

Predicting short-term extinction risk for the declining Little Bustard (*Tetrax tetrax*) in intensive agricultural habitats

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Abstract

Populations of Little Bustard (*Tetrax tetrax*) have shown pronounced declines in European farmland landscapes over the last 25 years due to the intensification of agricultural practices. In France, the number of breeding males in agricultural habitats has declined by 92% since 1980 as a result of decreases in insect abundance and nest destruction during harvesting. We formulate an age- and sex-structured stochastic model for the remaining Little Bustard population in SW France that has been studied since 1997 and, using actual values of demographic rates, we estimate its extinction risk over a time period of 30 years to be of 0.45. At the level of local populations, the extinction risk ranged between 0.66 and 0.90, largely depending on the initial population size and local fecundity of each population. A comprehensive sensitivity analysis evaluated the influence of uncertain demographic rates and of aspects of the spatial dynamics (sex and age dispersing individuals, sex-biased dispersal and different dispersal rates) on the predicted extinction risks and showed that our model was robust to changes of a wide range of combinations assessed. Given the severity of the current decline, and the spatial issues raised by our analysis, implications of our findings for the conservation of this endangered species are suggested.

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1. Introduction

European-farmed landscapes have traditionally consisted of complex mosaics of extensive crops that sustained high levels of biodiversity (Potter, 1997; Walk and 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 and Sutherland, 2002) that has entailed a loss of biodiversity judged to be similar to loss expected from climate change. A similar situation occurs as well in North America (Jobin

et al., 1996; Herkert, 1997). In Western Europe, plants, insects, and more especially birds have declined at the community level (Tucker and Heath, 1994; Pain and Dixon, 1997; Bouma et al., 1998; Söderström and Pärt, 2000; Chamberlain et al., 2000), and declines of 50% of population size have been measured for some bird species over the last 50 years. Perhaps not surprisingly, farmland habitat hosts the highest proportion of bird species with unfavourable conservation status in Europe (Tucker, 1997).

The Little Bustard *Tetrax tetrax* is a Palearctic, medium-sized bird (average body mass ≈ 900 g) belonging to the family Otididae (Del Hoyo et al., 1996) which was a common bird of open fields in most of Europe until the early 1900s, but it has disappeared from most of its former range over the last century (Cramp and Simmons,

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1980; Schulz, 1985, 1987; Tucker and Heath, 1994). Remaining populations have shown continuous declines, especially in France, Italy, Ukraine and some parts of Spain (Goriup, 1994; Del Hoyo et al., 1996; De Juana and Martinez, 1996; Jolivet, 2001). Formerly considered as ‘Globally Threatened’ (Collar and Andrew, 1988), it is currently classified as ‘Near Threatened’ at the world level (BirdLife, 2000) and ‘Vulnerable’ in Europe (Goriup, 1994). In France, Little Bustard is now red-listed (Rocamora and Yeatman-Berthelot, 1999) due to its precipitous decline during the last 17 years, from >7000 to an estimated total of 1285–1425 males in 1996 (Jolivet, 1997) and the associated reduction of its breeding range (Boutin and Métais, 1995). This decline has however only affected Little Bustard populations breeding in cultivated habitats, since those breeding in Southern France and especially the steppes of La Crau have remained stable over this period (Wolff et al., 2002). The decline and range reduction of the Little Bustard decline in the French cultivated habitats are thought to be due to a decrease of insects abundance as a result of agricultural intensification, and nest destruction during harvesting which can account for at least 25% of egg loss in some regions (Bretagnolle, V., unpublished data). The French Little Bustard population of cultivated areas was about 470 males in 2000 (Fig. 1), with a core area (Poitou-Charentes Region) covering approximately 9000 km² wherein 410–420 males were censused (Jolivet, C., and Bretagnolle, V., unpublished data). This population has shown on average 10–15% yearly decrease over the last seven years as well as increasing fragmentation thus raising serious doubts about its persistence.

Stochastic demographic models have become an important and increasingly used tool for assessing the degree of threat of natural populations and the effect of management actions (Beissinger and McCullough, 2002; Morris and Doak, 2002). These models allow exploration of the effect of factors that may place a population at the risk, among them demographic and environmental stochasticity, catastrophes, inbreeding depression, density dependence (reviews in Burgman et al., 1993; Beissinger and McCullough, 2002; Morris and Doak, 2002). The objectives of this article are four-fold. First, we formulate an age- and sex-structured stochastic model of a Little Bustard population, and given that estimates of several model parameters are uncertain or lacking, we carry out a sensitivity analysis of our model. Second, using a two-population model, we explore various aspects of the spatial dynamics and in particular, dispersal of adults and young, for this species. Third, using data collected at seven different breeding sites in SW France from 1997 onwards, we estimate the short-term risk of extinction of Little Bustards using real data. Fourth, we discuss conservation options in light of our simulations.

