

Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining little bustard (*Tetrax tetrax*) in agricultural habitats

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(Received 31 December 2003; resubmitted 6 June 2004; accepted 30 June 2004)

Abstract

The little bustard (*Tetrax tetrax*) has declined rapidly across European farmland landscapes due to agricultural intensification. In France, the number of breeding males in agricultural habitats has been reduced by 92% over the last 20 years as a result of decreases in insect abundance and nest destruction during harvesting. An age- and sex-structured stochastic metapopulation model was formulated for the remaining little bustard population in south-west France and, using actual estimates of demographic rates obtained after 1997, its extinction risk over the next 30 years was estimated to be *ca.* 0.48. Limited population reinforcement has thus appeared as a potential conservation strategy for this species in agricultural habitats, while agro-environmental actions have begun to have an effect on habitat quality at the landscape level. Different strategies for the reinforcement of fledglings, including the number and frequency of releases and the number of release localities in relation to four criteria for choosing the release points, were evaluated in terms of their effect in reducing the extinction risk of local populations and of the metapopulation. The reinforcement of 100 fledglings per year for 5 years and choosing the actual release points using the current abundance were found to be the optimal choices for reducing the estimated extinction risk of the remaining little bustard population in south-west France.

INTRODUCTION

Although translocations and reintroductions of individuals of threatened species are an increasingly common conservation measure (Scott & Carpenter, 1987; Griffith *et al.*, 1989; Beck *et al.*, 1994; see also Wolf, Garland & Griffith, 1998), these actions are generally carried out without previous careful evaluation of alternative options (Sarrazin & Barbault, 1996). Moreover, most reintroductions involve flagship or keystone species that, typically, are large and long-lived animals (Wilson & Stanley-Price, 1994; Saltz, 1998; Evans *et al.*, 1999; Meretsky *et al.*, 2000) and much less knowledge has been acquired for smaller species. In addition, reintroduction programmes are most often carried out from a single release site, while juvenile or adult dispersal is often sex-biased, females dispersing more than males in birds for instance (Greenwood, 1980). A strongly sex-biased dispersal pattern may affect release strategies, because males may not disperse while females may desert the release site, thus reducing the chances of mating. Although it is widely acknowledged that dispersal patterns may affect metapopulation and population persistence (e.g. Serrano & Tella, 2003), the paucity of empirical estimates

for most wild and endangered species precludes the evaluation of their general importance in the context of translocation, introduction or reinforcement conservation programmes.

Stochastic demographic modelling is an important and increasingly used tool for assessing the degree of threat to natural populations and the effect of management actions (Beisinger & McCullough, 2002; Reed *et al.*, 2002). Under the generic name of Population Viability Analyses (PVA), these models allow the effect of environmental or ecological factors that may place populations at risk to be explored, as well as allowing the evaluation of the consequences of conservation actions on these populations. A simulation approach can provide an alternative way to explore to what extent the limited knowledge on the spatial scale and the rates of dispersal of a bird species might determine various aspects of the release strategy, such as the number and the criteria for selecting different release sites. Moreover, exploring the sensitivity of different conservation strategies to the (usually) partial knowledge on dispersal patterns of target species is especially warranted given the diversity of cues and factors used by birds for leaving a local population and selecting a new patch (see e.g. Ens, Weissing & Drent, 1995; Matthysen, Adriaensson & Dhont, 1995; Cale, 2003).

The little bustard, *Tetrax tetrax*, was a common bird of open fields in Europe until the early 1900s but it

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has since disappeared from most of its former range (Cramp & Simmons, 1980; Schulz, 1985, 1987; Tucker & Heath, 1994). Remaining populations have, moreover, shown continuous declines, especially in France (Jolivet, 1996, 1997), where the species is now red-listed (Rocamora & Yeatman-Berthelot, 1999). In France, the reduction in the geographical range (Boutin & Métais, 1995) and the precipitous decline in numbers (> 80%) during the last 20 years (Jolivet, 1997) have, however, only affected populations breeding in cultivated habitats (Wolff *et al.*, 2002) where the decline in numbers has reached *ca.* 92% in just 20 years. The main reasons suggested for the decline of the little bustard are the decrease in insect abundance as a result of agricultural intensification and the destruction of nests during harvesting, which can account for *ca.* 40% of egg loss in some regions (V. B., unpublished results).

Intensive monitoring in south-west France has revealed that the current decline of the little bustard has been more than 10% per year (V. B., unpublished results) between 1997 and 2002. Such a decrease has led to the estimate that the extinction risk at the metapopulation level (*ca.* 850 birds in 2000) is *ca.* 40% in the next 30 years and up to 90% in some of the populations (Inchausti & Bretagnolle, 2005). Several agro-environmental actions, aimed at increasing habitat quality (insect resources) at the parcel level, are currently being implemented in order to reverse population trends (Jolivet, 2001; Jolivet & Bretagnolle, 2002). However, in order to be effective, those measures will have to affect insect abundance at the landscape level, since female little bustard home ranges typically cover several hundreds of hectares (V. B. & F. Jiguet, unpublished results). Changes in habitat quality at this spatial scale are not expected to occur in just a few years, thus questioning the long-term success of habitat management for this species given its fairly high probability of extinction. Limited population reinforcement has thus appeared to be a potential conservation strategy for this species in agricultural habitats (Jolivet & Bretagnolle, 2002; Inchausti & Bretagnolle, 2005) while agro-environmental actions begin to have an effect on habitat quality at the landscape level.

