

## Viability of the endangered Little bustard *Tetrax tetrax* population of western France

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**Abstract.** Stochastic computer simulations are used to evaluate the sensitivity of Little bustard population parameters, estimating the survival probabilities of the seven endangered Little bustard populations of central-western France for which conservation actions are currently being or have been implemented. Different scenarios of parameter compensation for those nuclei to establish parameter levels assuring population viability are discussed. Adult survival, productivity per female, initial population size and carrying capacity were the most sensitive parameters in a hypothetical, isolated population. Juvenile survival also affected population survival, although its sensitivity was lower. Sex ratio did not have a linear effect on population survival, but probability of extinction increased for extreme values. Productivity per female and initial population size, varied strongly among the populations studied, determining their average time of extinction and growth rate. When a metapopulation scenario was simulated, the survival probabilities of each population and the metapopulations stayed close to 1.0 if no mortality was associated to migration. When mortality during migration was included in the simulations, the metapopulation's probability of survival significantly decreased under 90%. This approach may help managers to correctly address conservation measures and design effective strategies, which should be directed mainly to improve productivity, enhance female survival, and minimise mortality during migration (e.g. promoting insect-rich nesting substrates, avoiding female killing and nest destruction at harvesting, reducing the risk of collision with powerlines, or controlling poaching).

### Introduction

The Little bustard *Tetrax tetrax* is a palearctic, medium-sized, lekking steppe bird from the *Otididae* family that has suffered a strong population decrease throughout its range during the last century (Goriup 1994; Del Hoyo et al. 1996), and even disappeared from many European countries (Schulz 1985, 1987). Due to this decrease, it is currently classified as 'Vulnerable' (Tucker 1991; Goriup 1994, Heath et al. 2000) in Europe. In western Europe, only France, Italy, Portugal and Spain hold relatively

important populations (Tucker and Heath 1994). Among the latter, the French population has recently shown a particularly severe decline. The estimate of the French population's size was 7200–8500 breeding males in 1978–1979, falling to 1400 displaying males in 1995, according to the national census co-ordinated by LPO/Birdlife-France (Jolivet 1996), which represents a decrease of almost 80%. The regression continued up to 2000, when the population size was estimated at 1300 displaying males (Jolivet and Bretagnolle 2002). The decline has affected only birds breeding in cultivated areas, the population breeding in the steppe area of La Crau, Southern France, having remained stable since 1972 (Cheylan 1985; Jolivet 1997). Conversely, the number of displaying males inhabiting cultivated plains has fallen dramatically from 7800 to 700 in 18 years, which represents a decline of 90%. This has been associated to a corresponding range reduction (Boutin and Métais 1995).

The main reason suggested to explain Little bustard decline and range reduction in France are habitat loss and/or degradation as a result of agricultural intensification (Lecomte and Voisin 1991; Goriup 1994), including increasing application of agro-chemicals (Goriup and Batten 1990; Hellmich 1992), which reduces food availability. Food reduction seems to be particularly important in the case of arthropods, which are almost the only prey of fledglings (Jiguet 2002), and thus a main limiting factor on productivity and a critical component of the carrying capacity of agricultural habitats. Most conservation efforts in France have been directed to increase insect availability (Jolivet and Bretagnolle 2002). Additionally, agricultural intensification also affects adult survival, by killing incubating adult females at mowing-harvesting, although this is apparently relatively uncommon.

In spite of the effort made to census and monitor declining Little bustard populations, information on basic population parameters such as productivity or adult turnover has only recently been gathered (Jiguet 2001; Morales and Bretagnolle in prep.). Furthermore, no attempt has so far been made to assess the viability of the remaining population nuclei, or to evaluate the sensitivity of these populations to changes in either productivity or adult survival. This analysis is however important, since knowledge of these aspects is critical to evaluate whether conservation measures based on increasing productivity (the ones currently taking place) may be enough to maintain populations, or whether different measures must be taken in different populations. In the present paper, we use stochastic computer simulations to evaluate the sensitivity of Little bustard population parameters and try to assess the survival probabilities of the seven Little bustard populations of central-western France for which conservation actions are currently planned, or have been implemented. We discuss different scenarios of parameter compensation through the simulation of increases in the level of parameters for those nuclei to establish values assuring population viability. This approach should help managers to correctly address conservation measures and design effective strategies.

## Methods

### *Study species and populations*

The Little bustard is a polygynous bird generally mating in exploded leks (Schulz 1985; Jiguet et al. 2000 see Hölund and Alatalo 1995 for the concept of exploded lek). The species shows sexual plumage dimorphism, but size dimorphism is only slight (700–900 g for females versus 800–1000 g for males, Cramp and Simmons 1980). Females lay up to 4 eggs and males do not provide parental care (Cramp and Simmons 1980). Males display interannual fidelity to mating territories (Jiguet and Ollivier 2002; Morales et al. unpubl.) but the degree of site fidelity among females is unknown. Families remain isolated until chicks are 6–8 weeks old when they gather with other individuals to form mixed post-breeding flocks. Until 3–4 weeks, young feed almost entirely on insects while adults depend basically on plant food (Jiguet 2002).