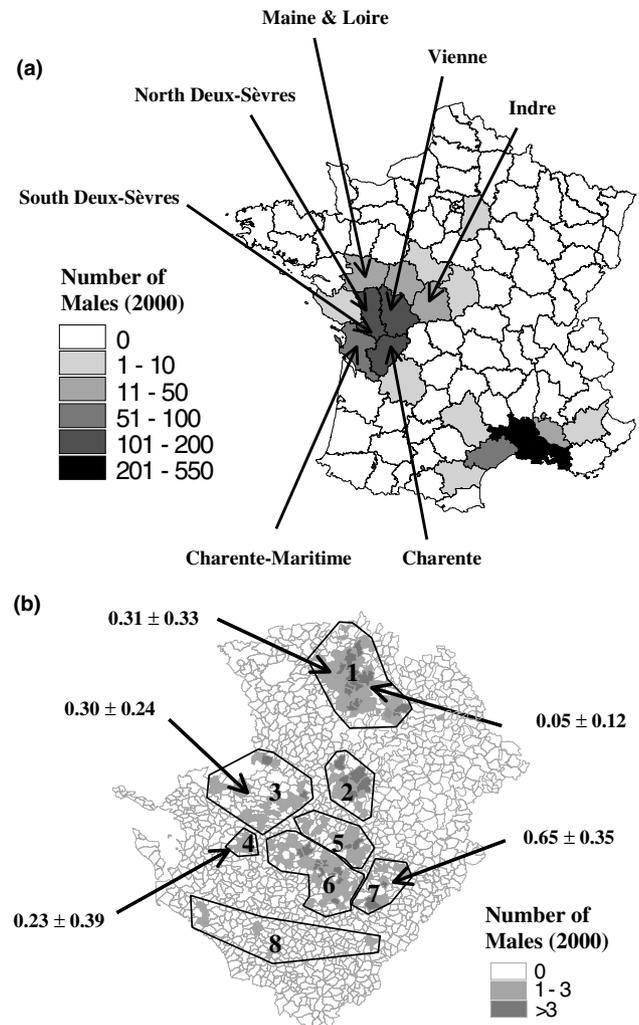


Fig. 1. Current distribution of Little Bustard by Departments in France in 2000 (Jolivet, 2001) (Panel a) and the location of the eight populations of Little Bustard defined in the Poitou-Charentes (Panel b) with the average fecundity, \pm SD between 1997 and 2002 for each of the five study sites indicated by the arrows. Numbers refer to the abundance of the eight populations considered in this paper.

2. Methods

2.1. Study species and study areas

The Little Bustard has an exploded lek mating system (Jiguet et al., 2000) in which males display in aggregated sites that females attend primarily for the purpose of mating (Jiguet et al., 2000). Populations of Little Bustards inhabiting SW France are migratory: males arrive first between March and April, while females arrive from April onwards.

Data were collected during the breeding seasons of 1997–2002 at seven different study sites that belong to six Departments in SW France (see Fig. 1, and Morales et al., *in press*, for additional information on methods and study sites): *South Deux Sèvres* (46°15' N, 0°30'

W), North *Deux Sèvres* (46°55' N, 0°10' W), *Vienne* (46°50' N, 0°20' W), *Maine and Loire* (47°07' N, 0°11' W), *Indre* (47°15' N, 1°50' E), *Charente* (45°49' N, 0°16' W) and *Charente Maritime* (46°02' N, 0°35' W). These sites, covering a total area of about 40,000 ha of agricultural habitat subject to varying degrees of intensive exploitation, hold generally low densities of displaying Little Bustard males (except in *Maine and Loire* and *Indre*). Land use is dominated by a mixture of winter cereal crops, other winter crops such as rape-seed and peas, spring-sown crops (mainly sunflower and corn), set-aside and pasturelands, and other permanent or semi-permanent crops for livestock rearing.

The study area was intensively surveyed by different experienced ornithologists on a weekly basis from late March to late August as part of a European Union LIFE-NATURE Program (Jolivet and Bretagnolle, 2002). All Little Bustards found were recorded and mapped, and during the nesting and chick rearing periods (June–August), a special effort was made to locate and map nests and families across the study area. Juveniles were also counted in several post-breeding flocks from August to October. These surveys provided field data that was used to estimate the population parameters (Morales et al., in press).

