broods, Fig. 4e). The main cause of chick loss or mortality was presumably starvation, since there was rarely any sign of egg or chick predation despite close observation of each monitored nest (Bretagnolle et al., 2011).

3.4. Temporal trends in breeding parameters

Over 1997–2009 (12 years), little bustards showed preferences in habitat selection with regard to vegetation type, in particular the proportion of nests found in alfalfa was inversely related to the area of alfalfa in the nesting zone (Fig. 5a). In addition, since 2010 when alfalfa was very much reduced (Fig. 5e), some nests were found or suspected in arable habitats: organic wheat, barley and flax. When the availability of alfalfa (the preferred crop) was high, little bustard females bred almost exclusively in alfalfa with a lower hatching success due to high nest

destruction rate (Fig. 5b).

Breeding parameters showed trends along the study period, e.g. clutch size showed a non-linear variation over the 12 years (Fig. 5c). There was also a significant shift in laying dates over the 12 years: on average, little bustards laid their eggs 1.27 days earlier every year between 1998 and 2009 ($\beta = -1.27 \pm 0.53$, $P = 0.019$, $\chi^2_{(1)} = 5.66$, $P = 0.017$), even when accounting for vegetation type ($\chi^2_{(2)} = 15.20$, $P = 0.0005$). Breeding failure showed strong variation from year to year (Fig. 5e).

4. Discussion

4.1. Little bustard nesting ecology in intensive farmland habitats

Little bustard breeding biology was virtually unknown in the 90s, with only fragmentary (Cramp and Simmons, 1980) or unpublished information (Schulz, 1985). Since then, additional data have been collected (Wolff et al., 2002; Morales et al., 2008), but with only two studies specifically dedicated to female breeding at chick rearing stage (Lapiedra et al., 2011; Morales et al., 2013). The number of nests surveyed was modest, between three and 19 (Lett et al., 2000; Lapiedra et al., 2011; Morales et al., 2013; Silva et al., 2014). Indeed most studies