The populations studied were located at seven different sites in central-western France (Figure 1). Two sites were located in the *Deux Sèvres* Department: South *Deux Sèvres* (46°15'N, 0°30'W) and North *Deux Sèvres*



Figure 1. Map showing the seven Little bustard study sites in central-western France considered in the present paper. (a) *Charente Maritime*; (b) *Charente*; (c) *Indre*; (d) *Maine et Loire*; (e) *North Deux Sèvres*; (f) *South Deux Sèvres*; (g) *Vienne*.

(46°55'N, 0°10'W). The remaining sites corresponded to the Departments of *Vienne* (46°50'N, 0°20'W), *Maine-et-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). All these sites correspond to intensive agricultural habitats holding low–medium densities of displaying Little bustard males. 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 pasture lands, and other permanent or semi-permanent crops for livestock rearing. Little bustards breeding in these areas are mainly migratory (Cramp and Simmons 1980), leaving their breeding grounds from roughly November–March, by the end of which they begin to arrive from wintering areas (Jiguet and Ollivier 2002), located as far as the Iberian southern plateau Morales and García de la Morena 2001).

Suitable agricultural habitat for Little bustard reproduction in central western France (mainly prairies, fallows and alfalfa fields, Salamolard and Moreau 1999) is fragmented (Jolivet and Bretagnolle 2002), so that favourable patches are isolated and surrounded by an unsuitable matrix of continuous and highly intensified cereal farmland (Wolff et al. 2001). On the other hand, radio-tracking has shown that individuals (mainly females) born in a given population can disperse and settle as breeders in a different patch (Bretagnolle and Jiguet, unpubl. data). Consequently, the Little bustard population of central-western France can be described as a spatially structured set of subpopulations connected through dispersal, and thus can reasonably be considered to function as a metapopulation.

#### *Demographic simulations*

We used Vortex 7.0, a stochastic simulation program (Lacy et al. 1995), to model Little bustard population dynamics. The following premises were used in the simulations: (1) no inbreeding depression, (2) polygynous mating, (3) females make their first reproduction attempt at age 1 year, while males do so at age 2 years (Jiguet 2001, author's unpubl. data), (4) lifespan of 10 years (von Frisch 1976), (5) sex ratio at hatching 1:1, (6) maximum number of hatchlings 4 (Cramp and Simmons 1980, authors' unpubl. data), (7) reproduction not density dependent, (8) individuals migrate between populations from age 1 year onwards, and (9) females are the migrating sex. Unless otherwise stated, simulations were run 100 times over 20 years.

To study the effect of different key demographic parameters on Little bustard population survival (calculated as  $1 - \text{probability of population extinction}$ ), we adopted an iterative procedure in which all parameters were held constant (at the 'default' values, see below) except the one under consideration. These simulations were performed on a hypothetical, isolated population of 20 individuals, which is the average size of the seven study populations. Given that females are the dispersing sex (Bretagnolle and Jiguet, unpubl. data based on

radiotracking) inbreeding can be considered generally low in such an average population, as presumed in the model premises. The parameters analysed were adult survival (assumed equal for females > 1 year and males > 2 years), juvenile survival (e.g. mortality of females < 1 year or males < 2 years), sex ratio (number of males divided by total population size), productivity per female (number of young fledged divided by total number of females), degree of polygyny (proportion of males copulating), population size and carrying capacity ( $x$  times the population size). The ‘default’ values of these parameters considered normal for a stable Little bustard population are presented in Table 1. Some of these values have been derived from the literature, some are based on data collected in these and other Little bustard populations, and some are educated guesses based on seven years working with the species. Mortality of juvenile females (< 1 year) and males (< 2 years) was considered to be the same and estimated at 75%, based on survey data from French populations (V. Bretagnolle and F. Jiguet, unpubl. data) and information from related species with similar life histories (e.g. 70–80% in the Great bustard, Morales and Martín 2003). We estimated adult mortality at 20% on the basis of data from 35 individuals radio tagged in France (V. Bretagnolle and F. Jiguet, unpubl. data). The estimate of 10% of males taking part in the breeding pool is derived from the observed frequency of females attracted by displaying males during a study of the mating system and sexual selection conducted at the population of *Deux Sèvres* (Jiguet 2001). Chicks can be considered ‘fledged’ at 30 days old, when they reach 3/4 of their mothers’ size and are fully able to fly and follow females, even to post-breeding flocks (Cramp and Simmons 1980, authors’ pers. obs.). We have estimated the percentage of females rearing no fledglings on the basis of nest failure in the stable Little bustard population of La Crau (South-eastern France), where 65% of females nesting in favourable habitat (steppe and fallows: Wolff 2001) succeed to hatch at least one egg. If we add a conservative figure of 15–20% mortality before fledging to the remaining 35% of nests, we can then consider that 50% of adult females rearing no chicks is a possibly correct figure for a stable population. Habitat carrying capacity

Table 1. Demographic and habitat parameters introduced in VORTEX to model Little bustard population dynamics ( $N_0$  = initial population size).

