Biodiversity and Conservation **13:** 1659–1674, 2004.

Distribution dynamics of a great bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment

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Received 11 February 2003; accepted in revised form 16 June 2003

Key words: Conspecific attraction, Great bustard, *Otis tarda*, Population dynamics, VORTEX simulations

Abstract. Dispersing individuals can use conspecifics as indicators of habitat quality and aggregate at traditionally occupied sites, leaving other favourable patches unoccupied. Here we test the predictions of the conspecific-based habitat selection hypothesis on a Spanish great bustard (*Otis tarda*) metapopulation, currently fragmented due to recent human-induced habitat changes. The number of birds had increased by 23% between 1988 and 1998, but not consistently among leks. Leks that were large in 1988 increased, while those that were small decreased, which suggests that dispersing individuals used the numbers of conspecifics as cues for breeding-site selection. Moreover, leks with high productivity increased, while those with low productivity decreased. Finally, lek distribution was markedly stable throughout the decade, with no establishment of new leks, and suitable habitat patches remained unoccupied, as predicted by the conspecific attraction hypothesis. These results were corroborated by a simulation model which incorporated natal dispersal rates between leks as obtained through radio-tracking of 15 birds that survived throughout their 4-year dispersal period. In conclusion, in spite of the apparent increase in total numbers throughout the decade, both conspecific attraction and local differences in reproductive success contributed to a more aggregated distribution, increasing the species' vulnerability to local catastrophes, and the risks of reduced genetic diversity and extinction of small leks.

Introduction

Although dispersal and colonisation have been generally assumed to be stochastic processes, influenced by dispersal rate, patch quality and distance between patches, recent studies have called attention to conspecific attraction as a factor determining settling patterns (Stamps 1988; Smith and Peacock 1990; Ray and Gilpin 1991; Reed and Dobson 1993; Danchin and Wagner 1997). The argument is that dispersing individuals can use conspecifics as indicators of habitat quality to select feeding (Beauchamp et al. 1997) or breeding sites (Baltz and Clark 1999; Ramsy et al. 1999; Löhmus 2001; Serrano et al. 2001). Additive aggregation is then predicted, that is, a clustering of individuals at some traditionally occupied patches, leaving other areas of suitable habitat unoccupied. Habitat selection based on conspecific cues has long been recognised as a mechanism producing feeding aggregations in the context of optimal foraging theory (Clark and Mangel 1984; Pulliam and Caraco 1984; Valone 1993), and more recently, to explain the evolution of breeding aggregations such as bird colonies (traditional aggregation hypothesis, Shields et al. 1988; Brown et al. 1990; conspecific reproductive success hypothesis, Boulinier et al. 1996; sexual selection or hidden lek hypothesis, Wagner 1993).

In this paper we test the conspecific attraction hypothesis on a fragmented great bustard (*Otis tarda* L.) population and discuss the consequences the dynamics observed in this population may have on the conservation of the species in our study area, as well as in other areas of its distribution range. The great bustard has suffered dramatic declines during the last decades and is now globally threatened (Collar and Andrew 1988; BirdLife International 2000). It seems that agriculture intensification and habitat fragmentation due to human activities may have played a decisive role in these declines. The Spanish population is estimated at 23 000 birds, which is more than half the world total (Alonso et al. 2003). It probably declined until hunting was outlawed in 1980 (Alonso and Alonso 1996) and is now thought to be stable. Its conservation is still threatened by habitat fragmentation in most of Iberia, and particularly in our study area around Madrid city due to urban expansion. The species is here distributed in a series of patches (leks), with unoccupied areas of both suitable and unsuitable habitat in between. Thus, the metapopulation concept and the conspecific attraction hypothesis seem an appropriate framework to study the dynamics of this population and try to prevent its extinction.

