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Status and extinction probabilities of great bustard (*Otis tarda*) leks in Andalucía, southern Spain

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Abstract. Great bustards (*Otis tarda*) commonly occur in isolated populations consisting of only a few tens of individuals. Knowing where these are, and understanding the factors affecting their persistence, is necessary to save this declining species. A census (Spring 1999) was therefore made of possible great bustard lek sites in Andalucía, southern Spain. Forty-six males and 79 females were observed and a total of 180 conservatively estimated for the areas we visited. These were distributed among five, possibly six, leks, but most (66–72%) were recorded at only two localities. Through interviews with local people we established that at least two, possibly three, leks had become extinct within the last two decades, and also learned of another lek of 50–70 birds in the north of the region. The precarious status of the four largest visited leks was demonstrated through computer simulation (VORTEX). This showed that under *status quo* conditions their likelihood of extinction within 100 years is 85–99%. Further simulations demonstrated the disastrous consequences of poaching with extinction probabilities of 95% reached in 8–70 years. However when a hypothetical management scheme was modelled the results were encouraging. In these simulations the number of chicks per female per year was increased from 0.14 to 0.18 and annual mortality of females was reduced from 7.5 to 5%. This resulted in extinction probabilities of only 20% within 100 years at the larger leks. Simple, practical conservation actions to enhance annual recruitment and increase female survival are suggested.

Key words: Andalucía, extinction, great bustard, management, population viability analysis, Spain, VORTEX

Introduction

The great bustard *Otis tarda* is a large, predominantly herbivorous, bird occupying grassland habitats from eastern Asia, westwards, to Iberia and northern Morocco. Although widely distributed, it is categorised as 'Vulnerable' (10% chance of going extinct in 100 years; IUCN criterion) in Collar et al. (1994) since individuals commonly occur around lek sites as small, separated, populations of a few tens to a few hundred birds. Leks are areas at which males display and copulate with females and, in the great bustard, adults of both sexes show high fidelity to a particular lek (Alonso et al. 1995, 2000a; Morales 1999; Morales et al. 2000).

Alonso and Alonso (1996) estimated the Spanish great bustard population to be approximately 20,000 birds. Despite these seemingly large numbers, the future status of great bustards in Spain remains uncertain since a precedent exists for large declines in relatively short periods. In Hungary the population decreased from 8557 in 1941 to 1100 in 1993, whilst in Germany the 4100 present in the 1940s is now (1999) reduced to just 50–60 (Nicolai 1993; Faragó 1993, 1996; Litzbarski and Litzbarski 1996; H. Litzbarski, personal communication). Hunting and changes in agricultural land management in the last 50 years causing general range fragmentation are widely regarded as central to these declines. The recent population trend in Spain is unknown, though until hunting was banned in 1980 the trend was probably downward since over 2000 birds were shot annually (e.g. 2057 in 1969 and 2036 in 1970; E. Trigo de Yarto, personal communication). Alonso and Alonso (1996) suggested that numbers are currently stable in some large populations in appropriately managed areas, but that there may be a tendency for the smaller, more isolated groups to decline to extinction. For example in Villafáfila, NW Spain, a population of approaching 2000 birds has remained broadly constant over a decade of monitoring (Alonso et al. 1996), whilst a population of 40 individuals reported at Navalcarnero, Madrid province, in 1980 (Domínguez and Vigal 1982) no longer existed in 1998 (J.C. Alonso et al., unpublished data).

In a recent article we argued that management of great bustards should particularly be directed at conserving the current number of lek sites (J.C. Alonso et al., unpublished manuscript). We suggested that since the distribution of great bustards in central Spain is apparently not limited by the availability of suitable habitat (Lane et al. 2001), dispersing juveniles might judge habitat suitability on the presence of conspecifics. Consequently settlement patterns should be strongly influenced by the prevailing distribution of the birds. Moreover no establishment of new lek sites has been observed in a ten year study in the same area suggesting that great bustards have very limited capacity to expand their range (J.C. Alonso et al., unpublished manuscript). Indeed the opposite has occurred in central Spain. Larger leks are increasing, but smaller leks are decreasing in size, leading to a more clumped distribution and increasing extinction probabilities of small leks. Aggregation of all birds at larger leks and concomitant loss of smaller ones is undesirable since it may lead to a decrease in genetic diversity and increase the chance of a catastrophic event threatening a whole metapopulation.

To maintain existing leks a first step must be to establish where they occur. Recent surveys in the regions of Extremadura (Sánchez et al. 1989, 1994), Castilla La Mancha (ETI, 1994), Castilla-León (ETI, 1999), and our own work in Madrid (J.C. Alonso et al., unpublished manuscript), and with colleagues in Navarra (A. Onrubia, M. Sáenz, and P. Osborne, unpublished data) and northern Morocco (Hellmich 1999; Alonso et al. 2000b) have verified the status and distribution of much of the Iberian great bustard metapopulation (see Figure 1 for the location of areas mentioned in the text). However reliable or recent data are still lacking for several regions where leks