Parameter	Value	Source
Mortality of females < 1 years	75%	Estimated, Bretagnolle et al. (unpubl. data)
Mortality of males < 2 years	75%	Estimated, Bretagnolle et al. (unpubl. data)
Adult mortality (males and females)	20%	Estimated, Bretagnolle et al. (unpubl. data)
% of males in breeding pool	10	Estimated, Jiguet (2001)
% females with 0 fledglings > 30 days	50	Estimated, Wolff (2001)
% females with 1 fledgling > 30 days	20	Estimated, Wolff (2001)
% females with 2 fledglings > 30 days	15	Estimated, Wolff (2001)
% females with 3 fledglings > 30 days	10	Estimated, Wolff (2001)
% females with 4 fledglings > 30 days	5	Estimated, Wolff (2001)
Habitat carrying capacity	$1.5 * N_0$	Assumed

was tentatively set at 1.5 times the initial population size, so that population behaviour was not conditioned by this parameter.

Secondly, we evaluated the influence of connectivity on population survival. We simulated the fate of the hypothetical population described above (initial size of 20 individuals, and with 'default' values for population parameters) when it was connected through bilateral migration to one or various other identical populations. Rate of migration between two populations was defined as the proportion of individuals that migrate bilaterally between two or more populations.

To simulate the viability of our study populations we used data on population size and productivity collected over a 4-year field study (1997–2000) at the seven sites considered (Morales and Bretagnolle in prep.) which are detailed in Table 2. For the remaining parameters we used 'default' values. These simulations were run over 30 years in order to have a longer-term view of the populations' fate.

Once we determined the most sensitive parameters and assessed the viability of study populations, we ran the corresponding simulations on the latter to establish which parameters can be more easily compensated to help populations reach viability values, as well as the range of values of such parameters assuring the viability of the populations considered.

## Results

On a graphical basis, the most sensitive parameters (i.e. those for which population survival changed more drastically according to the variation of these parameters) in the hypothetical, isolated population considered were adult survival, productivity per female, initial population size and carrying capacity (Figure 2). Juvenile survival presented also an effect on population survival, although the slope of the corresponding curve was smaller, and thus its sensitivity lower (Figure 2b). Sex ratio did not have a linear effect on population survival, but if sex ratio was lower than 0.3 or higher than 0.5, probability of population extinction increased (Figure 2e). Finally, the percentage of males taking part in the breeding pool did not have any influence in population survival (Figure 2f).

Two of the most sensitive parameters, namely productivity per female and initial population size, varied strongly among the populations studied (Table 2). These differences determined their respective growth rate and survival probability (Figure 3). Only one population, *Maine et Loire*, which had both relatively high initial population size and high productivity, seemed to reach year 30 with reasonable probabilities to survive (0.57, and an average size decrease of 21%). The interpolation of the seven populations of study in the 3-dimensional space formed by population survival with productivity and initial population size, respectively (both parameters are known for all seven sites) is shown in Figure 4.

Table 2. Initial population size ( $N_0$ ), habitat carrying capacity ( $1.5 * N_0$ ), percentage of females rearing each of the possible number of fledglings, and average productivity (no. of fledglings/female) in the seven study populations considered.

Population	$N_0$	$K$	% 0 fledg.	% 1 fledg.	% 2 fledg.	% 3 fledg.	% 4 fledg.	Average productivity
South Deux Sèvres	43 ± 11.7	65	79.2 ± 13.2	17.3 ± 8.9	2.3 ± 2.3	1.3 ± 2.5	0.0	0.258
North Deux Sèvres	12 ± 1.6	18	71.3 ± 32.2	16.3 ± 11.1	12.5 ± 25	0.00	0.0	0.413
Vienne	17 ± 0.5	26	92.9 ± 14.3	3.6 ± 7.1	3.6 ± 7.1	0.00	0.0	0.108
Maine et Loire	28 ± 2.16	42	66.8 ± 12.9	10.1 ± 8.1	12.4 ± 8.4	8.6 ± 12.9	2.1 ± 4.2	0.691
Indre	20 ± 2.6	30	63.8 ± 12.3	21.7 ± 4.1	11.5 ± 15.7	3.1 ± 6.3	0.0	0.54
Charente	13 ± 1.5	20	38.8 ± 19.3	26.3 ± 18.9	28.8 ± 21.7	6.3 ± 12.5	0.0	1.028
Charente Maritime	6 ± 1.71	9	66.7 ± 38.5	16.7 ± 31.5	16.7 ± 31.5	0.0	0.0	0.501

Values are means ± SDs for  $n = 4$  years of study (1997–2000).