2.2. Model structure and parameter estimates

2.2.1. The basic model

We built an age- and sex-structured, post-breeding, stochastic population model (hereafter the basic model) that considered males and females in separate stages. Males were separated from females because we chose to model separately male and female dispersal abilities, and also because there is a biased sex-ratio in our study populations. The basic model also considered the polygynous mating system of Little Bustard in which at least some males can potentially mate with a fairly large number of females (Jiguet, F., and Bretagnolle, V., unpublished data). This model included nine age classes for both sexes, with reproduction starting at one and two years old for females and males, respectively (Schulz, 1985; Bretagnolle, V., Jiguet, F., and Wolff, A., unpublished data). While the basic model could have included fewer age classes, we chose nine age classes based on two considerations. First, most available approaches for estimating survival rates when individuals can remain variable amounts of time in each age class require knowing in advance the long-term, deterministic growth rate (see Caswell, 2001). This poses a problem when dealing with real populations since the long-term, deterministic growth rate can substantially differ from the realised population growth rate whenever demographic rates have important stochastic variation over time which can bias the survival rates of age classes having variable duration. Second, using the only available data of recap-

Table 1

Annual, age-specific demographic rates (mean \pm SD) of the basic model of the Little Bustard for individuals of both sexes

Age	Survival rate		Female fecundity	
	Males	females	Sons	Daughters
Fledglings	0.72 \pm 0.11	0.68 \pm 0.11	0	0
Young adults, 1 year old	0.72 \pm 0.11	0.68 \pm 0.11	0.14 \pm 0.09	0.14 \pm 0.09
Adults, 2–7 years old	0.72 \pm 0.11	0.68 \pm 0.11	0.22 \pm 0.13	0.22 \pm 0.13
Old adults, 8+ years old	0.60 \pm 0.06	0.60 \pm 0.06	0.22 \pm 0.13	0.22 \pm 0.13

Fecundity rates are expressed as the number of sons or daughters per female per year, and calculated as fertility rates times survival rates (see main text for the methods used in the estimation of each demographic rate).

tured and resighted individuals for the Little Bustard and the current abundance in central western France, the estimates of annual survival rates (see below) assure that <5% (\approx 32 individuals) of the population would be older than nine years old and thus the basic model would adequately depict the life cycle of this species.

The estimates of averages and temporal variation of the age- and sex-specific survival rates are shown in Table 1. Adult survival rates were obtained from 35 adult Little Bustards colour-ringed and radio-tagged in Poitou-Charentes in summer, and resighted either in Poitou-Charentes in summer or in Spain in winter, between 1998 and 2002 (Bretagnolle, V., and Morales, M., unpublished data). We used the software MARK (White and Burnham, 1999) for the estimation of survival rates; the best fit was obtained for a constant over time survival rate without sex effect (but see below). Individuals were assumed to have a non-zero probability of remaining at the last age class; the latter however should not be construed with assuming that the birds were immortal since the chances of remaining in the last age class diminishes each year at a rate of $(1 - S_{\text{adults}})$. Survival of last age class was set to 0.60 (compared to 0.70 on average) with a similar relative temporal variability to that of the other adult age classes for both sexes (Table 1).

The estimates of yearly fertility in each of the seven study areas were based on the number of juveniles detected and older than 30 days. It was assumed that juvenile mortality after that age was considerably lower than during previous stages of chick development because Little Bustard chicks have already reached their mother's size and they are perfectly able to fly with the adults (Bretagnolle, V., unpublished data). Yearly fertility was calculated as the number of chicks older than 30 days per year divided by the number of females recorded at each study site. In an post-breeding stochastic population model, fertility rates are then converted into fecundity rates, i.e. fertility rates times the age-specific survival rate (Caswell, 2001). We also considered that

youngest females would lack experience of breeding and thus set their average fecundity to be lower than that of older females (Table 1). Adult sex ratios on the seven study sites were similarly biased across years and sites: 1.47 (± 0.12 ; $n = 7$ years on all sites) males per females; this biased sex ratio may originate either from a natal bias (primary or secondary) or as a result of differential adult survival. We modelled a survival bias according to sex, as survival rates, although not significantly, differed between males and females (Table 1).

Environmental stochasticity was modelled by drawing the values of the age-specific survival and fecundity rates from lognormal distributions whose parameters (means and standard deviations) reflect the average value and the temporal variability of each demographic rate of each population. Using the lognormal 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 that would be induced by using the normal distribution and truncating biologically impossible values (i.e. negative fecundity, survival higher than one) of the demographic rates (Akçakaya, 1998). Given that, presumably, food provisioning by the mother (chicks mainly feed on insects) determines chick survival rates, we 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 at each time step of the simulations (Akçakaya, 1991). Unless otherwise indicated, all models were analysed by Monte Carlo simulation using RAMAS/METAPOP (Akçakaya, 1998) for 30 years using 2000 replications for each model.

2.2.2. Sensitivity analysis of the basic model

We assessed the extent to which the predicted extinction risk of the basic model was affected by changes of several key model parameters in separate simulations while keeping the remaining ones unchanged. All models considered in the sensitivity analysis had the same sex-, age-structure as the basic model (Table 1) and a total initial abundance of 50 individuals (assuming a balanced sex ratio) with the initial age structure set to the stable age distribution corresponding to the demographic rates of each model. Seeking to keep the sensitivity analysis to a reasonable size, we divided the strictly local demographic components from the spatial aspects of the model into two separate parts.