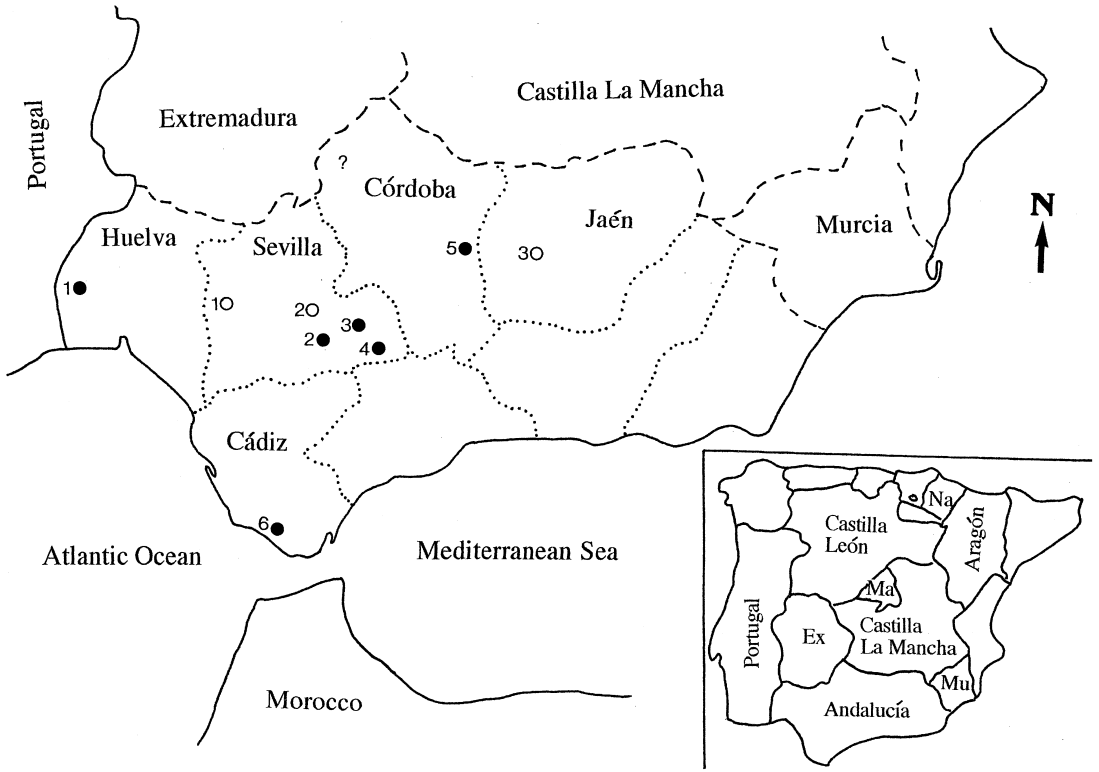

Figure 1. Locations mentioned in the text. Main map depicts Andalucía and surrounds: Solid lines represent coastlines or international border, dashed lines are regional boundaries, and dotted lines delimit provinces. Filled circles show locations of extant great bustard leks or possible leks: 1, Villanueva; 2, Paradas; 3, Lantejuela; 4, Osuna; 5, Bujalance; 6, La Janda. Open circles show extinct or possibly extinct leks: 1, Aznalcóllar; 2, Carmona, 3, Cazalilla. ? indicates the approximate location of a possible lek at Los Blázquez which we did not visit. Inset map shows political divisions of Iberia: Ex, Extremadura; Ma, Madrid; Mu, Murcia; Na, Navarra.

are known or thought to occur including Andalucía, Aragón, Murcia, and much of Portugal. To partly address this situation, the first aim of this work was to make spring visits to all reported great bustard leks in the Andalucían region, where numbers are thought to be small (*ca*. 200, Alonso and Alonso 1996), and individuals are distributed in an unknown number of vaguely described localities (e.g. Inés et al. 1995). Our precise objectives were to establish lek locations, and the size and structure (age/sex) of flocks.

Our second aim was to demonstrate the vulnerability of small, isolated, great bustard leks via computer simulation. Effective management of great bustards will require an understanding of the factors affecting lek persistence. In general terms, smaller populations are at greater risk of extinction than larger ones as a result of various factors operating synergistically. These include deterministic threats (human activities such as poaching or incompatible land use), environmental stochasticity (leading to variable breeding success), demographic stochasticity (chance extinction), and, if isolated, reduced fitness through inbreeding. Using the VORTEX population simulation software, which was written specifically to address the impact of these factors (Lacy et al. 1995), we calculated the persistence probability of four Andalucían leks over a period of 100 years under *status quo* conditions of no active management. After extensive sensitivity testing of the model we then demonstrated the disastrous consequences of illegal hunting of adult males for trophies, and, on a brighter note, the very positive benefits of a hypothetical management scheme. Though these models are specific to the leks we found in Andalucía, we present all parameters used in their construction so that researchers interested in management of great bustards elsewhere may apply VORTEX to their own populations.

Location and status of great bustard leks in Andalucía

Methods

This field work took place during 8–23 March 1999 in the five Provinces of Andalucía where we knew or thought great bustards occurred (Figure 1). The time of year was chosen since most great bustards gather in flocks at or near lek sites by mid-March. Approximate locations of leks, or suspected leks, have been published for the Provinces of Sevilla (Inés et al. 1995; Garrido 1996; Inés et al. 1996), Cádiz (Alonso 1985), Huelva (Garrido 1996) and Córdoba (Redondo and Tortosa 1994). We also knew of one more potential site in Jaén. In these areas we searched for leks by one of two methods. In the early morning (dawn to *ca*. 1000 h GMT) or evening (*ca*. 2 h before dusk) we surveyed extensive areas by telescope from suitable highpoints. At these times great bustards are generally active and males sometimes display conspicuously. Over midday we interviewed local people who were often able to indicate approximate areas in which great bustards occurred. In Córdoba, Alberto

Redondo (Universidad de Córdoba) kindly showed us where the birds occurred most frequently at his study area (Redondo and Tortosa 1994). We then searched these areas until we found the birds or were confident that none were present, which sometimes necessitated follow up visits. On three occasions we failed to find birds reported to us due to difficult terrain but in two of these we considered the local information specific enough to include in the results.