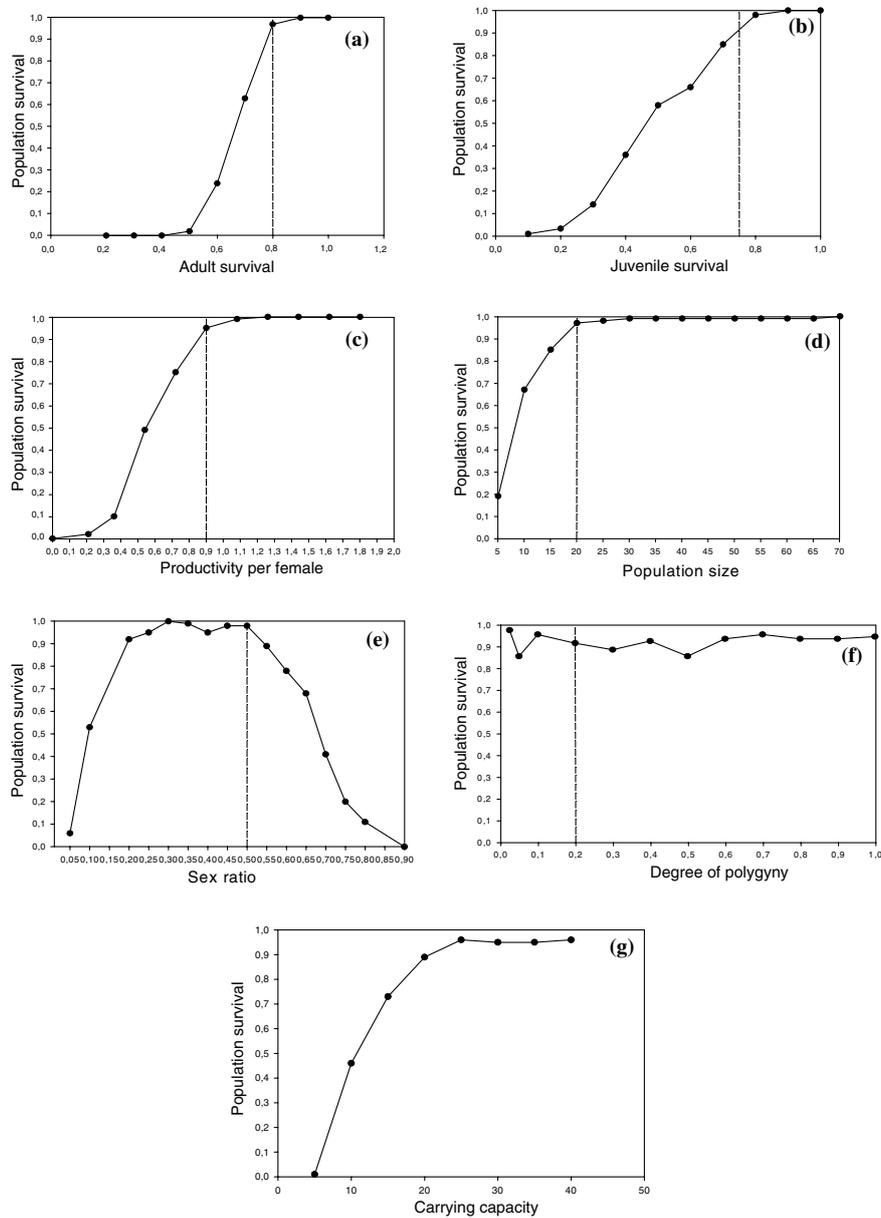


Figure 2. Sensitivity of population survival to the different parameters considered in a hypothetical Little bustard population of 20 individuals. (a) adult survival; (b) juvenile survival; (c) productivity per female; (d) initial population size; (e) sex ratio; (f) degree of polygyny; and (g) carrying capacity. Dashed vertical lines indicate threshold values for which population survival is 0.9.

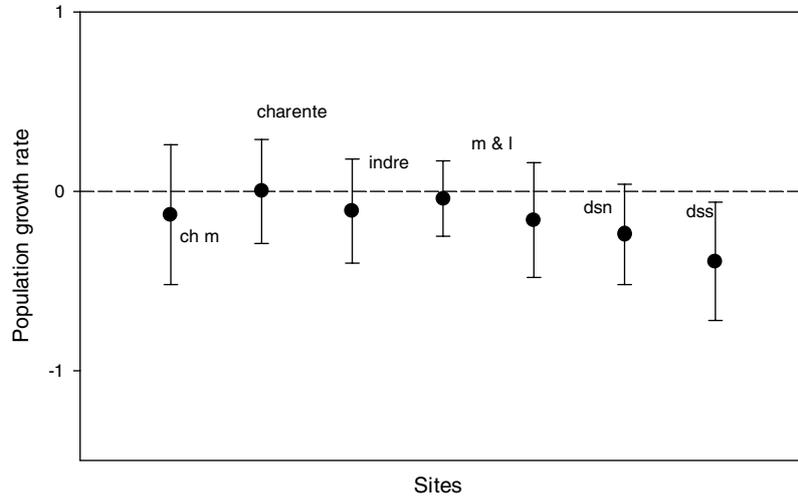


Figure 3. Average growth rate ( $\pm$ SD) of the seven Little bustard populations of central-western France considered in the present paper.