In the first, we assessed the effect of changes of 0, ± 0.02 and ± 0.05 in average adult fecundity, adult survival and fecundity of the youngest adult age (Table 1) forming ($5^3=$) 125 parameter combinations for which we modelled the Little Bustard as a single population, leaving the complications arising from dispersal for the

second part. This part of the sensitivity analysis aimed to establish the influence of main demographic parameters on the extinction risk and the extent to which changes in one can be compensated by changes in another.

In the second part, we examined the potential that dispersal between populations (i.e. metapopulation dynamics) would lower the risk of extinction of the Little Bustard at a regional level. While there is little quantitative information on inter-population dispersal for the Little Bustard, anecdotal evidence suggests that both adults and juvenile can disperse over large distances (e.g. a tagged breeding male dispersed by >200 km during a breeding season). The two most critical parameters determining whether dispersal events would affect local population dynamics are the dispersal rate and the environmental correlation between populations (Burgman et al., 1993; Hanski, 1999). We explored the behaviour of a simple system of two populations having the same sex-, age-structure and the demographic rates (Table 1) as the basic model. Each population was started with a total abundance of 50 individuals (assuming a balanced sex ratio) and their initial age structures were set to the stable age distribution, and only dispersal rate, environmental correlations and the relative dispersal rates of individuals of different ages and sex were varied. As before, the results are expressed as the extinction risk of the source or the sink population. Two extreme cases were considered: a balanced case wherein the two populations had identical demographic rates, and source-sink case in which the fecundity rates of one population were three times higher had those of the other. Dispersal rates, expressed as the (symmetrical) proportion of fledgling individuals successfully switching populations per year, varied from (0.01, 0.03, 0.05, 0.07 and 0.09), and environmental correlations, expressing the similarity of fluctuation of environmental conditions of two populations, assumed values in (0.1, 0.3, 0.5, 0.7, 0.9), thus forming 25 combinations of these parameters for each of the two extreme cases. The variation of dispersal rates according to the age (fledglings and/or adults) and the sex of dispersing individuals (with female rates being equal, twice, triple or four times that of males) in this two-populations system were also evaluated for three pairs of values of the dispersal rates and environmental correlations forming 15 parameter combinations in separate simulations.

2.2.3. Extinction risk of the Little Bustard in SW France

Based on the results of the sensitivity analysis, we formulated a metapopulation model with eight Little Bustard populations in the Poitou-Charentes region, to estimate the extinction risk of the metapopulation and of each local population in this area. Based on a detailed map of the male Little Bustard distribution on the four Departments of the region in 2000, we defined eight

Table 2
Annual demographic rates (mean \pm SD) for the eight Little Bustard populations in SW France, Fig. 1

Population	Initial population size	Total fecundity	Population growth rate
1	273	0.296 \pm 0.133	0.811
2	103	0.544 \pm 0.231	0.946
3	80	0.292 \pm 0.116	0.801
4	30	0.228 \pm 0.114	0.772
5	98	0.464 \pm 0.163	0.904
6	212	0.384 \pm 0.201	0.861
7	50	0.544 \pm 0.170	0.946
8	15	0.384 \pm 0.201	0.861

Fecundity rates are expressed as the observed number of sons + daughters per female per year assuming 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 main text for the methods used in the estimation of each demographic rate. The population growth rate was calculated by eigen-analysis of the age-, sex-transition matrix of each population. Initial population sizes were based on a complete survey of the study area performed in 2000, see Fig. 1.

different subpopulations (Fig. 1) whose contours were decided using natural boundaries for Little Bustards such as forests and rivers, and discontinuities in their spatial distribution. We also considered a model with 16 populations (results not shown) which provided very similar results. In this part of the sensitivity analysis, we used the actual fecundity rates obtained from the five study populations that belong to this region (see Table 2 for values). Fecundity rates were obtained by using actual data if a study population was included into a subpopulation or by averaging values from the two closest study sites (Fig. 1).

The metapopulation model had a sex-, age-structure and density dependence functions identical to the basic model and the demographic rates and initial population abundance of each population shown in Table 2. We assumed that the dispersal rate of fledglings of both sexes between pairs of populations declined exponentially with the distance separating them, a common assumption in metapopulation modelling (Burgman et al., 1993; Beissinger and McCullough, 2002; Morris and Doak, 2002). The dispersal rates between populations were established by considering eight combinations of the parameters a and b of the dispersal function = $a^* \exp[-(1/b)*\text{distance}]$ where a is the proportion of individuals remaining at the population of origin, and b is the mortality rate per unit distance that defines the rate at which dispersal declines with the distance separating two populations (Akcakaya, 1998). Lower values of the parameters a and b of the dispersal function mean that fewer individuals will disperse between a pair of local populations. The eight combinations were formed using the values for a in (0.2, 0.4, 0.6, 0.8) and for b in (50, 100). The environmental correlations between pairs of populations were established using the same function used for dispersal rates with $a = 0.9$ and $b = 250$ which