When a flock was located, we recorded the number of individuals, habitat and UTM co-ordinate. For each bird we determined sex, and, in the case of males, age class (<1 year, probably 2–4 years, probably ≥5 years). Alonso and Alonso (1990) provide a commentary on sexing and ageing great bustards. Flocks usually consist of individuals of the same sex and mixed flocks are rare at this time, except for 1st year males occurring with their mothers in female groups. We consider the location of male flocks in March to be indicative of the lek site at which they will display and copulate in April. When found, female flocks were assigned to the lek closest to them. These assumptions are based on an extensive data set, spanning 15 years, at sites in central and NW Spain (Morales 1999; J.C. Alonso et al., unpublished data).

Results

A total of 125 great bustards was recorded in Andalucía (Table 1). They were distributed among five or possibly six lek sites in the Provinces of Córdoba, Sevilla, and Huelva but most (66% of those observed) were recorded at lek sites near Bujalance (Córdoba) and Osuna (Sevilla; Figure 1). At two other locations in Sevilla, Lantejuela and Paradas, we observed 3 and 24 birds respectively, and near Villanueva (Huelva) one male was seen and a flock of 14 females was independently reported to us by two local people. Since only three birds were present at Lantejuela we are not certain that this is a lek.

The lek status of two additional sites remains uncertain in as much as we failed to observe great bustards in these areas although local people said they were present. Near Aznalcóllar (Sevilla) several people insisted great bustards were normally present all year but nobody had seen them for the three weeks prior to our visits on 22–23 March 1999. We were consistently told of the occurrence of two flocks in the area, one of two birds and the other of 11. These have not been included in Table 1 since the sexes could not be ascertained reliably. At La Janda (Cádiz) a gamekeeper informed us that one male occurred in the area but no females. We have subsequently learned that some birds may also still occur 3–4 km to the south-west of the area we surveyed (J.A. Alonso, personal communication). If so, it is likely to be a female flock.

Forty-six males were recorded of which 83% were adults ≥5 years old, while the remainder were aged between 2 and 4 years. Females cannot be aged at this time of year, but the total of 79 seen is less than expected. At great bustard leks, numbers are naturally biased in favour of females (Alonso et al. 2000b), for example in central

Table 1. Approximate location and status of 10 great bustard *Otis tarda* leks in Andalucía. Data were obtained during March 1999 except for Los Blázquez. Numbers in italics are reliable recent counts by local people; otherwise all data are our own observations. The estimated number of females is derived by assuming that all males in the lek have been counted and that a sex ratio exists of 1:2.5 in favour of females (Alonso and Alonso 1990). The question mark indicates uncertainty in the existence of female great bustards at La Janda, Cádiz.

Province	Town nearest the lek site	Adult males	2nd–4th year males	1st year males	Females	Est. no. females[a]	Total birds recorded	Total birds estimated	Comments
Córdoba	Bujalance	13	7	0	15	50	35	70	Perhaps the largest lek in Andalucía
	Los Blázquez							55–70	Not visited in Spring 1999[b]
Sevilla	Osuna	17	0	0	30	43	47	60	
	Carmona	0	0	0	0	0	0	0	Extinct since *ca*. 1990[c]
	Paradas	4	1	0	19	–	24	24	
	Lantejuela	2	0	0	1	5	3	7	Uncertain if true lek site
	Aznalcóllar	0	0	0	0	0	0	0	Uncertain if true lek site or extinct
Cádíz	La Janda	*1*	0	0	0?	3	1	4	Verging on extinction
Huelva	Villanueva	1	0	0	*14*	–	15	15	Ostrich farm built on/near lek site
Jaén	Cazalilla	0	0	0	0	0	0	0	Extinct since *ca*. 1985[c]
Total		38	8	0	79	134	125	235–250	

[a] No value calculated if number of females observed exceeded sex ratio of 1:2.5.

[b] Information obtained during a visit in December 1999 suggested 15–20 males and up to 50 females might occur during spring (C. Palacín, personal communication). This requires confirmation.

[c] According to information from local people which we judged reliable.

Spain the average adult sex ratio in 1998 was 1:2.5. We have used this ratio to estimate the number of females present at the four leks where males were recorded, but where the number of females seen was less than expected from this sex ratio. Thus, the estimated number of females in the areas we visited is 134 (Table 1). No first year males were seen which suggests successful breeding did not take place in 1998, though some first year females might have been present in the female flocks.

As a result of talking to local people we were able to establish the former existence of leks near Cazalilla (Jaén) and Carmona (Sevilla). Many local people were familiar with the males' display and one man recalled finding a nest and accurately described an egg. Local estimates of the last years in which great bustards were seen displaying in these areas were generally consistent, and extinction dates can be estimated at 1985 and 1990 respectively.

After our survey was completed, we were made aware of a possible lek at Los Blázquez, in the northwest of Córdoba. In December 1999 a cursory inspection of the area suggested 55–70 birds were present, and local people said a similar number occur each spring (Table 1; C. Palacín, unpublished data).