In two earlier studies on habitat selection in our study area we showed that several unoccupied areas are ecologically inseparable from used sites, and that the species shows fidelity to sites regardless of the availability of suitable habitat elsewhere (Lane et al. 2001; Osborne et al. 2001). In the present study we hypothesise that the changes in numbers and distribution of birds throughout the decade 1988–1998 have been determined by intrinsic characteristics of each lek, mainly annual productivity of young, and by conspecific attraction. We suggest that conspecific attraction operates as follows. Habitat deterioration at a lek would favour juvenile and adult dispersal to neighbouring leks, which would increase in numbers. Radio-tracking studies carried out in other Iberian populations have shown extensive juvenile dispersal between leks, as well as partial migratory movements and some breeding dispersal of adults (Alonso et al. 1998, 2000; Morales et al. 2000). The additive aggregation rule of conspecific attraction implies two testable predictions: (a) we should expect a positive correlation between the initial numbers at each lek and the increases observed, because dispersing birds would prefer to settle at larger leks (*Smith and Peacock prediction*, Smith and Peacock 1990; see also Ray and Gilpin 1991; Stamps 1988; Reed and Dobson 1993; Danchin and Wagner 1997); and (b) no birds should establish at new, previously unoccupied patches of suitable habitat (Smith and Peacock 1990; Stamps 1988; Danchin and Wagner 1997). If conspecific attraction does not occur, dispersing birds would establish randomly at other leks, independently of the bird numbers at them, and should be expected to colonise new suitable sites available.

We also tested productivity as another cause of changes in numbers. The breeding success is very variable in great bustards, depending on local predator abundance and weather factors (Martín 1997; Morales et al. 2002). In population viability models of small great bustard populations, productivity has proved to be the main variable determining extinction probability (Lane and Alonso 2001; J. Streich, personal communication). Since females generally return to their natal sites after juvenile dispersal (Alonso et al. 1998), areas with high reproductive success would be expected to show higher increases in numbers throughout the period of study.

The effects of both factors, mean annual recruitment and conspecific attraction, were tested by correlating the changes in numbers of birds observed after a decade with initial numbers and average productivity at each lek. To corroborate the results, we performed computer simulations of the metapopulation, respectively ignoring and considering differential natal dispersal rates as obtained through radiotracking of individually marked great bustards.

Study area and species

Great bustards occur east of Madrid (Figure 1), in farmland habitat cultivated mainly with cereal wheat and barley, and minor crops of vetch *Vicia* spp., olives and grape vines. The human population of the region amounts to 5.5 million, with ca. 90% concentrated in the capital city and its immediate surroundings. The sites used by the great bustards are generally located in areas of lower population density, although in some of these, suitable habitat is being lost and fragmented continuously through the building of new roads and rapid expansion of villages.

The great bustard is polygynous and sexually dimorphic. Between late winter and early spring males concentrate at traditional arenas where they display in a dispersed lek system, to attract females for mating. Both sexes behave as partial migrants between the lek and postbreeding areas (Alonso et al. 2000, 2001; Morales et al. 2000), and show strong interannual fidelity to lek sites in spring. Females take over all brood caring duties, rearing usually 1–2 chicks. Juvenile dispersal is male-biased, and dispersing males establish as adults at up to 117 km from their natal sites, females usually at <5 km (Martín 2001).

Methods

Censuses and productivity estimates

We carried out three censuses of the great bustard population breeding in Madrid province: 23–25 March 1988, 13–18 March 1997 and 13–20 March 1998. The second half of March is the period of highest concentration of both males and females at leks and so the reliability of the censuses is maximised in this period. Additionally, we made several surveys throughout the rest of the year at all leks. In the present paper we compare only the results obtained in the 261 km^2 surveyed with equal effort in all three censuses. Censuses were carried out by 2–4 observers