yielded environmental correlation values in the range (0.48, 0.90). Using the metapopulation model thus formulated, we also evaluated the effect of the lek mating system of the Little Bustard on its extinction risk by comparing it with a model including all individuals (i.e. the sex ratio and the social do not affect breeding events) and a monogamous mating system for the same values of the demographic parameters. From the point of view of population dynamics, the mating system determines the degree to which each sex can limit reproduction (Legendre et al., 1999). In polygynous breeding such as the lekking mating system of Little Bustards, females are more limiting than males, because the dominant male mates with multiple females while females take exclusive care of the young and thus the number of mating events would be mostly constrained by the minimum number of breeding females each year on each population.

3. Results

3.1. Single population basic model and sensitivity analysis of key-parameters

Little Bustard annual survival rate has been estimated to be 0.72 for males and 0.68 for females respectively (Table 1), without significant differences between sexes (Bretagnolle, V., unpublished results) while fecundity rates in the seven monitored populations averaged 0.44 young fledged per female between 1997 and 2002 (Table 1) For the range of values tested in the sensitivity analysis, fecundity rate had a strong impact on the asymptotic population growth rate (Fig. 2(a)). Starting with a hypothetical population of 50 individuals, these average values of the demographic rates (Table 1) yielded an extinction risk at 30 years of 0.844. For the range of values assessed, changes in the adult survival rate had a relatively stronger effect on the extinction risk than changes in fecundity rates: changes in ± 0.05 in adult survival changed extinction risk roughly 10-folds whereas similar changes of fecundity rates only changed extinction risks three folds (Fig. 2(b)).

3.2. Two-populations basic model and effects of dispersal and environmental correlation

The basic spatial model showed, as expected, that the effect of dispersal events on decreasing extinction risk increased with dispersal rate and were more pronounced for lower values of the environmental correlation (Fig. 3). Compared with a closed population, dispersal lowered the extinction risk for all combinations of dispersal rate and environmental correlations assessed (Fig 3(a)). However, when the basic spatial model included two populations with different fecundity (a source-sink

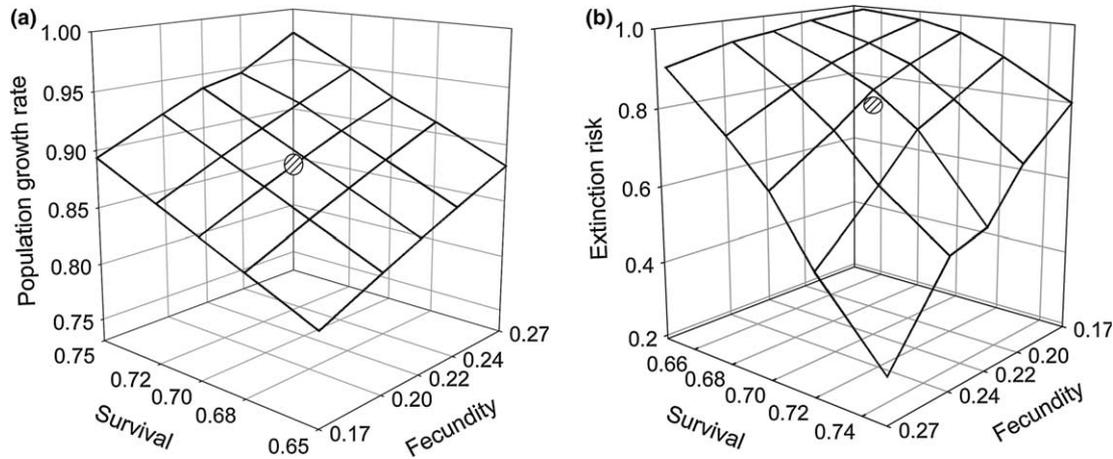


Fig. 2. Sensitivity analysis of the basic model of Little Bustards. (a) Effect of changing adult fecundity and survival on the deterministic growth rate of the basic model. The results shown in *a* and *b* were obtained by eigen-analysis of the basic model. (b) Importance of varying the adult survival and fecundity on the extinction risk predicted by the basic model, see text for details of the simulations. The circle in each panel marks the average values of the demographic rates of the basic model (Table 1).