Extinction probabilities of great bustard leks in Andalucía

Method

To demonstrate the vulnerability of the four largest, visited, leks in Table 1, population viability models were constructed in which their probability of persistence over a 100 year period was calculated using VORTEX 7.0 (Lacy 1993; Lacy et al. 1995). VORTEX is a program that simulates the viability of small populations based on information given for appropriate life history parameters and the variation around these. The parameters required, and our best estimate for each, are given in Table 2. Some values were calculated from the literature, some were based on data from long term studies of marked birds (J.C. Alonso, unpublished data), and others were educated guesses based on nearly two decades of field work.

The ages at which males and females first breed is estimated from field observations of birds marked as chicks. The longevity estimate is based on a report of a captive female living to 28.5 years (Gewalt 1959), though the oldest known individuals in a marked population, two females, were 14 years old when last seen (J.C. Alonso, unpublished data). The percentages of females with one, two or three egg clutches were derived from Faragó (1992). We assumed that each year 24% of females did not lay eggs (Alonso and Alonso 1990). Percentage mortalities of birds less than one year old include eggs that did not hatch. Percentage mortalities of birds older than one year are based on the mortality rate of birds marked as chicks dying in their second year and on a limited number of birds marked as adults. The percentage of 33% adult males in the breeding pool is based on intensive observations of 12 marked

Table 2. Data and data sources, used in VORTEX to construct the *status quo* model.

Parameter	Value (± SD)	Source
Age females first breed	3 years	Estimated, J.C. Alonso and co-workers[a] (unpublished data)
Age males first breed	5 years	Estimated, J.C. Alonso and co-workers[a] (unpublished data)
Maximum age	30 years	Estimated, Gewalt (1959)
Sex ratio (eggs laid)	50:50	H. Litzbarski (unpublished data)
Maximum clutch size	3	Gewalt (1959), Faragó (1992)
% females with clutch of 1 egg	15.7	Derived from Faragó (1992)
% females with clutch of 2 eggs	49.8	Derived from Faragó (1992)
% females with clutch of 3 eggs	10.5	Derived from Faragó (1992)
% females which are nonbreeders	24.0 (± 12.5)	Alonso and Alonso (1990) ± VORTEX default value
% mortality females 0–1 year	89.4 (± 6.28)	Derived from Faragó (1992), Morales (1999), J.C. Alonso and co-workers[a] (unpublished data)
% mortality females >1 year	7.5 (± 11.81)	Derived from J.C. Alonso and co-workers[a] (unpublished data)
% mortality males 0–1 year	92.1 (± 6.36)	Derived from Faragó (1992), Morales (1999), J.C. Alonso and co-workers[a] (unpublished data)
% mortality males >1 year	13.3 (± 12.0)	Derived from J.C. Alonso and co-workers[a] (unpublished data)
% adults males in breeding pool	33	J.C. Alonso and co-workers[a] (unpublished data)
Emigration rate	0	Assumed
Immigration rate	0	Assumed

[a] J.A. Alonso, S.J. Lane, M. Magaña, E. Martín, C.A. Martín, M.B. Morales, C. Palacín.

males of which four were seen to copulate. Finally, an ongoing study (since 1997) of juvenile dispersal in an isolated great bustard population in Navarra, northern Spain, has yet to reveal an incident of emigration (J.C. Alonso, A. Onrubia and P. Osborne, unpublished data). We assume the same to be the case for immigration, so a rate of zero was set for both in all models.

At a more general level VORTEX offers a variety of additional options for which we made the following decisions: (a) reproduction is not density dependent up to an arbitrary carrying capacity of 1000 individuals; (b) environmental variations in reproduction and survival are correlated, and (c) the effects of inbreeding depression should be incorporated (VORTEX default values). Great bustards have a polygynous breeding system.

For each of the four leks, VORTEX was instructed to calculate the age distribution since we did not know the ages of individual birds attending leks (other than the estimates for males given in Table 1). However, to more accurately reflect the structure of the leks as we had seen them in the field two adjustments were necessary. First, we found that VORTEX incorporated too many males into the models and so, for each lek, we adjusted the sex distribution by subtracting males from the older age

classes and adding females to the younger classes until the sex ratio and total were the same as that in Table 1. Secondly, VORTEX structured the age populations such that between one and four individuals were placed in the 'age 1' category. However our surveys showed no males of the year were present at any lek suggesting failure of recruitment during the year prior to the census. Consequently we adjusted the age distributions in the models by adding one bird to each successive age class for every individual subtracted from the 'age 1' category until the total in the latter was zero. The resulting age distributions obtained for each lek and used in the models are given in Table 3.

For each lek VORTEX was programmed to run 1000 simulations over a 100 year timespan. From these, the probabilities of persistence at ten year intervals were

Table 3. Adjusted number of female, F, and male, M, great bustards in age classes 1–30 calculated by VORTEX for the four largest leks surveyed in Andalucía.