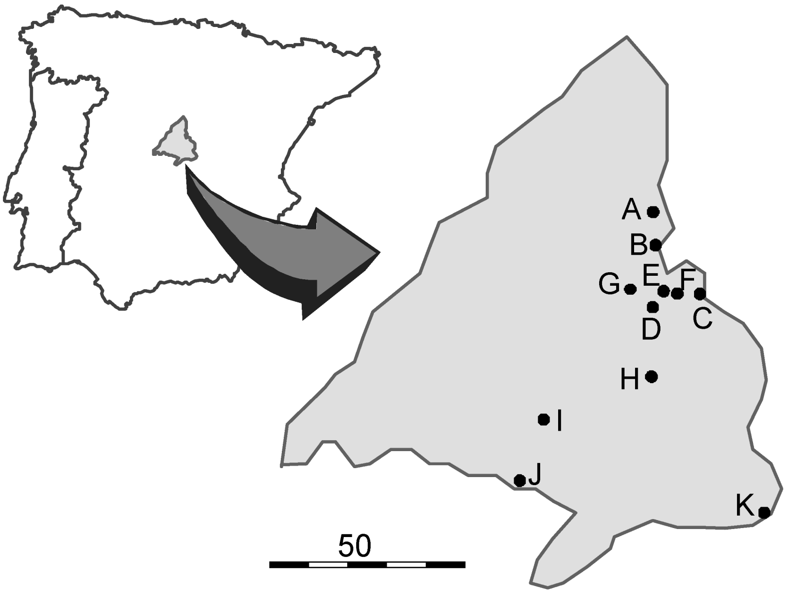

Figure 1. Location of great bustard leks in the Madrid region. A: Talamanca-Valdetorres, B: Ribatejada-Valdetorres, C: Meco, D: Daganzo, E: Camarma-Daganzo, F: Camarma, G: Cobeña, H: Campo Real, I: Pinto, J: Torrejón de Velasco, K: Estremera-Fuentidueña de Tajo. The first six are included in Special Protection Area for Birds no. 139 (335 km^2, Important Bird Area no. 064; Grimmet and Jones 1989), and lek J is included in a Nature Reserve since 1994.

with four-wheel drive vehicles, using the same routes, which had been selected according to previous experience. The census was interrupted at midday (10:00–15:00 GMT) when birds often sit down and are difficult to see.

Productivity was defined as the number of chicks surviving up to September, divided by the number of females older than 1 year. From September on productivity estimates cannot be made, since juvenile females cannot be distinguished from adult ones. As mean productivity for each lek through the period 1988–98 we used the mean of the 4–6 years for which we had data. In great bustards productivity is highly variable between years (0.04–0.29 chicks per adult female in September; Morales et al. 2002), which may distort interpretation of population trends. So in interannual census comparisons (Table 2), birds < 1 year old were omitted.

As a measure of lek-site fidelity for the period 1988–1998 we used the distance between the locations of male flocks at each lek site in both surveys. In March, males belonging to the same lek are generally found in a single flock. When more than one male flock was found, we considered the location of the largest one.

To test the hypothesis of conspecific attraction and the effect of differential productivity we correlated (after log-transformation) the changes in total numbers (expressed as percentage increase with respect to initial numbers) and densities of birds observed at each lek with numbers and densities at the beginning of the 10-year study period, as well as with the average productivity at each lek during the decade. To estimate lek areas we used all bustard locations recorded during spring censuses as well as during several complementary surveys carried out throughout the breeding season.

Radiotracking dispersing birds

In the summers of 1995–1997 we marked 107 young with wing-tags and radio-transmitters (Biotrack) at their natal sites. Birds were later located from ground and aircraft at least once per month during their juvenile dispersal, until they settled definitively to carry out their first breeding attempt, usually at an age of 2 years in females, 3–4 years in males. Juvenile mortality and some transmitter failures reduced our initial sample size to 28 birds (13 females and 15 males). Since the marking effort was equally distributed among leks, dispersal results should not be biased to favour final settling at particular leks.

Computer simulations

We used Vortex 7.0 (Lacy 1993; Lacy et al. 1995) to simulate the dynamics of the metapopulation. Our best estimates for all parameters required for the model are given in Table 1. Some values were calculated from the literature, some based on data from our long-term studies of marked birds in this and other areas, some measured during the present study, and others were educated guesses based on nearly two decades of field work. We set the same value for longevity, mean clutch size, age of first breeding, mortality and % adult males in the breeding pool, for which we did not have evidence of variation between leks. For the remaining parameters we could assign lek-specific values in the model. Initial population sizes and sex ratios were taken from our 1988 censuses (Table 2), and age distributions were assumed to be stable. For first-year mortalities (including non-hatched eggs) we used the values derived from average productivities at each lek (Table 2). For migration rates between leks we used the rates obtained through radiotracking of 15 males marked as young and followed throughout their dispersal phase until they settled to breed. Female great bustards are strongly philopatric, natal dispersal being performed mainly by males (Alonso et al. 1998), so in this study we only used male dispersal rates. For example, the dispersal rate from lek A to lek D was 0.17, since only one of six males hatched and survived at lek A dispersed to lek D ($1/6 = 0.17$). We set the initial and final dispersal age at 2 years, since this is the most frequent age at which males begin dispersal. Although adult bustards may also perform breeding dispersal occasionally (unpublished data), this was ignored in the present study since the Vortex software does not allow for differential juvenile and adult dispersal rates.

Table 1. Data and data sources used in VORTEX to construct the metapopulation model.