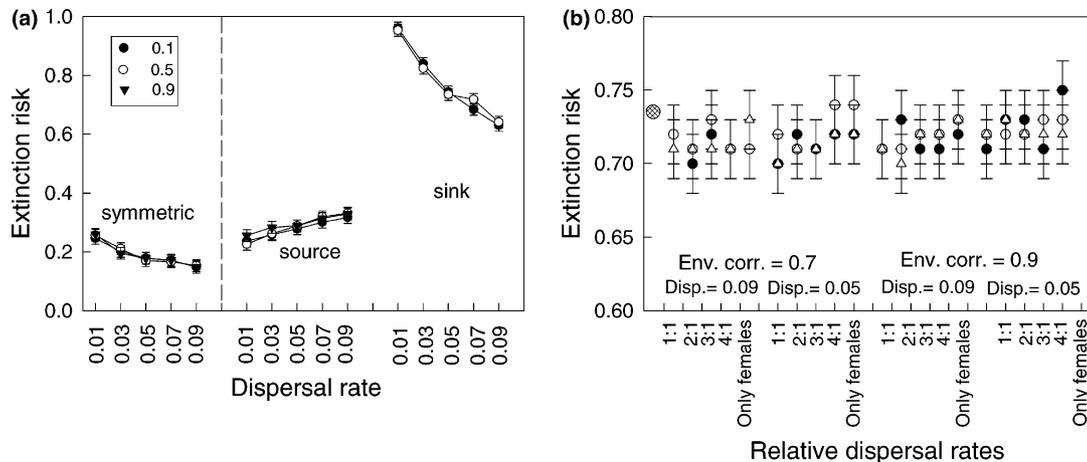


Fig. 3. Sensitivity analysis of the basic spatial model. (a) Effect of changes in the dispersal rate and environmental correlations (values used are shown in the insert) on the extinction risk for a symmetric and a source–sink cases, having a 3:1 ratio in their fecundity rates when only fledglings disperse between populations, see text for details. (b) Effect of the relative dispersal rates of individuals of different ages and sex, filled circles: only fledglings; empty circles: only adults; triangles: both fledglings and adults from even to progressively more female-biased dispersal rates for selected values of environmental correlations and dispersal rates. Only results for the symmetric model, both populations had the same demographic rates are shown. The extinction risk of the source population without dispersal is indicated at the left of the plot. The extinction risk for each condition or combination of parameters was obtained in separate simulations, see text for details.

system), dispersal rates had contrasting effects on the extinction risk and the importance of environmental correlations was smaller than when the two populations had identical demographic rates (Fig. 3(a)). Differences in dispersal rates between males and females had a relatively minor (less than 5%) influence on the extinction risk regardless of age of the dispersing individuals and typically the lowest extinction risk was obtained when dispersal rate was similar for both sexes (Fig. 3(b)). Overall, we found that the dispersal of both adults and fledglings regardless of any differences in dispersal rate between sexes lowered the predicted extinction risk (Fig. 3(b)).

3.3. Metapopulation model with real data from central western France

The extinction risk increased monotonically with the duration of simulation (Fig. 4). The choice of a time horizon of 30 years appeared as a sensible compromise between short-term prediction showing moderate extinction risk and a longer time horizon in which current conditions will almost certainly change thus reducing the usefulness of the predicted extinction risk.

The age- and sex-structured model for the eight populations showed that the extinction risk of the metapopulation in Poitou-Charentes (Fig. 1) over 30 years

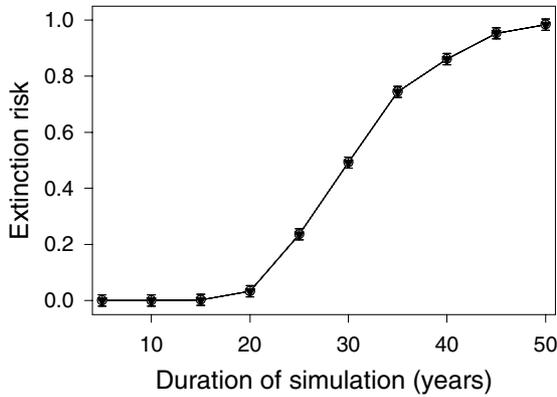


Fig. 4. Sensitivity of the extinction risk predicted by the age- and sex-specific metapopulation model to changing the time horizon of the simulations, using the values $a = 0.6$ and $b = 100$ in the dispersal function, see text for details. The extinction risk for each time horizon was obtained in separate simulations.

was about 0.45 for most combinations of parameters of the dispersal function, and 0.288 in the absence of dispersal (Fig. 5). The extinction risk of the metapopula-