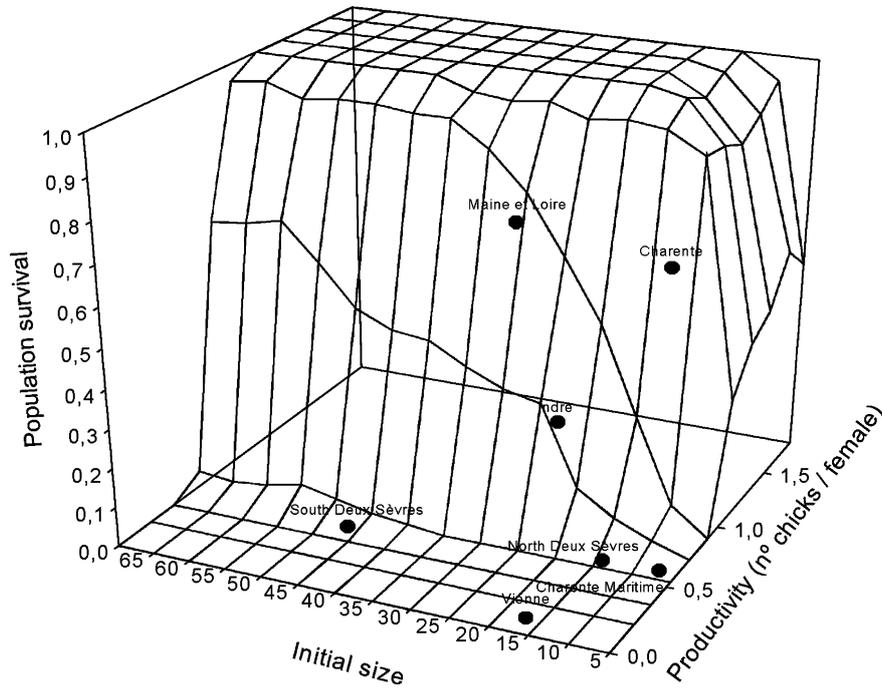


Figure 4. Three-dimensional space resulting from variation of population survival in relation to productivity per female and initial population size of a hypothetical Little bustard population and interpolation of the corresponding values of the species' populations studied in central-western France.

Figure 5 shows the changes in population survival probability that would be experienced in the study populations if they experienced increases in three critical population parameters: an increase in productivity would have strong influence on population survival on most of the study populations, whereas increases in adult or juvenile survival only would not have such a strong effect.

Given that very little information on individual exchange between our study populations is available, their fate was simulated in the absence of connectivity. In order to explore the potential effect of migration, the hypothetical population was bilaterally connected by the same migration rate with another identical one, thus forming a metapopulation. Their survival probabilities (and the metapopulation's) stayed close to 1.0 in a scenario where no mortality was associated with migration. However, when mortality during migration was included in the simulations, the probabilities of survival of the metapopulation significantly decreased for values of survival during migration under 90% (Figure 6).

## Discussion

### *Key demographic parameters in Little bustard population dynamics*

The results of our analyses yield adult survival, productivity, and initial population size as the demographic parameters more intensively affecting population survival, while juvenile survival showed lower sensitivity. The behaviour of these parameters fits the life-history of a species with features intermediate between 'K' and 'r' selected demographic strategies. The Little bustard could be considered as one such intermediate strategist. Its average lifespan is probably longer than that of similarly sized, ground nesting, plant-eating birds such as some grouse and ducks, while its average clutch size is much smaller (von Frisch 1976; Cramp and Simmons 1980; Johnsgard 1983). Additionally, second clutches are very rare due to the prolonged chick rearing period (von Frisch 1976; Cramp and Simmons 1980). On the other hand, females are sexually mature at age 1 year (2 years for males, Jiguet 2001) and thus the non-reproductive fraction of the female population is negligible. Juvenile mortality is generally high and population breeding success may undergo important inter-annual oscillations (Morales and Bretagnolle in prep). These intermediate life-history traits are shared by some closely related species like the Great *Otis tarda* and Houbara Bustards *Chlamydotis undulata* (Morales et al. 2002; Morales and Martín 2002, Combreau et al. 2002). In these type of species, high juvenile mortality rates can be compensated through a high life-time reproductive success, achieved after consecutive breeding attempts facilitated by relatively low adult mortality rates, although annual productivity should still be important to assure population viability (see reviews in Clutton-Brock 1988 and Newton 1998). It is therefore reasonable to expect both adult survival and productivity to have greater influence in Little bustard population viability