Parameter	Value ± SD	Source
Age females first breed	3 years	J.C. Alonso and coworkers[1]; Morales et al. (2002)
Age males first breed	5 years	J.C. Alonso and coworkers[1]
Maximum age	30 years	Glutz et al. (1973)[2]
Sex ratio eggs laid	50:50	H. Litzbarski, personal communication, sample of 531 eggs
Maximum clutch size	3	Glutz et al. (1973); Farragó (1992)
% Females with clutch of 1 egg	15.7	Alonso and Alonso (1990); Faragó (1992)[3]
% Females with clutch of 2 eggs	49.8	Alonso and Alonso (1990); Faragó (1992)[3]
% Females with clutch of 3 eggs	10.5	Alonso and Alonso (1990); Faragó (1992)[3]
% Females which are nonbreeders	24.0 ± 12.5	Alonso and Alonso (1990) ± VORTEX default value
% Mortality females 0–1 year	69.6–92.9[4] ± 6.28	J.C. Alonso and coworkers[1], present study
% Mortality females >1 year	7.5 ± 5.0	Derived from J.C. Alonso and coworkers[1] ± VORTEX default value
% Mortality males 0–1 year	77.1–94.7[4] ± 6.36	J.C. Alonso and coworkers[1] and present study
% Mortality males >1 year	13.3 ± 5.0	Derived from J.C. Alonso and coworkers[1] ± VORTEX default value
% Adult males in breeding pool	33[5]	J.C. Alonso and coworkers[1]
Emigration/immigration rate	0–1.00[6]	Present study

[1] J.A. Alonso, C.A. Martín, S.J. Lane, C. Palacín, M. Magaña, E. Martín and M.B. Morales, unpublished data based on marked birds.

[2] The longevity estimate is based on a report of a captive female living to 28.5 years (Glutz et al. 1973).

[3] The percentages of females with 1, 2 or 3 egg clutches were derived from Faragó (1992) assuming that 24% of females did not lay eggs (Alonso and Alonso 1990).

[4] First year mortality values varied between leks according to average young productivity 1988–98, see Table 2 and Methods, section Censuses and productivity estimates.

[5] Based on our intensive observations of 12 marked males of which four were seen to copulate.

[6] Natal dispersal rates (i.e., emigration/immigration) between leks were measured through radiotracking, see Methods.

Table 2. Comparison between spring census results of 1988 and 1997–98 in the 261 km^2 surveyed intensively in the 3 years. Young birds <1-year-old were excluded to avoid interannual variations in productivity.

Lek	km^2 surveyed	Birds(♂,♀)			Difference 1988–1997/98[1] *n*(%)	Average productivity[2] 1988–98	Distance between lek centers 1988–98 (km)
		1988	1997	1998			
A	34	89 (21,68)	158 (47,111)	183 (53,130)	+82(+92)	0.20	0.8
B	37	43 (12,31)	75 (19,56)	75 (16,59)	+32(+74)	0.40	0.6
C	26	40 (12,28)	31 (12,19)	40 (10,30)	−4(−10)	0.26	0.7
D	12	47 (10,37)	73 (15,58)	110 (18,92)	+45(+96)	0.43	0.5
E	25	34 (18,16)	45 (18,27)	39 (19,20)	+8(+24)	0.33	1.8
G	30	51 (16,35)	33 (5,28)	16 (4,12)	−26(−51)	0.10	0.7
H	37	91 (29,62)	94 (33,61)	82 (38,44)	−3(−3)	0.11	0.8
I	33	80 (30,50)	80 (28,52)	77 (28,49)	−1(−1)	0.19	0.9
K	27	55 (18,37)	51 (17,34)	37 (17,20)	−11(−20)	0.17	0.3
All leks	261	530 (166,364)	640 (194,446)	659 (203,456)	+120(+23)	0.21	0.8

[1] 1997/98 values are averages of both years.

[2] Number of young per female counted in September.

We simulated the behaviour of a metapopulation including the nine leks for which we had values for all relevant parameters (Table 2). Vortex was programmed to run 100 simulations over periods of 100 years. In order to check the effect of conspecific attraction independently from that of productivity at each lek, we ran the model both ignoring and considering the lek-specific values for dispersal between leks obtained through radiotracking. First we ran the model using identical emigration/immigration rates between all pairs of leks (we used the default values of Vortex, 0.02 birds migrating between leks). In a second run we introduced the specific natal dispersal values observed between each pair of leks. We then compared the changes in numbers predicted by the model for each lek through the first 10 years with those observed between our censuses of 1988 and 1998, after log-transformation of all values. If conspecific attraction was important, the second run was expected to give more similar results to those observed in our censuses than the first run.