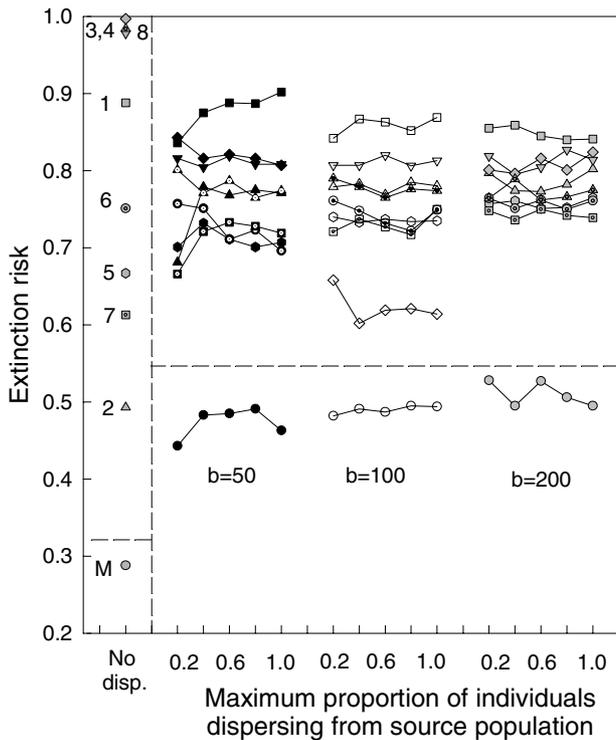


Fig. 5. Extinction risk of the metapopulation and the eight Little Bustard populations, (indicated by M and by their number) in Poitou-Charentes for different values of the parameters, a : proportion of the fledglings not dispersing and b : rate of decay of proportion of dispersing individuals with the geographic distance between two populations of the dispersal function. The extinction risk for each condition/combination of parameters was estimated in separate simulations, see text for details. The extinction risks of each local population and of the metapopulation without dispersal are shown at the left of the dotted line in order to assess the impact of dispersal on their extinction risk.

tion is largely determined by the abundance of three populations (1,2,5) that concentrate almost 70% of all individuals of the metapopulation which, in the absence of dispersal, do not function as source of dispersing juveniles to other local populations as discussed below. Dispersal had different effects on the extinction risk of local populations depending on their local fecundity and initial population abundance when compared with the predicted extinction risk not including dispersal. Three cases could be distinguished. (a) Populations 3, 4 and 8 that had low local abundance and fecundity for which dispersal decreased their extinction risk. (b) Populations 1, 2, 5, 6 and 7 that had both relatively high abundance and fecundity that served as the source of dispersing individuals and for which dispersion increased their extinction risk. The effects of dispersal on the extinction risk at the level of the metapopulation and of the local populations depended also on the values of the parameters of the dispersal function that determined the proportion of dispersing individuals amongst local populations. In general however, lower values of a and b leading to fewer dispersing individuals (Fig. 5), increased the extinction risk of populations functioning as sources (1, 2, 5, 6, 7), though these increases were mostly noticeable for $a = 0.2$ and 0.4 (Fig. 5). At the level of the metapopulation, larger values of the parameters a and/or b were associated with rather modest increases in extinction risk. Overall, extinction risk in local populations varied from 0.66 to 0.90.

Table 3
Effect of the mating system on the extinction risk of the metapopulation and of local populations of Little Bustards in Poitou-Charentes

	Polygynous	Monogamous	All individuals
Metapopulation	0.487	0.698	0.278
Population 1	0.863	0.958	0.808
Population 2	0.769	0.910	0.703
Population 3	0.820	0.916	0.733
Population 4	0.801	0.928	0.738
Population 5	0.737	0.874	0.617
Population 6	0.732	0.841	0.480
Population 7	0.727	0.890	0.583
Population 8	0.765	0.913	0.651

Each mating system was considered in separate simulations using the demographic rates shown in Table 2, the proportion of dispersing fledglings between pairs of populations was determined by the function $a \cdot \exp[-(1/b) \cdot \text{distance}]$ where a and b were set to 0.6 and 100, see main text for the biological interpretation of these parameters and other conditions of the simulations. Only the number of breeding events differed between the three sets of simulations. All individuals: the number of breeding events is determined by the total number of individuals but is not affected by either the sex ratio or social system. Polygynous-lekking system: the number of breeding events is determined by the minimum number of females of each age class. Monogamous system: the number of breeding events is determined by the minimum number of either females or males of each age class.

We finally assessed whether the number of breeding events determined by the mating system would affect extinction risk of the metapopulation and of the local populations. We found that, for the same parameter values, the extinction risk of the polygynous mating system was intermediate between a monogamous system and all-individuals model in which the mating system do not affect the number of breeding events of a population (Table 3).

4. Discussion

4.1. Extinction risk of Little Bustard in south-western France

With an estimated annual decline rate >10%, the current status of the Little Bustard in French cultivated areas is of considerable conservation concern, and recent data from Spain suggest that the species might also be declining in this country (Morales, M., personal communication). Using the first available information on most demographic parameters for this species, our age- and sex-structured stochastic model for the remaining Little Bustard population in SW France allowed estimating its extinction risk over a time period of 30 years to be of ≈ 0.45 . Moreover, using fecundity rates collected during six years on five different study sites and fine-grained counts of males obtained in 2000 we were able to formulate a spatially explicit metapopulation model. At the level of local populations, the extinction risk (0.66–0.90) depended largely on the initial population size and local fecundity.