The objectives of this article are twofold: first, to assess the effect of a conservation strategy, the reinforcement of individuals (fledglings), using the extinction risk of the little bustard in south-west France as a baseline for comparison; second, to compare several scenarios in view of the almost total lack of knowledge of a key-parameter, fledgling dispersal. Besides the basic issue of how many individuals should be released, and based on a real case study, we specifically address the critical questions of the number (if several) of release sites that should be chosen and which criteria should be used to select these release sites.

METHODS

Study species and study sites

The little bustard is a Palearctic, medium-sized bird (average body mass of *ca.* 900 g) belonging to the Otidae

family (Del Hoyo, Elliot & Sargatal, 1996) that has an exploded lek mating system (Jiguet, Arroyo & Bretagnolle, 2000) in which males congregate in aggregated display territories of a few hectares in size and which females primarily attend for the purpose of mating. Populations of little bustards inhabiting south-western France are migratory: males arrive first between March and April, while females arrive from April onwards. Both sexes winter in Central Spain (V. Bretagnolle, unpublished data), *ca.* 1500 km south of the breeding grounds.

Between 1997 and 2002, data on breeding biology, population size and trends have been collected in seven study sites (Fig. 1; and Inchausti & Bretagnolle, 2005). These surveys provided field data that were used to estimate the population parameters (see also Morales, Bretagnolle & Arroyo, 2004). Adult sex ratios were similar and biased across years and study sites: 1.47 (± 0.12 ; $n = 8$ years on all sites) females per male.

Model structure and parameter estimates

We built an age- and sex-structured, post-breeding, stochastic metapopulation model of the little bustard in south-west France. The model considered males and females separately to account for the polygynous breeding of the lekking mating system of little bustards (Jiguet *et al.*, 2000). From a population dynamics point of view, the number of females is likely to constrain the number of breeding events in the polygynous breeding system of little bustards (Legendre *et al.*, 1999), since the dominant male mates with multiple females while females take exclusive care of the young (Cramp, 1985). The model included nine age classes for both sexes, with reproduction starting at 1 and 2 years old for females and males, respectively (Schultz, 1987; V. B., F. Jiguet and A. Wolff, unpublished results).

Estimates of averages and the temporal variation of the annual age- and sex-specific survival rates were derived from our unpublished results. The survival of the oldest adults of both sexes was set at 0.60 (compared to 0.68 for females and 0.72 for males), with a similar relative temporal variability to that of the other adult age classes for both sexes; this should not be construed as assuming that the birds were immortal since the chance of remaining in the last age class diminishes by 40% per year. Annual estimates of fecundity in study sites were calculated as the number of chicks older than 30 days divided by the number of females recorded at each nesting site (Table 1). We considered that the youngest adults of both sexes would lack experience and thus set their average fecundity at 15% lower than that of other adult age classes. There is evidence from field data that 1-year old females lay smaller clutches (one egg less on average) than older females, although the sample size ($n = 3$ clutches of 1-year old females) is currently very small (V. B., unpublished data).

The model included environmental stochasticity by drawing the values of the age-specific survival and fecundity rates from log-normal distributions whose parameters (means and standard deviations) reflected