Results

Population trends between 1988 and 1998

All leks found in 1988 were also active in 1998, and the mean distance between the March locations of male flocks was only 0.8 km (Table 2). No lek was completely abandoned, nor did we see birds establish new leks, in spite of the availability of suitable unoccupied habitat patches (Lane et al. 2001; Osborne et al. 2001).

Within the 261 km^2 surveyed intensively, the numbers of great bustards older than one year increased by 23% between 1988 and 1997–98 (Table 2). However, local increases in numbers and productivity varied substantially between individual leks. Sex ratio remained fairly stable within each lek. We performed a multiple regression analysis to examine the relative importance of initial bird density and mean productivity at each lek for the observed change in bird density. Both independent variables were statistically not correlated ($r = -0.59$, $p = 0.091$). The resulting model was highly significant ($p = 0.005$, $r^2 = 0.83$, $n = 9$ leks), both variables showing a significant positive effect on changes in bird density ($p = 0.009$ for initial bird density, and $p = 0.016$ for productivity, Figure 2). These results support the additive aggregation prediction of the conspecific attraction hypothesis and also the prediction that local values of annual recruitment are important. This suggests that the changes in numbers between 1988 and 1998 at each lek were influenced by both local productivities and a partial re-distribution of birds due to conspecific attraction.

To exclude the possibility that this result was influenced by the differences in the sizes of the areas occupied by each lek, we repeated the multiple regression analysis using the percentage increase in bird numbers with respect to initial numbers at each lek, instead of the change in bird densities. The resulting model was highly significant for change in total birds ($p = 0.003$, $r^2 = 0\ .86$, $n = 9$ leks). When males and females were considered separately, the model was significant for females but

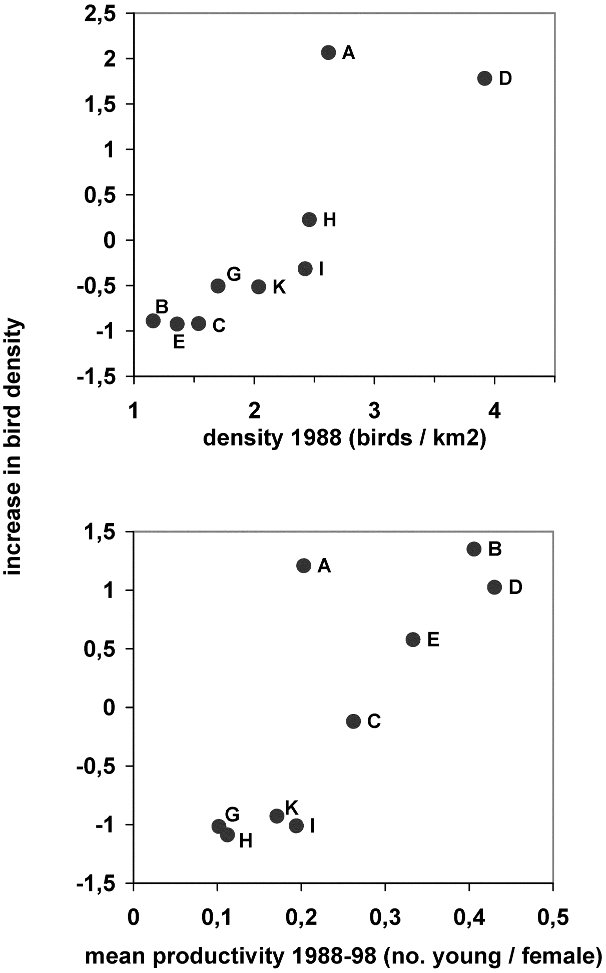

Figure 2. Component effects of the two independent variables included in the multiple regression analysis, initial bird density in 1988 and mean young productivity during the study period, on the observed change in bird density at each lek between 1988 and 1998.

not for males (respectively, $p = 0.001$, $r^2 = 0.90$, and $p = 0.44$, $r^2 = 0.24$; $n = 9$ leks in both cases). The effects of both independent variables, initial numbers of birds and productivity, were highly significant in the models for total birds and females ($p < 0.01$ in all cases), and not significant in the model for males ($p = 0.47$ for number of males, $p = 0.22$ for young productivity).