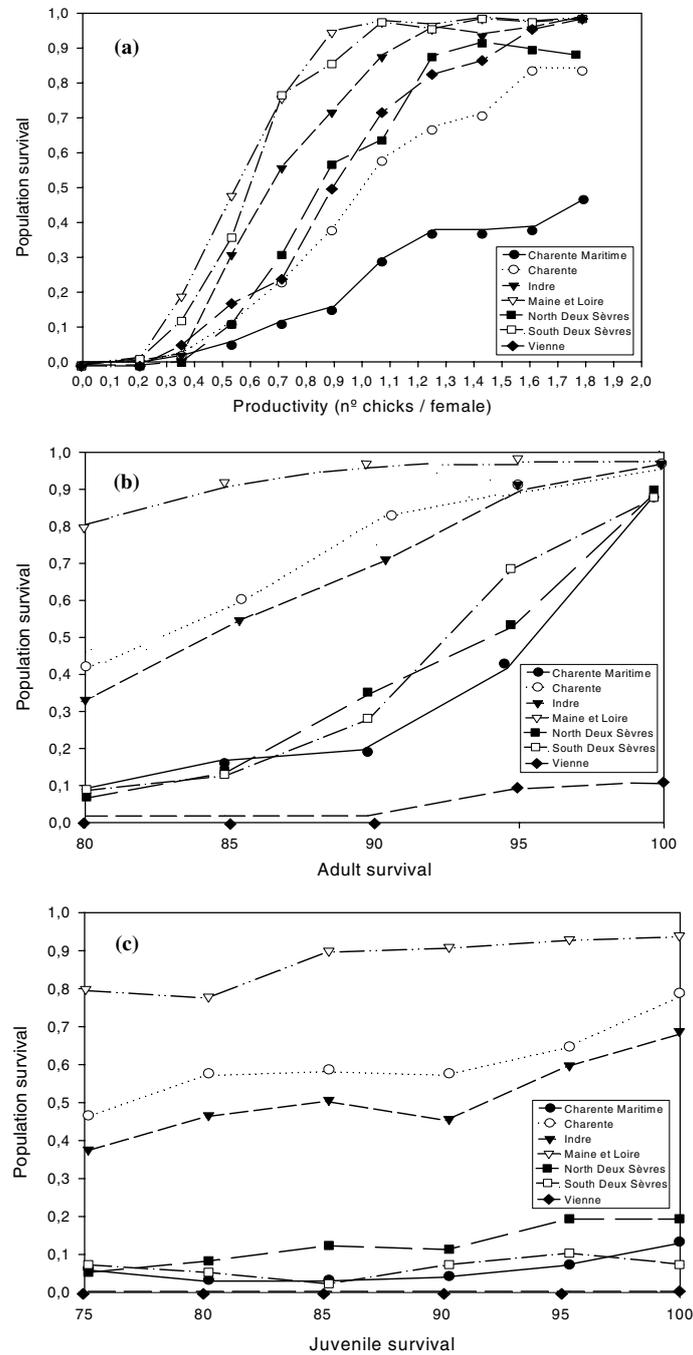


Figure 5. Effect on the studied Little bustard populations of central-western France of the compensation of three key parameters. (a) productivity per female; (b) adult survival; (c) juvenile survival.

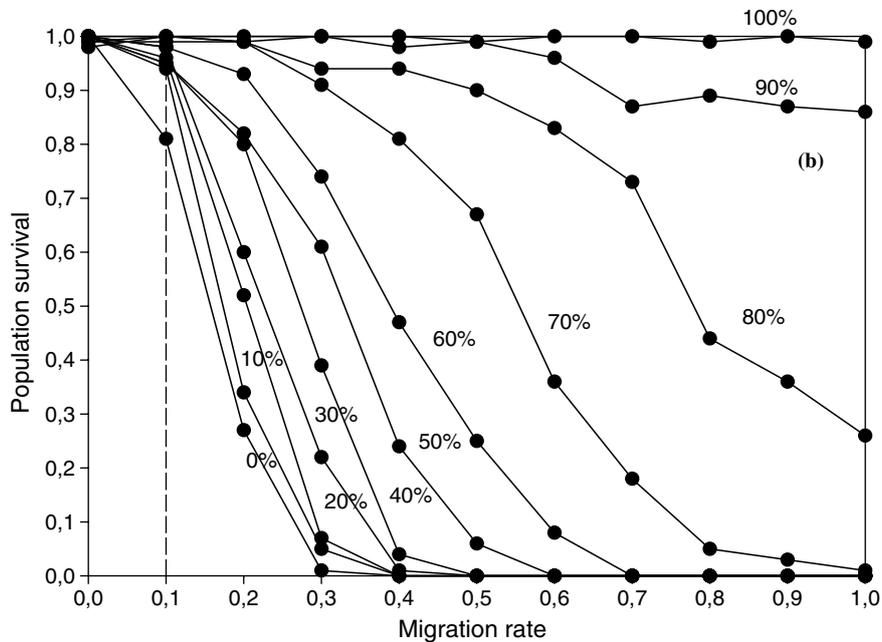


Figure 6. Relationship of population survival with the migration rate between two bilaterally connected identical Little bustard populations, and survival during migration presented as increasing percentages for each survival curve.

than juvenile survival, as shown by our sensitivity analysis, in which adult survival values smaller than 60% generated population survival probabilities under 0.3, while an increase of less than 10% in the former would raise population survival over 0.6 (Figure 2a). Similarly, an increase in productivity of 0.5 young per female produced a 85% increase in population survival probability (Figure 2c). The effects of increasing juvenile survival were, conversely, much less pronounced, with maximum population survival increases of only 22% for every 10% rise in that parameter. The pattern shown by initial population size also seems to fit an intermediate demographic strategy, since small values (less than 20 birds in our case) do have a significant effect on population survival, thus limiting its potential for recovery, as could be expected from a K-selected species (Newton 1998). Further population increases only seem to produce, however, a low asymptotical growth towards 1.0 population survival.

Population survival was highly sensitive to variations of sex ratio of the adult population at values of even moderate female shortage, but only of extreme male deficit, which could have been expected from a lekking mating system (Partridge & Endler 1997). In our simulation, the probability of extinction begun to rise when the proportion of females was smaller than 0.45, while population survival was higher than 0.9 when males represented only 20% of

the adult population. Moreover, the proportion of males entering the breeding pool, i.e. the operational sex ratio, was not a sensitive parameter. In lekking species, females usually mate with a small fraction of reproductive males (Bradbury et al. 1986; Höglund and Alatalo 1995) and therefore reproduction may be guaranteed as long as a few males are able to copulate with all or most sexually mature females.

When connectivity between populations was taken into account, population survival logically increased. However, when mortality during migration was considered, population survival significantly decreased (Figure 6). It can therefore be concluded that, although connectivity should improve metapopulation survival, when mortality during migration or dispersal increases over a certain level (around 30% in our case), the metapopulation would be at a considerable risk of extinction. Consequently, mortality sources during migration or dispersal should be minimised for the metapopulation to survive. Although its real influence in population viability is currently unknown, a scenario of no mortality during migration movements does not seem, however, very realistic due to the need to act on different potential causes (collision with powerlines, poaching, predation, lack of food) and at a large geographical scale (regional or national).