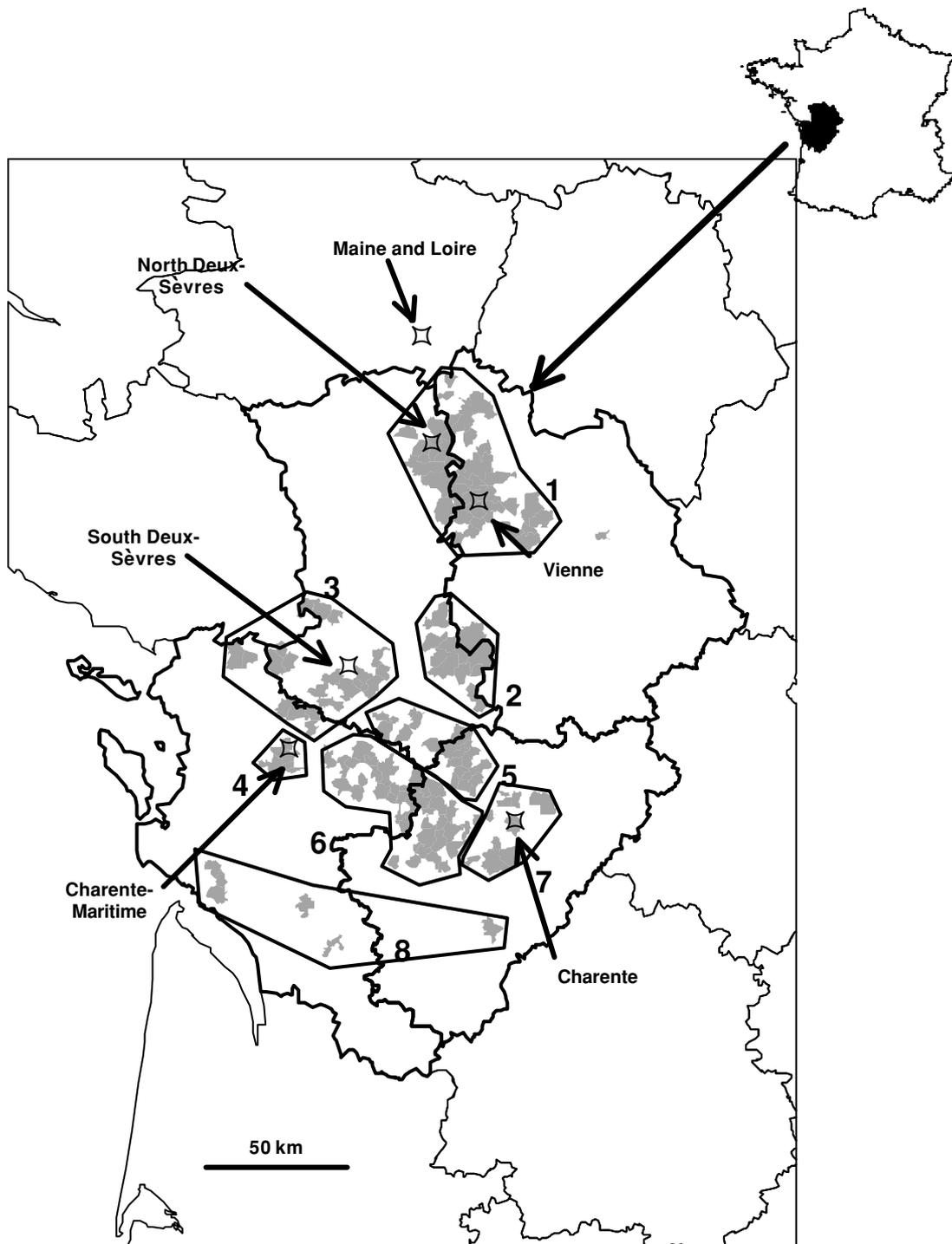


Fig. 1. Distribution of the little bustard (*Tetrax tetrax*) within the Poitou-Charentes region (black area on small map, upper right), based on an exhaustive, large-scale survey conducted in 2000. Also shown (with black symbols and their names) are six out of the seven study sites surveyed between 1997–2002 (the seventh study site is located *ca.* 200 km west of the site ‘Vienne’). The contours and numbers represent the eight defined populations here considered. Note that subpopulation 8 consists of four patches of less than two males each, which were lumped for simplification.

the average value and the temporal variability of each demographic rate in each population. Using the log-normal distribution to model environmental stochasticity is recommended whenever the average survival and/or fecundity rates are either close to zero or to one in order to avoid biases in the average realised rates, which

would be induced by using the normal distribution and truncating biologically impossible values (i.e. negative fecundity, survival higher than 1) of the demographic rates (Akçakaya, 1998). Given that the breeding success of little bustards strongly depends on the food provisioning of fledglings by their mother (Jiguet *et al.*, 2000), we

Table 1. Annual fecundity rates (mean \pm standard deviation (SD) over time) for the eight little bustard populations in south-west France (see Fig. 1 for location)

Population	Initial population size	Total fecundity	Asymptotic population growth rate	Extinction risk	
				With Dispersal	Without Dispersal
1	273	0.296 \pm 0.133	0.810	0.869	0.888
2	103	0.544 \pm 0.231	0.946	0.780	0.493
3	80	0.292 \pm 0.116	0.810	0.813	0.978
4	30	0.228 \pm 0.190	0.772	0.809	0.997
5	98	0.464 \pm 0.163	0.904	0.735	0.667
6	212	0.384 \pm 0.201	0.861	0.749	0.751
7	50	0.544 \pm 0.170	0.946	0.750	0.613
8	15	0.384 \pm 0.201	0.861	0.774	0.984
TOTAL	861	0.347 \pm 0.169	–	0.494	0.288

Fecundity rates are expressed as the observed number of sons + daughters per female per year assuming a balanced sex ratio at birth. Annual survival rates for all populations were 0.68 ± 0.11 for females and 0.72 ± 0.11 for males (see the text for the methods used in the estimation of each demographic rate). Initial population sizes are based on a complete survey performed in 2000 (Fig. 1). The population growth rates were calculated using an eigen-analysis of the age- and sex-transition matrix of each population. The extinction risk of local populations and of the metapopulation was calculated using the age- and sex-transition model for 25 years using the local survival and fecundity rates and 2000 replications. The dispersal rates of fledglings between populations were calculated for the parameters $a = 1.0$ and $b = 100$ of the dispersal function (see the text for details) and using the geographical distance between populations.

assumed that fecundity and adult survival were correlated. Demographic stochasticity was modelled by sampling the number of survivors of each age class and the number of young birds from binomial and Poisson distributions using the method described by Akçakaya (1991). All models were analysed using Monte Carlo simulation with RAMAS/METAPOP (Akçakaya, 1998) for 30 years using 2000 replications. Previously, we (unpublished results) have shown that 30 years is a reasonable time frame for assessing both the extinction risk of the little bustard in south-west France and the effects of reinforcement of the populations, and it is also a reasonable time frame for agro-environmental measures to become effective: a shorter time frame (e.g. 10 years) is not enough given the inertia of the EU-Common Agricultural Policy, while a longer one is unrealistic because the agricultural landscape would not remain stable over such time span.