The changes in numbers observed did not correlate with non-conspecific habitat quality estimators like size of the area (Table 2, $p > 0.05$), or substrate composition, which was similar among leks and not different from that of nearby, non-occupied areas (Lane et al. 2001).

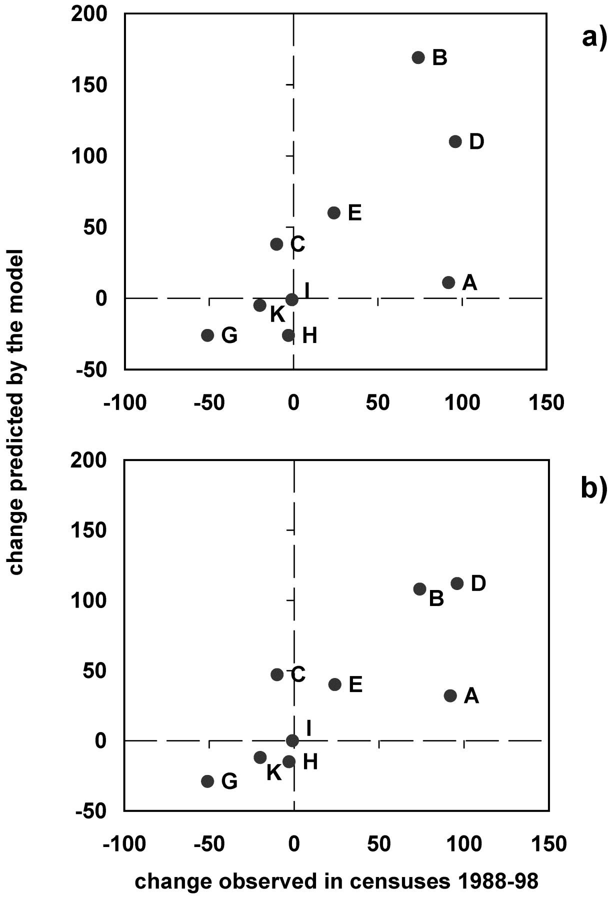

Figure 3. Relationship between changes in numbers observed at each lek in our censuses 1988–1998 and those predicted by the metapopulation model, respectively without considering (a) and considering (b) real natal dispersal data as obtained through radiotracking 15 marked individuals. Correlation (a) was marginally significant ($r = 0.66$, $p = 0.054$), and (b) was very significant ($r = 0.79$, $p = 0.012$). The variance explained by correlation (b) ($r^2 = 0.618$) was 43% higher than that explained by correlation (a) ($r^2 = 0.433$).

Dispersal between leks and simulation results

The changes predicted by the metapopulation model in numbers of birds at each lek after a decade were very similar to those recorded in our censuses (Figure 3). The sign of the predicted change (increase or decrease) coincided with the trend observed between 1988 and 1998 except for lek C, where the model predicted an increase and we observed a slight decrease. The correlation between final lek sizes predicted and those censused did not reach the 0.05 significance level for the model with identical dispersal rates between all pairs of leks (i.e., without considering the

Table 3. Numbers of radiotagged birds (males, females) dispersing from their natal lek to other leks. Other means a lek outside our study area. Missing values mean no dispersal was recorded. Data are from a sample of 28 birds (15 males, 13 females) marked as young in 1995–96 and radiotracked throughout ≥4 years until they settled as mature birds.

Natal lek	Lek where birds settled									
	A	B	C	D	E	G	H	I	K	Other
A	4, 5			1, 0			1, 0			1, 0
B	2, 1	0, 4								1, 0
C										1, 0
D				0, 1						0, 1
E							1, 0			
G										
H							1, 1			
I										1, 0
K										1, 0

effect of conspecific attraction; Figure 3a), whereas it was very significant for the model incorporating the specific natal dispersal rates between each pair of leks obtained through radiotracking (i.e., considering differential dispersal among lek pairs as predicted by the additive aggregation rule of conspecific attraction; Figure 3b). Most predicted lek sizes were very similar in both models, with the exception of leks A, B, E and H, for which the model with real dispersal rates gave more accurate values than the model with identical dispersal rates. This was so because as our radiotracking results showed, most dispersal occurred between these leks (Table 3).