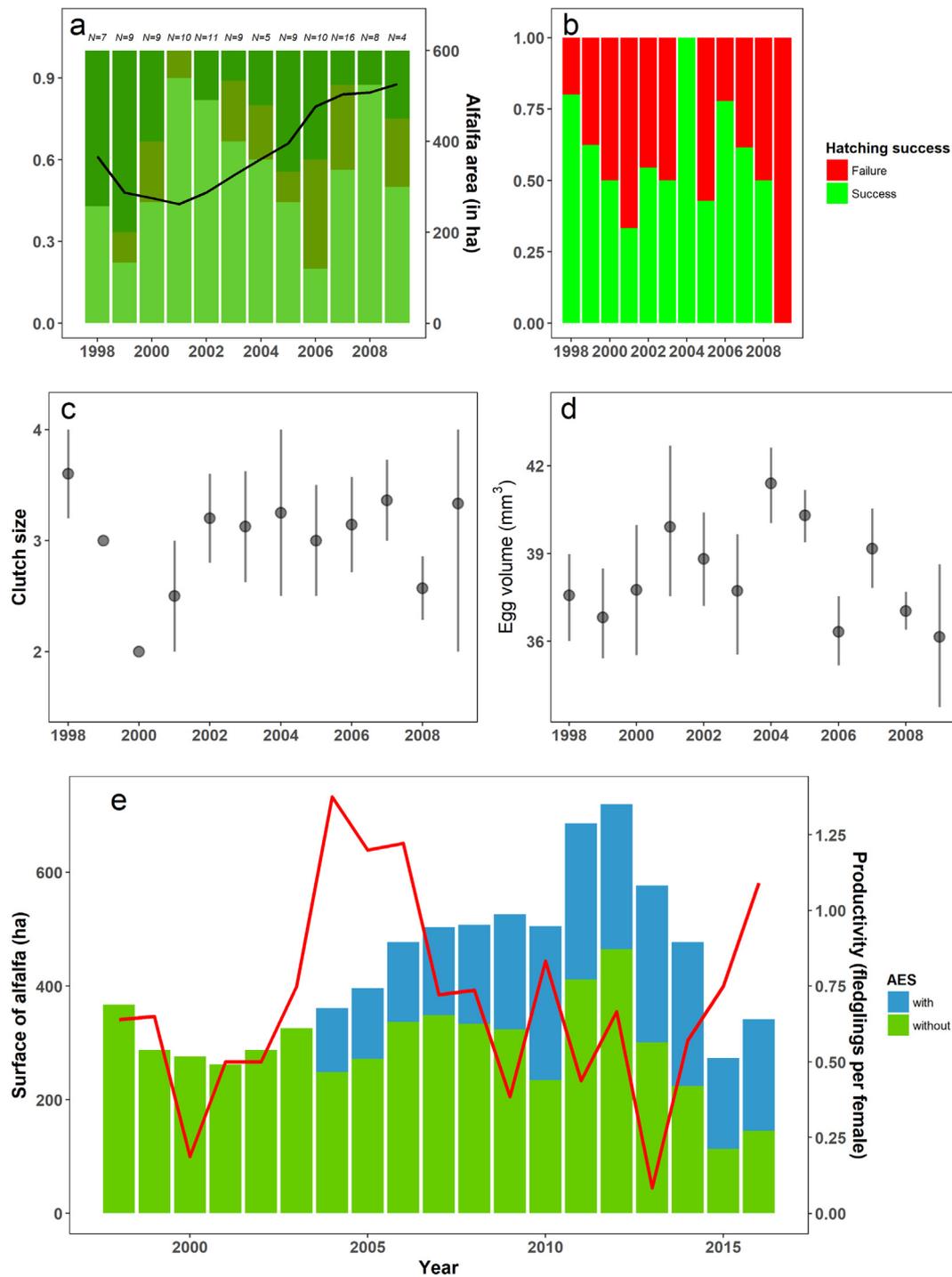


Fig. 5. Little bustard breeding parameters over the study period.

- a) Nesting vegetation type (sample sizes above the column). Light green (grey) is for alfalfa, with the area of alfalfa in the nesting zone (see Fig. 1) shown by the black line.
- b) Hatching success.
- c) Clutch size (mean \pm 1SD).
- d) Egg volume (mean \pm 1SD).
- e) Breeding productivity (N. fledglings/female, red line) with total area of alfalfa in the nesting zone, with or without AES. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

investigating female nesting ecology were based on female sightings or radio-tracking (Wolff et al., 2002; Morales et al., 2008), and targeted female breeding habitats (Faria et al., 2012; Morales et al., 2013; Silva et al., 2014) rather than breeding ecology sensu stricto (but see Lapedra et al., 2011). Our study presents the largest data set ever

collected for the little bustard, although it is still modest (7–8 nests per year) due to the extreme difficulty of locating little bustard nests. Some important results emerged from our study, as well as information relevant to the conservation of this and other large-bodied species breeding in intensive agriculture landscapes.

Our results first point out the importance of meadows in intensive cereal landscapes. Female little bustards select a rare habitat for breeding (< 15% in this study). In less intensive cereal landscapes, such as in the Iberian Peninsula, females also strongly prefer large pseudo-steppe habitats (Silva et al., 2010) or fallows and set-asides (Morales et al., 2013; Silva et al., 2014). Over the past 50 years, the farmland landscapes of Western Europe have experienced dramatic changes, with oversimplification through huge reduction of meadows, set-asides, fallows and semi-natural habitats (Duncan et al., 1999; Benton et al., 2003). Therefore, the main breeding habitat of little bustards has shrunk in quantity, but also in quality (Morales et al., 2013; Silva et al., 2018), suggesting the species is now strongly habitat limited. In intensive farming areas, female bustards have shifted to sub-optimal habitats, alfalfa when present (this study) or cereal fields when meadows are almost absent (e.g., all nests in Lapiedra et al., 2011).