Spatial dynamics of the model

Based on a detailed map of the male little bustard distribution in south-west France obtained in 2000, we defined eight subpopulations (Fig. 1; see also Inchausti & Bretagnolle, 2005) whose contours were defined using natural boundaries for little bustards such as forests and rivers, discontinuities in their spatial distribution and the presence of a study population from which fecundity data were obtained. There is, therefore, subjectivity in delineating some of the subpopulations, but simulations based on 16 populations gave similar results to those of the eight-subpopulation model presented here, and we also systematically report the results of a single-population

model. Fecundity rates for each local population were obtained by using actual data if a study population was included in a subpopulation or by averaging the values from the two closest study sites (Fig. 1).

We assumed that only fledglings of both sexes dispersed (natal dispersal; Greenwood & Harvey, 1982), although there is also evidence for adult dispersal in this species, but we found that the effect of adult dispersal on extinction was moderate (Inchausti & Bretagnolle, 2005). The rate of dispersal was set to decline exponentially with the distance separating pairs of populations, a common assumption in metapopulation modelling (Burgman, Ferson & Akçakaya, 1993; Morris & Doak, 2002). The (symmetrical) dispersal rates of fledglings were established using:

$$\text{dispersal function} = a * \exp \left[- \left(\frac{1}{b} \right) * \text{distance} \right]$$

where a was the maximum proportion of individuals leaving a local population and $1/b$ was the rate at which dispersal declined with the geographical distance separating two populations, as estimated from their respective centroids (Akçakaya, 1998). Lacking direct estimates of the dispersal rates, we considered 10 combinations of a (0.2, 0.4, 0.6, 0.8, 1.0) and b (50, 100; Fig. 2(a)). The value of $b = 100$ was selected because it allows one-half of the dispersal events by females to occur between local populations (Fig. 2(a)) and the values $b = 50$ and $b = 200$ were used only for comparison with the chosen value $b = 100$. We assumed that the maximum dispersal rate of females was twice that of males (Fig. 2(a)), since females usually disperse more than males in many bird species (Greenwood & Harvey, 1982). The

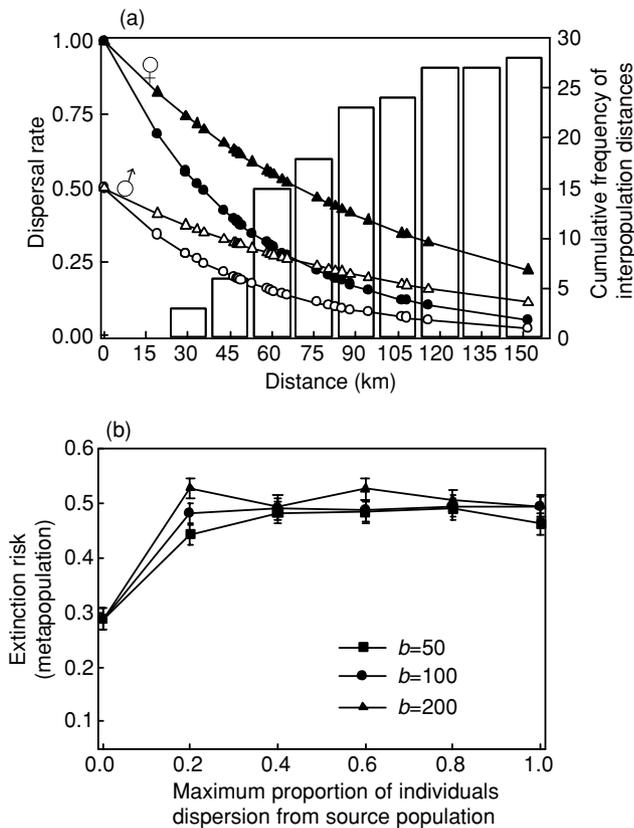


Fig. 2. (a) Predicted values of dispersal rate (proportion of dispersing individuals per year; left ordinate) for all pair-wise distances between populations in Poitou-Charentes (shown as a cumulative frequency distribution; right ordinate) for two values of the parameter b (circles, $b=50$; triangles, $b=100$) from the dispersal function. $1/b$ is the change in the dispersal rate with distance. Also shown is the difference in the maximum dispersal rate of male and female little bustards as different values of the parameter a of the dispersal function (see the text for further details). (b) Shows the extinction risk of the metapopulation for different values of a and b (symbols as before) using the demographic rates given in Table 1 (see the text for the full details of the model and its implementation).

environmental correlations between pairs of populations (i.e. similarity in the fluctuations of demographic rates) were set using the same exponential function used for dispersal rates with $a=0.9$ and $b=250$, which yielded values of environmental correlations in the range 0.48–0.90.

Reinforcement of little bustard populations

We started by estimating the extinction risk of the metapopulation of the little bustard in south-west France in order to have a baseline for comparing the results of the different scenarios of reinforcement. We first considered a non-spatial model with all little bustards of south-west France constituting a single breeding population whose survival and fecundity rates corresponded to the regional averages and standard deviations calculated over all local populations. We used this non-spatial model to

determine the total number of fledglings to be released and the optimal release frequency in the area by comparing the extinction risk obtained in separate simulations for different numbers or frequencies of fledglings released.