These models required an important amount of field information and the making of assumptions for parameters for which there was little or no empirical information. Whilst the sensitivity analysis showed that the extinction risk predicted by the basic model changed little for different combinations of values of the demographic rates assessed, there remains important uncertainties regarding the actual dispersal rates and the individual fidelity to local breeding sites after their winter migration to Spain. Although the actual values of the dispersal rates did not have too much impact on the extinction risk of the metapopulation, they can affect the predicted extinction risk of local populations, particularly those functioning as a source of dispersing individuals.

Apart from being spatially explicit, our model took into consideration another critical aspect of the mating behaviour of the Little Bustard, its lekking system. Despite of the widely acknowledged importance that mating behaviour and its disruption may have on the long-term population persistence (Höglund, 1996; Sutherland, 1998; Caro, 1999), this feature has been explicitly incorporated into very few models of viability

using actual demographic data (Legendre et al., 1999). Our results illustrate the importance of accounting for the mating system for predicting the extinction risk of local populations: it was on average doubled compared to a non-lekking mating system. The lekking behaviour of Little Bustards tends to induce a distinctly aggregated spatial distribution of individuals (see Sutherland, 1996). Allee-like effects can be expected in lekking species because member individuals disperse whenever its total abundance becomes very low (Alonso et al., 2000; Morales et al., 2000; Dale, 2001) that would presumably increase local extinction risk (Stephens and Sutherland, 1998). In the case of the Little Bustard, the abandonment of the leks and the effective halt of reproduction have been observed in the region once the local lek size becomes smaller than six individuals (both sexes cumulated). The tendency of deserting leks once they become too small would accelerate the spatial contraction of local populations and lead to the progressive disappearance of a metapopulation system as individuals concentrate in fewer populations of high abundance (“hotspots”) where local resource depletion can then become limiting (as shown for the Great Bustard by Alonso et al., 2000). We did not however explicitly model this situation in our simulations.

4.2. Conservation perspectives

The reduction of the number of populations and their increasing fragmentation, accentuated by the mating behaviour of the Little Bustard, raise doubts about its prospects of long-term persistence in SW France in the absence of effective conservation actions. Our models suggest that the decline is mainly due to a low fecundity of females (≈ 0.5 chick at 30 days old per female). This is the demographic parameter on which conservation action should be focused, as for reaching an asymptotic growth rate around 1, adult survival, with such a fecundity rate, should equal approximately 0.9, a clearly unrealistic value for a bird of this size. The reason why fecundity is currently so low in French cultivated areas is due to nest destruction at harvesting (which accounts for 40% of clutch failure, $n = 104$ nests over the period 1997–2003), and food shortage for early chick rearing period, when chicks only depend on insects, mainly orthopterans. Between 7 and 15 days of age for a family, the probability of complete failure increases from 4% ($n = 47$ families) to 39% ($n = 28$), and the average family size (for those surviving) declines from 2.8 chicks per family at hatching, to 2.3 chicks per family at seven days old and 1.4 chicks per family at 15 days old, i.e. nearly one chick lost per week of rearing (Bretagnolle, V., unpublished data).

With such a high extinction risk at the metapopulation level, urgent action is needed to save French little Bustards breeding in cultivated areas. Large efforts were implemented experimentally between 1997 and 2001 (Jolivet and Bretagnolle, 2002), under a national LIFE-Nature program, in order to improve, at the parcel level, insect abundance and nest protection from harvesting. However, despite this effort, Little Bustards have continued to decline in nearly all experimental sites, probably because not enough parcels could be contracted by the LIFE-Nature program (Jolivet and Bretagnolle, 2002). While the ultimate causes of the precipitous decline (92% in 17 years) of the Little Bustard breeding in the French intensive agricultural areas lie with the decreases in the insect abundance and nest destruction, the mating system of the species, as well as high dispersal by fledglings, may have exacerbated the effects of these factors resulting from intensification of agricultural practices, as suggested by our models.

The average rate of decline at the Poitou-Charente region level is between 10% and 15% currently. New agro-environmental measures are taking place in France, at a more appropriate spatial scale (i.e., designation of eight Specially Protected Areas in the Region Poitou-Charentes, covering >160,000 ha, and eventually, the implementation of “*Contrats d’Agriculture Durable*”, from 2004). It is however quite likely that the Little Bustard population becomes extinct before those measures are effective, which has prompted the evaluation of additional conservation actions involving population reinforcement. Our model provides estimates of extinction risk for the metapopulation and the local populations, which are critical for assessing the effect of reintroduction of juvenile Little Bustards in the Poitou-Charentes: how many birds, how many release sites, and where, are considered elsewhere (Bretagnolle and Inchausti, 2005). Reinforcement has also been tested experimentally in 2003, at a very small scale. The future of the last migratory population of Little Bustard from Western Europe will probably depend on the simultaneous success of (i) improving habitat quality at a large spatial scale but, as this will take some time, also (ii) the reinforcement measures.

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