	Bujalance		Osuna		Paradas		Villanueva	
Age class	F	M	F	M	F	M	F	M
1	0	0	0	0	0	0	0	0
2	4	3	4	2	1	1	1	0
3	4	2	3	2	1	0	1	0
4	2	2	4	1	1	0	1	0
5	4	2	2	2	1	0	1	1
6	3	1	2	1	1	1	1	0
7	2	1	2	1	1	1	1	0
8	2	2	2	1	1	1	1	0
9	2	0	2	1	1	0	1	0
10	2	1	2	1	1	0	1	0
11	2	1	2	1	1	1	1	0
12	2	1	2	0	1	0	0	0
13	2	0	1	1	1	0	1	0
14	1	1	1	0	1	0	0	0
15	2	0	2	1	1	0	0	0
16	1	1	1	0	0	0	1	0
17	1	0	1	0	1	0	0	0
18	2	0	1	1	0	0	0	0
19	1	1	1	0	1	0	1	0
20	1	0	1	0	0	0	0	0
21	1	0	1	0	0	0	0	0
22	1	0	1	0	1	0	0	0
23	1	0	0	0	0	0	0	0
24	1	0	1	1	0	0	1	0
25	1	1	1	0	1	0	0	0
26	1	0	1	0	0	0	0	0
27	1	0	0	0	0	0	0	0
28	1	0	1	0	0	0	0	0
29	1	0	0	0	1	0	0	0
30	1	0	1	0	0	0	0	0
Totals	50	20	43	17	19	5	14	1

obtained. We suggest these models reflect the likelihood of these leks becoming extinct under the *status quo* conditions of no conservation management and assuming no birds are poached.

Having established these models we then performed a series of additional tests to determine how sensitive the ouputs were to small changes in key parameters. Using the age structured data for Bujalance (Table 3) we adopted an iterative procedure in which all parameters were held constant except the one under consideration. For this parameter successive values, incorporating the one used in the *status quo* model, were input at increments such that ten values spanned the range of values that might be considered reasonable. For example for 'maximum age' 10 values at increments of five years between the ages of 10 and 55 were used. Probabilities of extinction at year 100 were then recorded for each value based on 1000 simulations. Other parameters included in this analysis were ages of first breeding for males and females, percentage of females not breeding, percentage of adult males in the breeding pool, percentage mortality estimates with juvenile mortality based on the number of chicks raised per 100 adult females, and estimated standard deviations where appropriate (Table 2). Regression analyses were used to assess which changes across the independent variables had statistically significant effects.

Finally we modelled two realistic scenarios on the data from the four leks. In the first we examined how poaching great bustards affects probability of lek persistence. We programmed VORTEX to remove one adult male each year. This rate was chosen since it seems to reflect the attitude of poachers that the occasional shooting of a male has little appreciable effect on population persistence. Poaching regrettably involves selection of a large male as a trophy hence potential breeders ($\geq$5 years) were removed. In the second scenario we examined the benefits to each lek of an hypothetical management scheme in which the result was an increase of 0.14–0.18 chicks per female per year (equivalent to a three percentage point decrease in both male and female juvenile mortality) and a reduction in annual female mortality from 7.5 to 5%.

Results

The results of the sensitivity tests (Figure 2) indicated the model output was robust to values given for the percentage of adult males in the breeding pool ($P > 0.05$). Increasing the proportion of adult females not breeding, the ages at which males and females first breed, and the percentage annual mortalities of males and females, all significantly increased the probability of extinction at year 100 ($P < 0.05$ in each case). With regard to age at first breeding and mortality rates, the results for females tended to be more pronounced than for males, with the output being particularly sensitive to mortality of adult females. A second parameter whose values strongly influenced extinction probability is the number of chicks raised per female. Within the range of 14 to 26 chicks per 100 females, probability of extinction declined