Perhaps because of this habitat limitation, our second finding is that, surprisingly, females do not appear to be habitat selective. Rather, they show high flexibility in choice of vegetation type, field size, distance from edge, vegetation height, as well as an extremely long egg-laying period which spans over three months. We have no evidence that this extensive period is due to relaying, since relaying is relatively infrequent in little bustard (Lett et al., 2000; Lapiedra et al., 2011). An extremely long breeding period is unexpected for a migratory species breeding at such latitudes; indeed sedentary Mediterranean populations breed in a much more protracted season (Lapiedra et al., 2011; Faria et al., 2012). The main reason for this unusually long breeding period may be the harvest time of alfalfa, the main breeding crop here, which coincides with the peak laying period, forcing half of the females to wait for vegetation regrowth. Overall therefore, nesting females appear as “meadow specialist” in regard to available habitat, but as “meadow generalist” in regard to preferred habitat. This has two unfortunate consequences: first, meadows act as ecological traps for nesting females; second, because they do not show strong preferences, it is difficult to manage meadows to avoid the trap.

4.2. Temporary meadows as ecological traps

The concept of ecological trap has received theoretical attention (Battin, 2004; Robertson and Hutto, 2006), but surprisingly little empirical support (review in Suvorov and Svobodová, 2012) despite its strong conservation consequences (Delibes et al., 2001). Ecological traps are expected to occur in rapidly changing habitats, such as farmlands, and other habitats under strong anthropogenic influence (Suvorov and Svobodová, 2012). We argue here that meadows in intensive cereal farming landscapes are ecological traps, firstly because meadows are mown (Faria et al., 2016; Kershner and Bollinger, 1996) and secondly because temporary meadows are poor in prey items (especially large insects; Badenhausser et al., 2008). Such meadows can be considered to be attractive sinks because there is a mismatch between habitat selection and habitat quality. Despite being less numerous than permanent meadows in our site, temporary meadows, with about 75% of the nests, are mowed every four weeks in spring and summer. The frequency of mowing is clearly too high for females to select a field with vegetation height of about 40 cm and incubate the eggs. Indeed alfalfa is mown at ~60 cm (after the first mowing at the end of May, unpublished data), i.e. only 20 days on average after a female has selected the field for nesting (incubation = 21 days). Distinguishing ecological traps and sink habitats is difficult (Battin, 2004) but of paramount importance for conservation since ecological traps will always result in local population extinction. Females breeding in meadows do not produce enough chicks to be sustainable at our site, since half of the nests are destroyed and brood reduction further decrease family size to 0.3 female fledglings per adult female, approximately one third of replacement rate (Bretagnolle and Inchausti, 2005). The meadows habitat is thus not a sink but a trap, since females prefer meadows to other habitats (they could, for instance, lay eggs in the

safer cereal crop habitat, then rear their chicks in meadows). Moreover, though unreported (Marcelino et al., 2017), the death of incubating females during agricultural operations might not be uncommon: at our study site, two females were killed while incubating between 1997 and 1999, when ~20 female * year breeding attempts were radio-tagged.