Discussion

Status and recent trends

The results of multiple regression analyses of productivity and initial bird density at each lek show that both variables had a positive effect on the changes in local bird numbers after the decade of study. Differences among leks in other non-conspecific, intrinsic habitat quality estimators like carrying capacity or extent of the most preferred substrate types were not correlated with changes in bird numbers (Lane et al. 2001). The high increases observed at leks A, B and D led to extraordinary local densities which do not correspond to similar increases in intrinsic substrate quality.

Productivity was the first variable causing an increase. In our population viability analysis (see below), the importance of annual recruitment variations around critical values of ca. 0.15 young per female is shown. Leks with mean productivity close or below 0.15 decreased (Table 2: G, H, K), while those with values above 0.30 increased (B, D, E), and those with values between these extremes tended to be stable or to increase. The fact that young productivity was correlated with the change in number of females but not of males is explained by the high sex bias in natal dispersal in this species. Since females are more philopatric than males (respectively 75% and 31%; Martín 2001), leks producing more offspring would be expected to increase faster as a result of a higher female natal return rate, while male offspring productivity would not necessarily result in such a rapid growth of the local male flock. Our results confirmed these predictions.

However, local increases of over 90% (leks A and D) would hardly be expected due only to recruitment of juveniles hatched in these areas, assuming reasonable estimates for adult mortality (ca. 10%, based on our sample of radiotagged birds). Indeed, the initial number of birds at each lek contributed significantly and independently of productivity to the local changes observed. Leks that were large at the beginning of the study period increased, while smaller ones decreased, leading to a more aggregated distribution at the end of the decade. Part of the increases observed at the initially larger leks were due to immigration of birds coming from the smaller ones (four of six dispersal movements within our study area were to leks larger than the natal one; Table 3), as well as perhaps from some other leks outside our study area. These results agree with the additive aggregation predicted by the conspecific attraction hypothesis (Smith and Peacock 1990; Stamps 1988; Reed and Dobson 1993; Danchin and Wagner 1997). We have observed that dispersing immature individuals usually visit several lek sites before establishing as breeders. Juvenile dispersal thus provides the mobility necessary for the observed re-distribution pattern in the metapopulation. Two other predictions of the conspecific attraction hypothesis, the aggregation at traditionally occupied sites and the absence of new settlements, were supported by the marked fidelity to lek locations throughout the decade, and the lack of new leks.

In an optimal foraging theory context, Pulliam and Caraco (1984) also predicted additive aggregation. They showed that in most gregarious species equilibrium flock size would increase above the expected optimum predicted by basic ideal free distribution, and frequently to the maximum size allowed by habitat quality. This is also predicted by ideal free distribution theory when individuals differ in competitive ability (Parker and Sutherland 1986). Furthermore, among lekking species the skewness in male mating success tends to be reduced in larger leks, which probably favours preference for larger leks (Alatalo et al. 1992; Höglund and Alatalo 1995; Widemo 1998). Thus, larger leks should probably be selected by dispersing great bustards with preference over smaller leks. Our results were in line with this prediction.

Finally, it has been suggested that habitat fragmentation would reduce the movement between breeding sites in a metapopulation, by decreasing the probability that dispersers find groups to settle which are isolated (Smith and Peacock 1990). Two pieces of evidence support this assumption. First, the density of birds increased notably northeast of Madrid, where leks are closer to each other (Figure 1: leks A–G, 64% increase), while it slightly decreased in the more isolated areas in the south (leks H, I and K, 7% decrease). Second, overall dispersal rates were lower in this fragmented population than in another great bustard population living in a non-disturbed habitat in northeastern Spain, where 100% of the young males dispersed from their natal leks (Alonso et al. 1998).

Computer simulations

Simulations confirmed the census results, in spite of the small sample used to estimate dispersal rates. In eight of the nine leks studied the trends predicted by the model coincided with those observed, and the predicted final sum of birds (651 birds) was very similar to that censused (640 in 1997 and 659 in 1998; Table 2), suggesting that our model's assumptions and parameter values were quite realistic.