Based on the results of the non-spatial model, we used a metapopulation model to determine how many, and which, populations should be selected for the releases in order to minimise the metapopulation extinction risk. To examine the entire range of possible cases, we assessed all combinations of one, four and eight release localities for two values of the parameter b (50 and 100), keeping $a=1$ in all cases, in the dispersal function in separate simulations. The total number of individuals released per year during the first 5 years of the simulation was equal to 100 fledglings; only the actual number of individuals released per populations changed, depending on the number of release sites considered. We then evaluated four strategies for choosing the localities for the release of 100 fledglings per year (assuming an even sex ratio) in each population over a 5-year period using the same values of the parameter b as described above. These strategies consisted of selecting the populations with the four lowest (or the four highest) current abundance or fecundity rates (see Table 1 for values of fecundity rates per populations) for the release of a total of 500 individuals over a 5-year period. For each of these four strategies, we also considered, in separate simulations, the effects of concentrating the releases on one, two, three or four populations that amounted to a release of 100, 50, 33 and 25 fledglings per year in each population, respectively. Lastly, for the two best reinforcement strategies, we assessed whether positive density-dependent dispersal (i.e. more crowding, higher dispersal) affected the efficacy of each reinforcement strategy compared to the cases where dispersal rate was assumed to be unrelated to local population abundance.

RESULTS

The extinction risk of the metapopulation in south-west France over 30 years was 0.28 in the absence of dispersal and about 0.48 for most combinations of parameters of the dispersing function (Fig. 2(b)), with larger values of the parameters a and/or b being associated with rather modest increases in the metapopulation extinction risk. In the following, we kept $a=1$ (i.e. all fledglings disperse from their natal site, see Fig 2(a)) and used only two values for b (50 and 100).

Effects of the number and duration of releases

The results with a non-spatial model (i.e. a single population encompassing all little bustards from south-west France) showed that the reinforcement of 100 fledglings per year over 5 years might significantly reduce (i.e. halve) the extinction risk from *ca.* 0.28 to 0.15 (Fig. 3(a)). Increasing the number of releases only led to small further reduction of the extinction risk (0.15 with 100 fledglings versus 0.11 with 200 fledglings; Fig. 3(a)).

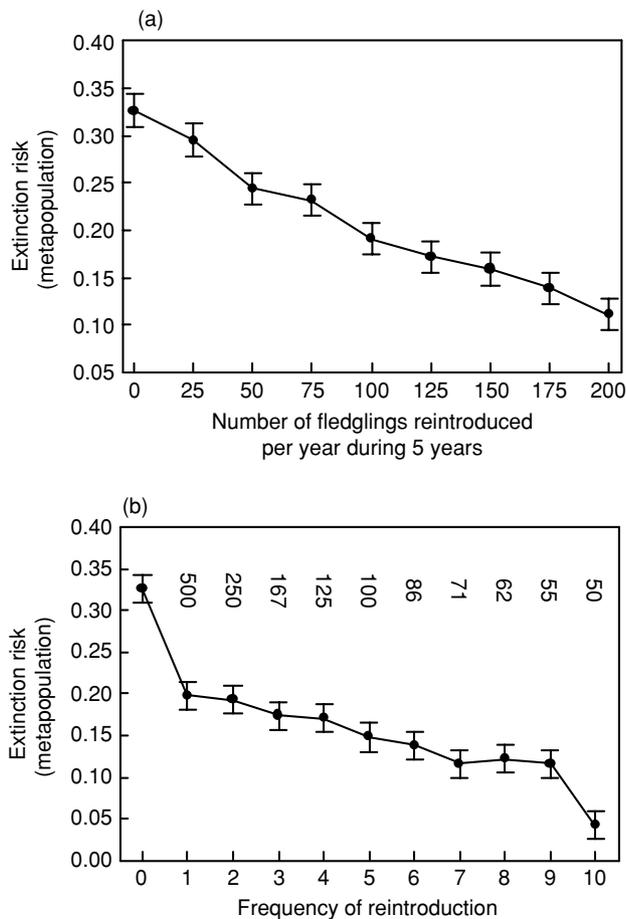


Fig. 3. Effect of the total number of fledglings reintroduced over 5 years and the duration of reintroductions on the extinction risk ($\pm 95\%$ confidence intervals (CI)) of the little bustards in south-west France. (a) Shows the effect of reintroducing a different number of fledglings in each of the first 5 years of the simulation. (b) Shows the effect of different frequencies of introduction of a total of 500 fledglings; the number of fledglings reintroduced per year is shown in the top of the panels. In all cases, we assumed an even sex ratio for the reintroductions and used the non-spatial variant of the model in simulations lasting 30 years. Each value for the number of fledglings reintroduced and the duration of reintroduction was obtained using 2000 replications in each set of separate simulations (see the text for details). For comparison, the baseline extinction risk of the non-spatial model is shown as the zero (i.e. no reintroduction) of each figure. All details of the model and its implementation can be found in the text.