4.3. A land-sharing conservation strategy

Such high nest failure has concentrated bustard conservation efforts on the two causes of decline, nest destruction during mowing and insect availability (Berthet et al., 2012). The main strategy relied on land sharing, in the form of AES which were designed to avoid nest destruction by delaying mowing by two months and improve food availability through a ban on pesticides ban and reduction in N inputs. Alfalfa was the main crop targeted because, in addition to being a main breeding crop for bustards, it provides benefits for farmers in crop rotation, improving soil fertility and reducing herbicide use (Meiss et al., 2010; Lechenet et al., 2014). The AES strategy had positive results since nests in AES fields were rarely destroyed by mowing (Bretagnolle et al., 2011), with a complete reversal of the population decline between 2004 and 2009 (Fig. 5e), though this also partly resulted from the population reinforcement program that started locally in 2007. However, we found no significant effects of the AESs on clutch size, egg volume and habitat choice, suggesting habitat quality was not improved by the AESs. In addition, females did not prefer AES fields for breeding. Unsurprisingly, as non-AES meadows were still present, female little bustards still bred in non-AES fields, with reduced breeding success as they were not protected. In this sense, the AESs strategy may further strengthen the ecological trap, depending on the proportion of suitable fields under AES protection: if all meadows are under AESs, there is no trap, but if the proportion is very low, as there is no preferential selection of AES fields (as shown by this study), most nests will be destroyed. The proportion of meadows covered by AESs depends on the available funds and farmers' willingness to accept that a significant part of their fodder becomes unavailable, since the meadow AESs delay mowing. In a mixed farming landscape, the AES strategy actually fails, because most meadows are not under AES. In dominantly cereal farming landscapes, it may work because it would be possible to contract most of the few meadows available for breeding. But in such cases, the area of AES fields will depend on the presence of low value land, and bustard breeding success will be limited by the availability of large insects (especially grasshoppers), limited to meadow areas (Badenhausser et al., 2008). Therefore for either agricultural system, little bustards are limited by mowing of the breeding areas or by the food supply. Other limitations exist in the AES strategy: firstly, it is not possible to completely avoid nest destruction in AES fields, given the extensive egg laying period: targeting zero nest destruction would mean that AES fields are withdrawn from agricultural production (which is no longer a land-sharing option). Secondly, the long-term survival of the AES policy is uncertain (Pe'er et al., 2014). In France for instance, after the European Union Common Agricultural Policy was reformed in 2014, the AES contract for all fields were terminated in early 2015 and as a consequence, many were ploughed up.

4.4. Conservation implications for large-bodied birds in intensive farmland habitat

The rise of agriculture has profoundly changed the environment and has impacted the Earth's biodiversity more than any other human activity. More food will even need to be produced from less land because of urbanization, desertification, and climate change while producing biofuels on agricultural land increases pressure (Godfray et al., 2010). Thus, trade-offs between the provision of food or other commodities and the conservation of biodiversity are inevitable (Godfray et al., 2010). The main approaches for managing the trade-offs have been land-sparing and land-sharing (Phalan et al., 2014). We concluded that

land-sharing was not efficient for conserving little bustard in intensive farming systems. We here argue that this is true for other large-bodied bird species, such as stone curlew, Montagu's harrier *Circus pygargus* (Santangeli et al., 2015) or great bustard *Otis tarda* which are facing very similar conservation dilemmas because they are ecologically demanding species. Large bodied species are long-lived, among the most severely threatened birds (Bennett and Owens, 1997), partially selective for habitat since they require complex mosaics with at least some semi-natural elements (including meadows), and have large to extremely large home ranges (e.g., several thousands of hectares for Montagu's harriers). Semi-natural habitats are critical for these birds because they provide food resources and breeding habitats for prey. Although there is no evidence so far that meadows may act as ecological traps for harriers and stone curlews, many of their nests are destroyed when meadows are mown (Santangeli et al., 2015). AESs may also have created ecological traps for grey partridges (Bro et al., 2004), through a predation trap mechanism. In addition, large-bodied birds in farmland habitats are shy, or at least shier than smaller species, so they need areas free of humans. Montagu's harrier and the great bustard keep up to up to 600–1500 m from any human constructions (deCornulier and Bretagnolle, 2006). We therefore suggest that our results support the adoption of land sparing. Land-sparing schemes have been proposed for large predators to limit human-wildlife conflicts (Chapron et al., 2014), and, in the same way, we need to limit interference between large-bodied bird species and farming activities, because farming practices are incompatible with their survival. However, since land-sparing has not been widely adopted for arable systems (mainly because land is considered to be prohibitively expensive), we still have to show that it can work in practice. In agricultural systems, land sparing has mainly been in the form of conservation easements (Brazza, 2017), aiming at conserving natural habitats from conversion to cropland. In practice, it requires a robust regulatory system to ensure that protected land is in fact protected (Phalan et al., 2014). Furthermore, these strategies may not be mutually exclusive, and several studies have suggested that compromise strategies could be the most effective for conserving biodiversity (Fisher et al., 2014).

Authors' contributions

VB designed the long-term study, conceived the ideas and designed the methodology. VB, AV & LD collected data (see also Acknowledgments). AV and LD performed analyses. VB & LD drafted a first version, and AV contributed to the following drafts. All authors gave final approval.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.09.031>.

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