Even without considering the effect of male natal dispersal (Figure 3a), the correlation between predicted and observed changes was quite accurate, almost reaching significance. This suggests that a considerable amount of the changes observed after a decade is probably explained by intrinsic characteristics of each lek. Viability analyses have shown that annual recruitment is the most important parameter in great bustard populations. A lek of 30 birds survived and increased when productivity was ≥ 0.30 young per female, but went extinct for values ≤ 0.15 (J. Streich, personal communication). A sensitivity analysis of all model parameters showed that the crucial range of values where extinction probabilities increased from 10 to 90% was 0.10–0.20 (Lane and Alonso 2001). These figures agree with our productivity and model results.

However, after incorporating the real dispersal rates between leks the variance explained by the correlation increased significantly (Figure 3b), which supports the predicted effect of initial numbers of birds at each lek. The small increase still predicted for lek A was due to a limitation of the Vortex model, which does not allow for simultaneous input of differential dispersal in both sexes. To check this, we calculated the number of females expected considering the actual female natal dispersal rates observed (one bird from B to A; Table 3), and obtained 129 females expected at A, very close to the 130 counted in 1998 (Table 2).

Conclusions

It is difficult to completely discard the hypothesis that dispersing great bustards use habitat quality characteristics other than conspecific cues to decide where to settle. However, the results of this study, together with our habitat selection analyses (Lane et al. 2001) suggest that long-term changes in lek size and/or density can largely be explained by differences in local reproductive success and conspecific attraction. Leks producing more offspring increased faster, and larger leks were preferred by dispersing bustards. Moreover, great bustards did not settle at new patches of suitable habitat, in spite of these being ecologically identical to used sites. The differences in breeding success and bird numbers may ultimately reflect the variable incidence of human-induced habitat deterioration at each lek, but we suggest that bustards use conspecific cues such as number of birds and breeding success during habitat selection.

Implications for conservation

The two largest leks hold 33% of birds, and the current trend is for these large leks to continue increasing at a faster rate than others, up to a limit eventually imposed by carrying capacity. Smaller or more isolated leks tend to remain stable or slightly decrease, and the smallest ones have only a few males and are seriously threatened with extinction. For example, a small lek reported only 20 years ago west of Madrid city is now extinct (Domínguez and Vigal 1982). Since great bustards seem unable to colonise new areas, at least in the short term, the consequence of this concentration process may imply serious risks (e.g., Verner 1992). First, metapopulations with a lower fraction of occupied patches are more vulnerable to total extinction through immigration–extinction stochasticity (Gilpin 1990; Hanski 1991). Second, concentration of the population in fewer areas increases the species' vulnerability to local catastrophes such as diseases, and loss or degradation of habitat due to agricultural policy changes. Third, it could contribute to decrease genetic diversity. Reducing the number of leks where dispersing males can establish as breeders increases the males' natal philopatry rate and thus, the probabilities of close inbreeding (Alonso et al. 1998; Martín 2001). Finally, concentration in some favourable areas might lead to the sometimes erroneous belief that the species is increasing over its whole distribution range (see Alonso et al. 2003).

In conclusion, the future of the great bustard population in the Madrid region is not guaranteed, in spite of the high number of birds still surviving. The increase in numbers observed during the last decade in the study area is probably a consequence of a higher concentration of birds in the better patches, a demographic growth at the latter due to local recruitment of young birds, enhanced philopatry due to habitat fragmentation, and perhaps some immigration from neighbouring areas, and a partial recovery of bustard numbers in the whole population after cessation of great bustard hunting in 1980. Smaller leks are particularly threatened with extinction in the near future, and an excessive aggregation at few leks makes the whole metapopulation more vulnerable to catastrophic events and loss of genetic diversity. Strict habitat conservation measures are urgently needed to secure the future of this endangered population, and should perhaps be particularly directed at preventing the decrease of the number of extant leks by protecting currently used sites rather than trying to establish new alternative suitable patches.

Acknowledgements

We thank the 42 Group at Getafe military base, and the Spanish Air Forces, for their generous collaboration in helping to locate radio-tagged birds from military aircraft, and E. Martín and M. Morales for their help during field work. Field work was financed by the Instituto Nacional para la Conservación de la Naturaleza, Dirección General de Investigación Científica y Técnica, and Dirección General de Medio Natural in Madrid. We also thank the Spanish Ornithological Society–BirdLife International for their support. During part of the study C.A.M. and

M.M.R. benefited from predoctoral fellowships of the Comunidad de Madrid, and S.J.L. was supported by a Marie Curie grant awarded under the EU Training and Mobility of Researchers Programme.

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