However, the metapopulation size (after 30 years of simulation) was still much smaller than the initial size (73 ± 168 SD, compared to 850 individuals initially). Releases of young adults in numbers similar to those shown in Fig. 3(a) showed marginal differences (*ca.* 0.05) from the extinction risk curve obtained for the release of fledglings (data not shown).

We also investigated whether other combinations of frequency and duration of the reinforcements of these 500 individuals could yield a better result in terms of reduction of the baseline extinction risk. The results showed that longer reinforcement programmes were only

marginally better and that shorter programmes involving the reintroduction of more birds per year never led to better results than the choice of 100 fledglings per year for 5 years (Fig. 3).

How many release sites, and according to which criteria?

Having established that releasing 500 fledglings over 5 years (i.e. 100 fledglings per year) was a reasonable choice to significantly decrease the extinction risk faced by little bustards in south-west France, we used the metapopulation model to evaluate different criteria for selecting an optimal number of release sites as well as different criteria for selecting these sites, based on a real and spatially explicit data set. Distributing the releases over several sites often resulted in smaller extinction risks than did distributing birds in all eight sites. Furthermore, some specific combinations of four release sites had a lower metapopulation extinction risk value than that predicted from the release over a single current population in Poitou-Charentes (Fig. 4(a)). However, no systematic differences were found between releasing birds in one or in four sites, i.e. some combinations of sites in the four-sites strategy had equal extinction risks compared with some of the single-site strategy simulations (Fig. 4(a)).

When comparing the different criteria for selecting specific combinations of four sites on the basis of their current highest/lowest abundance or highest/lowest fecundity, we found that the release sites to be chosen should be those having the highest fecundity, since this was the strategy that yielded the lowest metapopulation extinction risk compared to the baseline value of 0.48 (Figs 4(b), (c)). The three other release strategies, i.e. choosing the localities having either the four lowest abundance/fecundity rates or the lowest fecundity, never yielded a metapopulation extinction risk lower than the best release strategy (Figs 4(b), (c)). In order to verify whether two or three release sites would yield a lower extinction risk than the four-site strategy, we considered the entire range from one to four release sites chosen according to the above criteria in separate simulations. Overall, the metapopulation extinction risk of the strategies involving two or three release sites did not differ from the strategy of using four release sites. It is worth noting that concentrating the reintroductions into only population 2 or 7 (these having the two highest fecundity rates) yielded extinction risks of *ca.* 0.18, which are as low as those obtained for the best combinations of four sites.

The results shown in Fig. 4 were largely insensitive (data not shown) to changes in the maximum proportion of dispersing individuals (the parameter a in the dispersal function) since changing this parameter between 0.2 and 0.8 produced differences of, at most, 0.02–0.03 in the predicted metapopulation extinction risk for any release strategy. The efficacy of the two best release strategies (choosing the release localities having the largest current fecundity or population abundance) was not affected by the assumption that the dispersal rate was density