#### *Viability of the western France Little bustard populations, and implications for management*

In spite of the high sensitivity of population survival to productivity and adult survival considered independently, the joint analysis of those two parameters in relation to population viability shows that both must reach intermediate–high values to produce a significant increase in the population's probabilities to survive. In other words, only high values of one parameter will compensate the effect of low values in the other, although the compensatory effect of productivity seems weaker (a productivity of 1.8 chicks/female hardly compensates a 50% adult survival). On the other hand, even large initial population sizes will not compensate low productivity (below 0.7 chicks/female, Figure 4) or low to moderate adult survival levels. The results of the simulations run with data for the populations of central-western France fit these predictions. For the same estimated adult survival of 80%, the populations with the highest survival probabilities (*Maine et Loire* and *Charente*) were those presenting the highest average productivities, whereas the populations more rapidly falling into extinction, were those with the lowest productivity and/or initial size.

Productivity increases should have a compensatory effect on population survival, which would increase significantly in the seven populations studied (Figure 5a). This effect seems specially marked in the two largest nuclei, *South Deux Sèvres* and *Maine et Loire*, which would reach population survival probability over 0.95 for productivities of 1.1 and 0.9 chicks/female, respectively. Medium-sized populations like *Indre* and *Vienne* would only reach

probability values of population survival close to 1 with productivities of 1.3 and 1.6 chicks/female, respectively. The smallest nuclei, however, (North *Deux Sèvres*, *Charente* and *Charente Maritime*) would not reach total viability values and, in the case of the smallest population, even a maximum increase in productivity would hardly lead to a population survival probability of 0.50. These compensatory productivity values are not, however, realistic for the populations studied, where reproductive failure due to agricultural work and food shortage is very important (Jolivet and Bretagnolle 2002; Morales and Bretagnolle in prep.). Consequently, a potential recovery of these particular populations through productivity compensation does not seem plausible under the current management conditions of agricultural habitat. Moreover, as predicted by the corresponding 3-dimensional model, only high adult survival rates can increase population viability, while intermediate productivities may considerably rise their probabilities of survival. This suggests that conservation measures based on increasing productivity for the species are appropriate, although that aim would only be achieved through habitat management measures guaranteeing both the non-destruction of clutches and hatchlings during agricultural labours and a significant increase of arthropod supply for chicks. The analyses also suggest that such a strategy would be appropriate for all remaining populations, despite their differences in initial population size, so a global, regional-based strategy for increasing Little bustard productivity in western France would be appropriate. Finally a high breeding success in one of the populations is likely to affect positively all other populations, if they are connected through dispersion. Data existing for the species suggest that migration between populations may be relatively important for females, which also reinforces the previous statement. Consequently, management measures addressed at improving productivity, such as promoting agricultural practises that minimise nest losses and favour insect availability for chicks (e.g. fallow and field border maintenance, reduction of pesticide input) should be a priority in the conservation strategy of these Little bustard populations (in fact, their overall reproductive success between 1997 and 2000 was of only 19 chicks reaching age 30 days out of 101 eggs of known fate, mainly as a consequence of nest destruction during agricultural work and shortage of invertebrate preys for the young, Jolivet and Bretagnolle 2002). The reduction of nest losses by, for example, delaying mowing of prairies and alfalfa fields, which are the species preferred nesting substrates in the intensively cultivated plains of central-western France (Salamolard and Moreau 1999), would also contribute to lower adult female mortality. Simulations show that female shortage strongly reduces the viability of Little bustard populations. In fact, there is a general female deficit in the seven populations studied, all of which present a mean sex ratio of around 0.6 (Morales and Bretagnolle in prep.), which means that, on average only 40% of birds in the population are females, which is clearly below the viability threshold of 0.5. Consequently, any additional measure reducing female mortality (e.g. by avoiding female killing at harvesting) will improve population survival. Finally, population connectivity and survival of dispersing

individuals through adequate habitat management and elimination of mortality sources (powerlines, poaching etc.) should be favoured to guarantee the maintenance of the metapopulation.