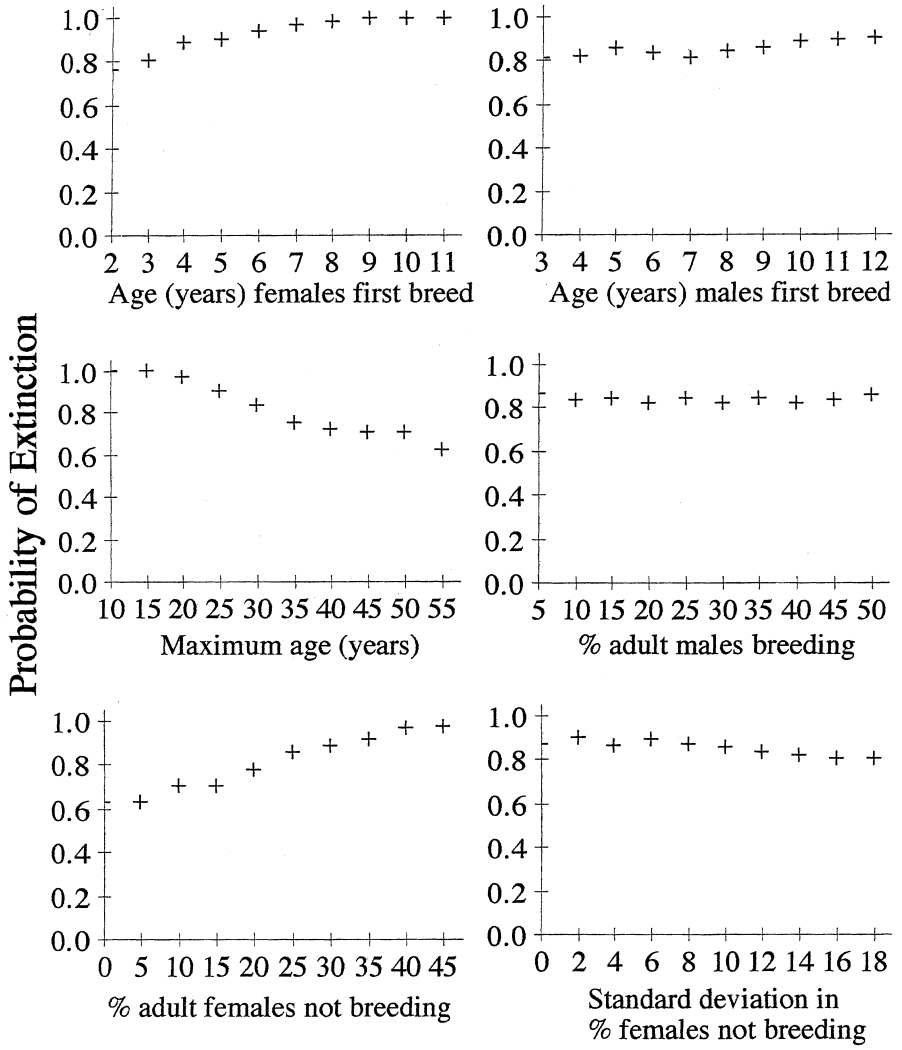

Figure 2. Results of sensitivity tests. Probabilities of extinction at year 100 based on 1000 iterations.

from 88 to 11% ($P < 0.001$). Increasing the maximum age above which all birds die also decreased the probability of extinction ($P < 0.05$).

Probabilities of extinction at year 100 were high for all four leks under the *status quo* model. In the larger leks of Bujalance and Osuna they were 84 and 85% respectively, whilst at the smaller leks of Paradas and Villanueva the prospects were even bleaker at 97 and 99% (Figure 3, squares).

The models in which the removal of just one male per year was simulated clearly indicated the disastrous consequences of poaching on the already small chances of population persistence. In the four leks the number of years elapsing before extinction

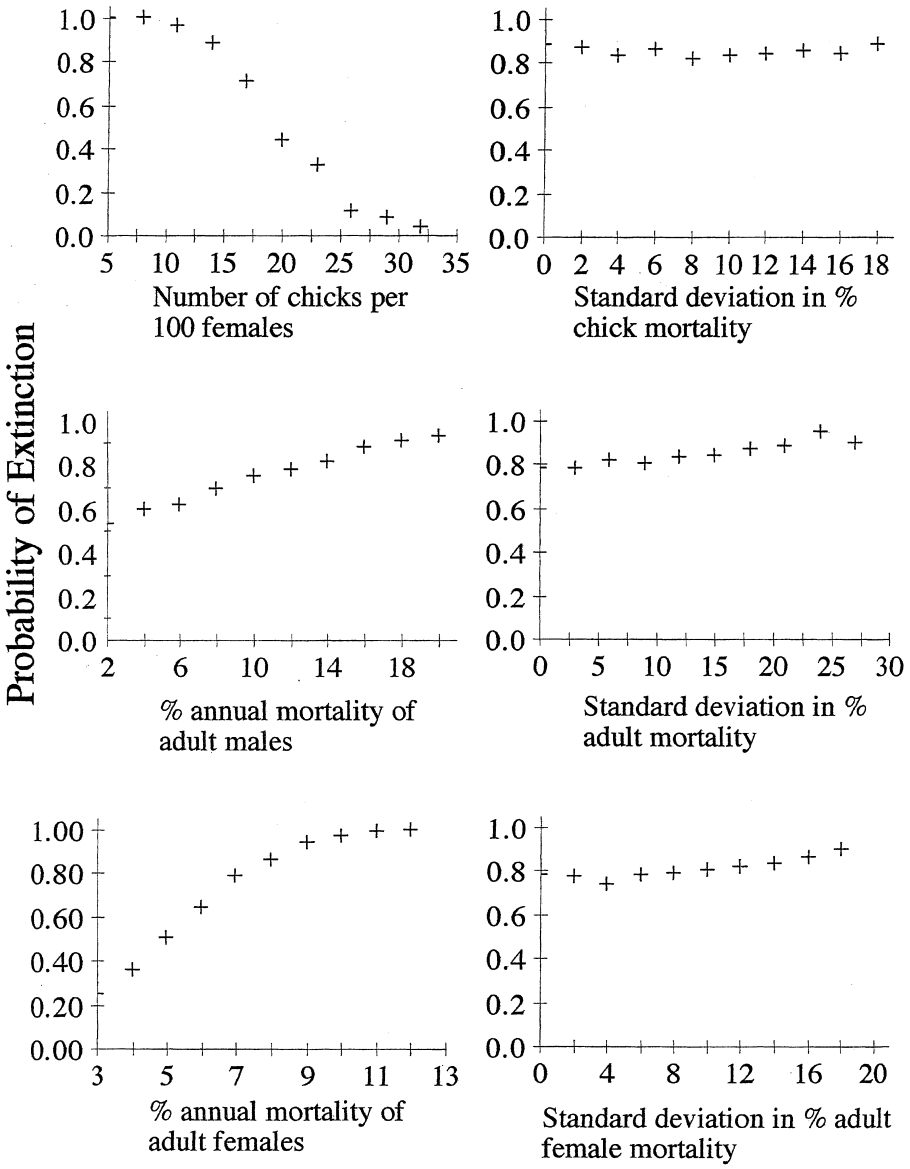

Figure 2. Continued.

probabilities approached unity were far fewer compared to the *status quo* (Figure 3, crosses). A 95% probability of extinction was reached at years 65 and 70 at the larger leks of Osuna and Bujalance, while at Villanueva and Paradas, which have fewer males, this probability was reached after just 8 and 17 years respectively.