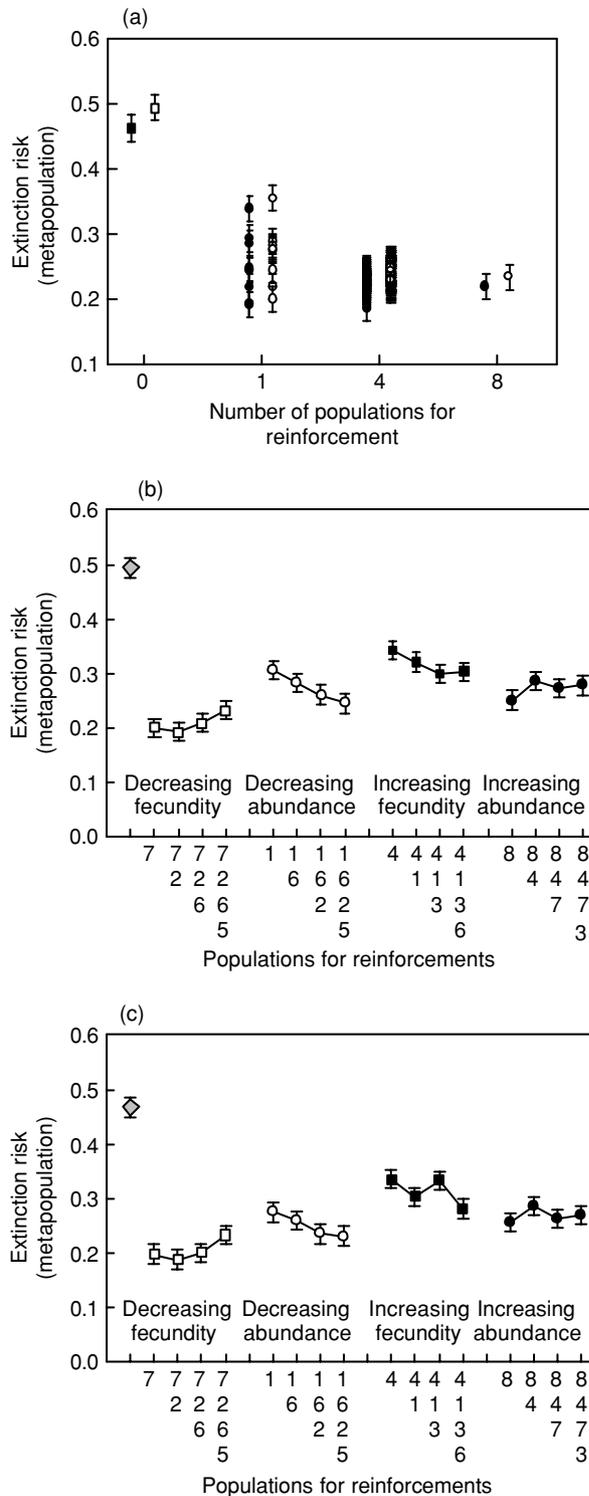


Fig. 4. Effect of the number and identity of release localities on the extinction risk ($\pm 95\%$ CI) of the metapopulation in south-west France. In all cases, a total of 100 fledglings per year (assuming an even sex ratio) were reintroduced during the first 5 years only (see the text for the full details of the model and its implementation). For comparison, the baseline extinction risk is shown as a diamond on the left of each graph. (a) Shows the results for all combinations of one, four and eight release localities for two values of the parameter b (filled symbols, $b = 50$; open symbols, $b = 100$; $a = 1$ in all cases) of the dispersal function in separate simulations. (b) and (c) show the effect of four criteria for choosing the sites for releasing little

independent. Additional simulations (data not shown) indicated that considering that the dispersal rate would increase with local population abundance could lead to a marginal change (of the order of 0.02–0.03) in the metapopulation extinction risk of each of the two best release strategies (sites having the highest fecundity/local abundance).

DISCUSSION

Validity of the model

Formulating an age- and sex-structured metapopulation model for the little bustard required making assumptions for parameters for which there was limited empirical information, especially dispersal rates. Available field data on dispersal in this species is anecdotal, but a small amount of data obtained in south-west France (subpopulation 3) since 1998 with colour-ringed birds suggests that fledglings disperse more than adults and females more than males. Out of 24 ringed chicks, only one was later recovered in the 350 km² study, while each year at least two one-year old, unringed birds of each sex are found. Conversely, only one adult has been recovered outside the study site, out of nearly 30 ringed. In addition, on the basis of recapture rate, adult females seem to disperse more than males, at least within this study site (V. B. & F. Jiguet, unpublished results), in sharp contrast to the great bustard, *Otis tarda* (Alonso *et al.*, 1997), where males disperse more than females. Therefore, based on scanty field evidence, we think it is reasonable to assume that fledglings disperse more than adults and females more than males.

Whether dispersal is symmetrical, or whether we should use the same function for each population cannot be discerned on the basis of the available empirical evidence in south-west France and elsewhere for this threatened species. We thus chose to use a simple model where dispersal depends solely on distance (i.e. is symmetrical and identical between populations) because we lack data that would suggest a different choice and because the available evidence in birds in general is contradictory, possibly because landscape structure affects dispersal patterns (see e.g. Ims, Rostad & Wegge, 1993; Matthysen

bustard fledglings in the local populations considering steep ($b = 50$) or shallow ($b = 100$) rates of decline in dispersal rate with distance. Each strategy consisted of ranking the populations in ascending/descending order according to either their fecundity or their local abundance (see the values in Table 1). Each strategy also considered releasing the fledglings in one to four populations as indicated at the bottom of each figure. As an illustration, the strategy 'decreasing fecundity' consisted of four possible releasing options: 100 fledglings per year to the population with the highest fecundity (population 7); 50 fledglings per year to the populations having the two highest fecundities (populations 7 and 2); 33 fledglings per year and 25 fledglings per year to the populations having the three and four highest fecundities, respectively. The four options for all release strategies were similarly constructed.

et al., 1995, Brooker, Brooker & Cale, 1999). Finally, we have shown (our unpublished results) that the actual values of the dispersal rate did not have too much of an impact on the extinction risk of the metapopulation, although they can affect the predicted extinction risk of local populations, particularly those functioning as a source of dispersing individuals. The existence of source populations is actually likely to explain the difference in the extinction risk predicted by the non-spatial and the metapopulation models (0.28 versus 0.48 in 30 years, respectively), which although paradoxical at first, may not be surprising. By considering the actual spatial subdivision of populations, the metapopulation model allows for local extinction of the smaller populations and their recolonisation from individuals dispersing from the larger ones. While three out of the eight populations (1, 2 and 6: Fig. 1) contain almost 70% of the individuals from the region and have a relatively lower extinction risk (Table 1), the remaining populations have high extinction risks due to their small initial size. Thus, the three larger populations would lose individuals as they disperse to the smaller, more extinction-prone populations (Table 1), which may explain the higher extinction risk predicted by the metapopulation model compared to the non-spatial model. In considering the little bustard in south-west France as a single breeding population, the non-spatial model had a much larger initial size and, not surprisingly, a lower predicted extinction risk than the metapopulation model. While the 'true' extinction risk of little bustards in south-west France probably lies between the estimates of these two models, we believe that the metapopulation model describes the social interactions related to the species mating system at the local scale and, thus, it provides a better portrait of the regional dynamics of little bustards. Therefore, rather than viewing the extinction risks predicted by the metapopulation and the non-spatial models in an absolute sense, they should be viewed as relative baselines for evaluating different aspects of the reinforcement of juvenile little bustards (see Burgman *et al.*, 1993 and Morris & Doak, 2002 for similar interpretations of predicted extinction risks). In conclusion, while our choices may not depict several imperfectly known features of little bustard dispersal in relation to its population dynamics, we feel that they constitute a reasonable first approximation for selecting between different conservation actions that need to be considered to minimise the currently high extinction risk. Future research with this species in agricultural habitats should allow refinement of the modelling of dispersal.