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### References

- Boutin J.M. and Métais M. 1995. L'outarde canepetière. Eveil Editeur, Saint-Yrieix.
- Bradbury J.W., Vehrencamp S.L. and Gibson R.M. 1986. Leks and the unanimity of female choice. In: Greenwood P.J., Harvey P.H. and Slatkin M. (eds), *Evolution: Essays in Honor of John Maynard-Smith*. Cambridge University Press, Cambridge, pp. 301–314.
- Cheyland G. 1985. Le statut de la canepetière en Provence. *Alauda* 53: 90–99.
- Clatton-Brock T.H. (ed.). 1988. Reproductive success. *Studies of Individual Variation in Contrasting Breeding Systems*. Chicago UP, Chicago.
- Cramp S. and Simmons K.E.L. (eds) 1980. *The Birds of the Western Palearctic*, Vol. II. Oxford University Press, London.
- Combreau O., Qiao J., Lawrence M., Gao X., Yao J., Yang W. and Launay F. 2002. Breeding success in a Houbara bustard *Chlamydotis [undulata] macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China, *Ibis* 144 (on-line): E45–E56.
- Del Hoyo J., Elliott A. and Sargatal J. (eds) 1996. *Handbook of the birds of the World*. Vol. 3. Hoatzin to Auks. Lynx Edicions, Barcelona.
- Goriup P. 1994. Little Bustard *Tetrax tetrax*. In: Tucker G.M. and Heath M.F. (eds), *Birds in Europe: Their Conservation Status*. Bird Life International, Cambridge.
- Goriup P. and Batten L. 1990. The conservation of steppic birds: a European perspective. *Oryx* 24: 215–223.
- Heath M. and Barggreve C. and Peet N. 2000. *European Bird Populations: Estimates and Trends*. Birdlife Conservation Series. Birdlife, Cambridge.
- Hellmich J. 1992. Impact of pesticide use: a case study on Great Bustard. *Ardeola* 39: 7–22.
- Höglund J. and Alatalo R.V. 1995. *Leks*. Princeton University Press, Princeton.
- Jiguet F. 2001. *Defense des Ressources, Choix du Partenaire et Mécanismes de Formation des Leks chez l'Outarde Canepetière*. Thèse de Doctorat, Université de Paris 6, Paris.
- Jiguet F. 2002. Arthropods in diet of Little bustard *Tetrax tetrax* during the breeding season in western France. *Bird Study* 49: 105–109.
- Jiguet F., Arroyo B. and Bretagnolle V. 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. *Behav. Process.* 51: 63–82.
- Jiguet F. and Ollivier D. 2002. Male phenotypic repeatability in the threatened Little bustard *Tetrax tetrax*: a tool to estimate turnover and dispersal. *Ardea* 90: 43–50.
- Jolivet C. 1996. L'Outarde canepetière *Tetrax tetrax* en déclin en France. Situation en 1995. *Ornithos*. 3: 73–77.

- Jolivet C. 1997. L'Outarde canepetière *Tetrax tetrax* en France: le déclin s'accroît. *Ornithos* 4: 73–77.
- Jolivet C. and Bretagnolle V. 2002. L'outarde canepetière en France: évolution récente des populations, bilan des mesures de sauvegarde et perspectives d'avenir. *Alauda* 70: 93–96.
- Johnsgard P.A. 1983. *The Grouse of the World*. University of Nebraska Press, Lincoln, NE.
- Lacy R.C., Kimberly A.H. and Miller P.S. 1995. *Vortex: a stochastic simulation of the extinction process*. Version 7, User's Manual. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN, USA.
- Lecomte P. and Voisin S. 1991. Dry grassland birds in France: status, distribution and conservation measures. In: Goriup P.D., Batten L.A. and Norton J.A. (eds), *The Conservation of Lowland Dry Grassland Birds in Europe*. Joint Nature Conservation Committee, Peterborough, pp. 59–68.
- Morales M.B. and García de la Morena E.L. 2001. Recherche des zones d'hivernage des outardes canepetières françaises hivernant en Espagne (hiver 2000–2001). Rapport, LPO/Life Nature/Ministère de l'Environnement.
- Morales M.B., Alonso J.C. and Alonso J.A. 2002. Productivity and female individual breeding success in a Great bustard *Otis tarda* population. *Ibis* 144: 293–300.
- Morales M.B. and Martín C.A. 2003. *Otis tarda* Great Bustard. *BWP Update* 4: 217–232.
- Newton I. 1998. *Population Limitation in Birds*. Academic Press, London.
- Partridge L. and Endler J.A. 1987. Life history constraints on sexual selection. In: Bradbury J.W. and Andersson M.B. (eds), *Sexual Selection: Testing the Alternatives*. Wiley, Chichester, UK, pp. 265–277.
- Salamolard M. and Moreau C. 1999. Habitat selection by Little Bustard *Tetrax tetrax* in a cultivated area of France. *Bird Study* 46: 25–33.
- Schulz H. 1985. Grundlagenforschung zur Biologie der Zwergtrappe *Tetrax tetrax*. Staatlichen Naturhistorischen Museum, Braunschweig.
- Schulz H. 1987. Biologie et protection de l'Outarde Canepetière *Tetrax tetrax*. Rapport de synthèse d'un projet de recherche des Communautés Européennes avec une bibliographie sur l'outarde canepetière.
- Tucker G.M. 1991. The status of lowland dry grassland birds in Europe. In: Goriup P.D., Batten L.A. and Norton J.A. (eds), *The Conservation of Lowland Dry Grassland Birds in Europe*. Joint Nature Conservation Committee, Peterborough, pp. 37–48.
- Tucker G.M. and Heath M.F. 1994. *Birds in Europe: their conservation status*. Bird Life Conservation Series, 3, Cambridge.
- Von Frisch O. 1976. Zur Biologie der Zwergtrappe (*Tetrax tetrax*). *Bonn Zool. Beitr.* 27: 21–38.
- Wolff A. 2001. Changements agricoles et conservation de la grande avifaune de plaine: Etude des relations espèce-habitats à différentes échelles chez l'Outarde canepetière. PhD. Thesis, Université Montpellier II, Montpellier.
- Wolff A., Paul J.P., Martin J.L. and Bretagnolle V. 2001. The benefits of extensive agriculture to birds: the case of the little bustard. *J. Appl. Ecol.* 38: 963–975.