Conversely the models which simulate the results of an active management program emphasise how much these leks would benefit from small increases in survival

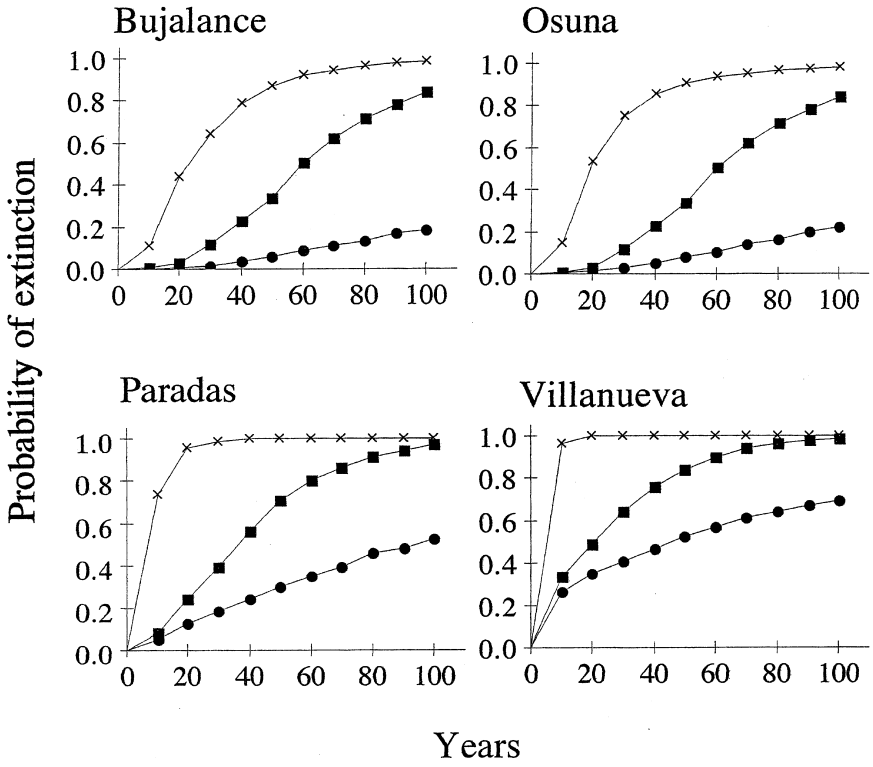

Figure 3. Likelihood of extinction over 100 years of four great bustard leks in Andalucía under (i) *status quo* conditions (squares), (ii) *status quo* plus a poaching pressure of one adult male removed per year (crosses), and (iii) a hypothetical management scheme that improved recruitment and reduced mortality of adult females (circles).

of adult females and enhanced breeding success, particularly at the larger leks (Figure 3, circles). Probabilities of extinction at year 100 were reduced to only 18.5 and 22% at Bujalance and Osuna. At Paradas and Villanueva probabilities of extinction were still relatively high at 52.5 and 70%, but are, nevertheless, below that attained in the *status quo* models.

Discussion

Location and status of great bustard populations in Andalucía

Assuming all males were recorded, and also all females at the leks of Osuna, Paradas and Villanueva (since the numbers seen fall within, or above, that expected from the normal limits of the sex ratio in small leks, see Alonso and Alonso 1990; Alonso et al. 2000b) then the total for the sites we visited in Andalucía is currently 46 males

and an estimated 134 females. This should be considered a conservative estimate for the Andalucía region since additional leks may exist. For example, this total does not include a possible lek in the north of Andalucía (Los Blázquez; Figure 1) where information gained in December 1999 suggested 15–20 males and up to 50 females might occur during spring (C. Palacín, unpublished data). This area is separated from the other Andalucían leks by the Sierra Morena mountain range and so, demographically speaking, may be more closely related to the nearby leks of Extremadura.

Most of the birds we recorded were in two localities (Bujalance and Osuna) and the status of the remaining leks must be considered critical. Unfortunately the precedent for extinction certainly exists with the last observations of male displays at Cazalilla (Jaén) and Carmona (Sevilla) probably occurring in 1985 and 1990 respectively. Viada (1998) gives 1995 as the year of extinction at Jaén. The lek at La Janda may also decline to extinction in the next year or so. At this site, interviews with local people gave an especially clear picture of how this lek has declined over recent decades. First an elderly shepherd told us that over 20 years ago there were 20–30 birds present, but they were regularly hunted and he had not seen any in recent years. Fifteen years ago there were still 12 birds known in the area (Alonso 1985), while seven years ago the total was nine according to a gamekeeper. Apparently one male still survives although we were unable to find it.

Specific threats at remaining leks include destruction of lek sites, illegal hunting, and unfavourable farming practices. At Villanueva (Huelva) for example, an ostrich farm has been constructed on or adjacent to the lek site. The lone male was observed flying through an area in which fence posts had recently been erected. Once the barbed wire is in place, collision with a fence seems likely. At Aznalcóllar (Sevilla) we observed aerial spraying of crops which is likely to have caused considerable disturbance and may be a reason why we did not find great bustards in the area despite spending two mornings searching and interviewing local people.

Also at Aznalcóllar, one man told us that there had been a great bustard hunt in the area in late February or March 1999 but declined to give further details. Our inability to locate any males at their lek site approximately four weeks after this event may indicate that the last males were shot at this time. Though one of our primary aims in this study was to locate leks precisely we have withheld these data because of the potential problem of poaching in some areas. UTM co-ordinates can be made available from JCA for bona fide purposes.