The reinforcement of little bustard populations in south-west France

The little bustard population of Poitou-Charentes is at the northern fringe of the current geographical range of the species and, unlike those from Southern France, individuals migrate before winter to southern and central Spain. Despite the fact that young adults have a higher reproductive value than fledglings (data not shown), using adults for reinforcement would not seem to be a viable

option for the little bustards in south-west France. This is because of the potential disruption of migratory patterns, since the fledglings would have to be kept in captivity during their first year, with the potential risk that they might not develop their migration abilities and have to endure severe winters in France.

It should be noted, however, that the approach followed to evaluate the effect of reintroductions assumed that all fledglings introduced become part of the breeding population, which is clearly unrealistic (mortality rates are about 40% in released hand-raised Houbara bustard, *Clamydotis undulata*: Combreau & Smith, 1998). Thus, a slightly higher number of juveniles should be released to account for potential difficulties of integration of these released individuals into the breeding population. We have also assumed that the reintroduced fledglings would acquire this migratory behaviour and thus that individuals raised in captivity would have the same chances of recruiting into the breeding population as those born in the wild.

Considering extinction risks in a relative sense allows informed choices to be made on the basis of quantitative criteria for deciding how many, where and for how long should the reinforcements take place. Despite the fact that translocations and reintroductions of individuals of threatened species are a common feature of conservation or species recovery plans (Scott & Carpenter, 1987; Griffith *et al.*, 1989; Wolf *et al.*, 1998), many such plans seem to resort to arbitrary or expedient approaches that are generally carried out without previous careful evaluation of alternative reintroduction strategies (Sarrazin & Barbault, 1996; Sarrazin & Legendre, 2000). Our results suggest that releasing 100 fledglings per year for 5 years would greatly decrease the extinction risk of the little bustard population in south-west France within the next 30 years. These results are consistent with our previous findings (Inchausti & Bretagnolle, 2005) that the low fecundity rates are the main demographic event underlying the precipitous decline of little bustards in south-west France. The populations whose local fecundity is currently high are those located in areas where the intensification of agriculture is amongst the lowest in the Poitou-Charentes region and those wherein traditional farming involving diverse crops and cattle raising is still practised.

Introducing fledglings using the criterion of decreasing local abundance could help to avoid Allee-like effects induced by the lekking mating system of little bustards, because member individuals disperse whenever the total abundance becomes very low (Höglund, 1996; Alonso *et al.*, 2000; Morales *et al.*, 2000; Dale, 2001). In the case of the little bustard, the abandonment of the leks and the effective halt of reproduction occur once the local lek size becomes smaller than six individuals (pers. obs.). The tendency to desert leks once they become too small would accelerate the spatial contraction of local populations and lead to the progressive disappearance of a metapopulation system. However, we did not consider Allee-like effects in our models because we currently lack direct factual evidence of their occurrence in the Poitou-Charentes region.

CONCLUSIONS: WHAT IS THE FUTURE FOR LITTLE BUSTARDS IN SOUTH-WEST FRANCE?

The ultimate causes of the decline in breeding of the little bustard in the French agricultural habitat lie with the decrease in insect abundance and with nest destruction (both of which result from agricultural intensification), although the mating and social system of the species may have exacerbated the effects of these factors. Therefore, the main targets of conservation programmes to enhance the persistence of the little bustard must consist of improving insect biomass and decreasing nest destruction. At best, the proposed reinforcements can only delay the currently observed population declines in south-west France in the event of no immediate changes in the intensive agricultural practices promoted by the current Common Agricultural Policy of the European Union. Despite the fact that new agro-environmental measures are currently being applied in south-west France, the little bustard population may become extinct in this region before those measures become effective. This eventuality further highlights the relevance of considering population reinforcement as an urgent conservation measure for little bustards in south-west France. Since reinforcement cannot be a solution for the long-term persistence of the little bustard, the best strategy would probably involve reinforcement as an urgent, short-term conservation measure, coupled with the implementation of agro-environmental measures in south-west France in the medium-term and finally acting in the long term towards changing the CAP into less detrimental practices for biodiversity in general and bustards in particular.

Acknowledgements

Collecting the data on the breeding of little bustards would not have been possible without the dedicated field assistance of Marie-Hélène Froger, Beatriz Arroyo, Alain Armouet, Christophe Jolivet, Jean-Michel Lett, Gilles Mourgaud, Didier Papot and Laurent Précigout who made them available. Particular thanks to M. Morales who analysed part of the data, C. Jolivet for making available unpublished information and B. Arroyo, F. Jiguet and A. Wolff for help at various stages of the LIFE program. To all we wish to express our gratitude. This study is part of a Conservation Program on the little bustard in France, co-ordinated by LPO/Birdlife and funded by Life-CEE, the French Ministère de l'Environnement, Région Poitou-Charentes, Départements des Deux-Sèvres, Charente and Indre and the CNRS.

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