Extinction probabilities of great bustard leks in Andalucía

There are several important assumptions in the VORTEX models used to generate the probabilities of extinction and these should be borne in mind when interpreting the results. Four stand out as being especially noteworthy but for which no provision was made. First, we have assumed that all females of breeding age are equally likely to successfully raise a brood. Yet Morales (1999) has shown that great bustard females

aged over eight years were more successful mothers than younger birds, based on the number of chicks surviving to September. Second, we have assumed that all eggs laid in a clutch of three are equally likely to result in a successfully reared chick. However it is generally accepted that birds sometimes lay an additional egg over the number of chicks they can expect to raise as an insurance against mishap. Thirdly, mortality rates of birds older than two years of age are not known reliably. Consequently we conservatively set an equal mortality rate for all classes aged over one year and in doing so may have overestimated adult mortality. Finally, up to an arbitrary carrying capacity of 1000, no density dependent effects were incorporated since this phenomenon has yet to be demonstrated for any great bustard population. Despite these shortcomings, which are anyway consistent in all analyses, the models usefully demonstrate (i) the extremely endangered status of Andalucían great bustards under the *status quo* with no conservation intervention, (ii) the emphatically calamitous consequence of poaching adult males for trophies and (iii) the potential benefits of active management.

It is quite possible that the Andalucían great bustards are entering the final phase of the extinction process. Most birds (66% of those observed) are estimated to occur in just two localities which may have resulted, in part, from the process of conspecific attraction acting over the region. We recently advanced the idea that small peripheral leks might become extinct if dispersing juveniles preferentially settle in leks where more conspecifics are present and found that this phenomenon is an important factor explaining the redistribution of great bustards among nine leks of various size in central Spain (J.C. Alonso et al., unpublished manuscript). We think the same mechanism could have contributed to the current Andalucían population being predominantly distributed at Bujalance and Osuna.

Although past dispersal patterns may have resulted in birds clumping at the larger leks, further immigration to these sites is less probable. This is predominantly because the other leks, from which birds may be recruited, are now few in number and small in size. Moreover the Bujalance and Osuna leks are unlikely to exchange dispersing juveniles because they are located far apart from one another (*ca*. 100 km). Separation and low recruitment rates are probably the reason why incidents of dispersal have yet to be recorded in a small, separated population of great bustards elsewhere (J.C. Alonso, A. Onrubia, P. Osborne et al., unpublished data). Hence, rates of zero were set for both emigration and immigration in the simulation models.

Hunting of great bustards was banned in 1980, but since then the Iberian population is not known to have increased. Moreover at least two leks have become extinct in Andalucía in recent years and post 1980 cases of extinction are known from elsewhere in Spain (e.g. Navalcarnero). The analyses on the impact of illegal hunting presented here suggests that even a very low poaching pressure is sufficient to markedly increase the chances of a small lek going extinct. Moreover, the surreptitious and illegal activities of poachers have important demographic consequences such as massively biasing the sex ratio in favour of females through the illegal hunting of males for trophies.

We found two leks in Andalucía which are apparently reduced to just one male (La Janda and Villanueva) and have seen one more in Morocco in the same critical situation even though 22 females were present (Alonso et al. 2000b).

Our results suggest strongly that consideration needs to be given to active management and protection of the remaining great bustard leks to offer any possibility of their persistence in Andalucía. Specifically the VORTEX simulations suggest that the key life history parameters to address should be increasing productivity and decreasing adult female mortality. Whilst the biology of the species in Andalucía is not sufficiently known to state unequivocally what measures need to be taken to achieve these goals, some sensible actions could and should be taken immediately. Provision of favoured food supplies by planting legume crops might improve female condition over the winter leading to enhanced productivity the following year. The area allocated need not be large. In central Spain a three hectare field sown with vetch *Vicia sativa* supported 60–100 great bustards over much of the winter in 1998/1999 (personal observation). Alternatively a similarly small area of alfalfa *Medicargo sativa* might be considered since this was found to be the dominant food at a site in NW Spain (Lane et al. 1999). In addition to enforcing hunting bans, decreases in both male and female mortality might be achieved by marking or eliminating powerlines since collisions with overhead cables occur infrequently but predictably in some areas (Alonso et al. 1994). Other sources of mortality, such as predation by eagles or foxes, are, admittedly, more difficult to manage, though shooting abandoned dogs would be straightforward.

More generally an action plan for the great bustard in Europe already exists (Kollar 1996) which gives 'high' or 'essential' priority to a number of useful conservation actions. Two of them seem particularly relevant to the Andalucían leks. First, reintroducing non-intensive farming practices and appropriate land management would be beneficial both to great bustards and steppe birds generally since this would provide feeding habitat in the form of overwinter stubble fields. Financial incentives for farmers to manage land in this way already exists in the form of payments within the Agri-Environment Program (EU Regulation 2078/92). The second action must include strict enforcement of the hunting ban in conjunction with raising public awareness of the endangered status of the species. In addition we suggest that the larger great bustard leks (e.g. Bujalance, Osuna, Paradas, Villanueva, and possibly Los Blázquez) should be included within the Natura 2000 ecological network (EU Birds Directive 79/409 and Habitats Directive 92/43) to provide them with enforceable legal protection.

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