Journal of Applied Ecology 2001
38, 193–203

Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied?

SIMON J. LANE*, JUAN C. ALONSO and CARLOS A. MARTÍN
Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain

Summary

1. Great bustards *Otis tarda* are globally endangered and 50% of the world population now occurs in agro-steppe habitats in Spain. An understanding of the relationship between land use and the species' habitat requirements is necessary to predict the consequences of land-use change on this declining species.
2. A 2-year study of great bustard substrate preferences was conducted in a large region in central Spain where most cereals are still cultivated in a traditional 2-year rotation.
3. Great bustards showed year-round selection of stubble fields, but avoided ploughed and uncultivated areas. Other substrate types were variously selected, avoided or used in proportion to availability depending on season. Patterns were consistent over 2 years.
4. Human artefacts such as roads, tracks and powerlines were avoided.
5. Variables correlating with flock locations could not discriminate between occupied and unoccupied but apparently suitable areas of traditionally managed cereal steppe. This suggests that great bustard distribution in central Spain is not limited by inappropriate land use in steppe areas.
6. The evidence suggests that great bustards show fidelity to sites regardless of the availability of suitable habitat elsewhere. Settlement patterns are probably determined by the presence of conspecifics rather than habitat cues. This result demonstrates the value of integrating observations of habitat use with knowledge of species' behaviour in order to understand distribution more fully.
7. We propose that conservation efforts should be directed towards securing traditional lek sites and we make three recommendations: first all great bustard lek sites should be identified; secondly, existing European Union legislation should be used to protect these and to ensure that compatible land management practices are applied or maintained; and finally, research programmes should be conducted that aim to enhance the conservation value of stubble fields rather than simply demonstrate their selection.

Key-words: farmland birds, habitat selection, lek sites, stubble fields, traditional agriculture.

Journal of Applied Ecology (2001) **38**, 193–203

Introduction

Great bustards *Otis tarda* L. are large (adult males to 18 kg, females to 5·25 kg), predominantly herbivorous, birds occupying dry grasslands from the Iberian peninsula and north-western Morocco to eastern Asia (Cramp 1980; Johnsgard 1991; Lane *et al*. 1999). The world population is probably in the order of 33 200–42 800 individuals, of which 44–57% occur in Spain (Collar, Crosby & Stattersfield 1994; updated with Alonso & Alonso 1996; Litzbarski & Litzbarski 1996; Chan & Goroshko 1998). Detailed population trends are known for only a few areas, but general declines are thought to be widespread and consequently great bustards are categorized as a globally threatened (vulnerable) species (Collar, Crosby & Stattersfield 1994). In the former East Germany, numbers decreased from an estimated 4100 birds in 1940 to just 90 in 1995 (Nicolai 1993; Litzbarski & Litzbarski 1996). A similar reduction occurred in Hungary, where an 87% loss during the period 1941–93 left an overall population of

*Present address and correspondence: Discipline of Biological Sciences, Department of Biological and Chemical Sciences, University of Newcastle, University Drive, Callaghan, New South Wales 2308, Australia (e-mail bisjl@alinga.newcastle.edu.au).

1100 birds (Faragó 1993, 1996). In Poland, former Yugoslavia and Bulgaria the species may already be extinct (del Hoyo, Elliot & Sargatal 1996). Although widely distributed, their range is highly fragmented and the species now occurs in distinct units in which it is common to find only a few tens of birds. Populations exceeding a few hundred are now rare and probably occur only in Spain and Russia.

The causes of these declines and range fragmentation are not fully understood. However, advances in arable agricultural technology, which improve yields at the expense of maintaining traditional practices compatible with bird conservation, are considered by many to have played a major role (Martínez 1991; Faragó 1996; Kollar 1996; Litzbarski & Litzbarski 1996). Detailed studies on the habitat preferences of great bustards in agro-steppe areas are therefore needed to provide information necessary to predict the consequences of future changes in agricultural policy and land management (Suárez, Naveso & de Juana 1997). In Spain, some studies on great bustard habitat selection already exist but these have either been limited in scope or conducted in areas that are not typical of the species' range and so are of limited utility. For example, Redondo & Tortosa (1994) made repeated observations on an isolated population of 24 birds or less, Peris *et al.* (1992) studied a larger population but conducted censuses mainly in the winter, and Martínez (1991) worked in an area where alfalfa *Medicago sativa* L. was grown and strongly preferred by great bustards. The first two studies purport to demonstrate habitat preferences without estimating availability or providing statistical support, while Martínez's study cannot be regarded as representative because great bustards more commonly occur in areas where alfalfa is not cultivated.

To gain a better understanding of habitat use in cereal farmland, we studied habitat selection over a period of 2 years in a large region of central Spain. The area was chosen because it holds an internationally important number of great bustards (893 in March 1997; J.C. Alonso *et al.*, unpublished data) and represents an intermediate stage between the vast areas of traditionally farmed cereal psuedosteppe to the north and the more intensively cultivated areas to the south.

Our objectives were two-fold: first, to establish the influence of substrate and human-made features on flock locations within cereal-growing areas, and secondly to determine whether the species is prevented from expanding into apparently suitable areas by one or more unrecognized habitat constraints. The first aim was tackled by comparing substrate use with availability during distinct phases of the annual agricultural cycle. This work continued over 2 years to assess constancy of substrate-use patterns. To accomplish the second objective, we used those variables identified as important in determining flock location to try to discriminate sites preferred by the birds from nearby, unoccupied, arable areas.

Study region and species

This study was conducted at sites in southern and eastern Madrid Province, and at nearby areas in Castilla La Mancha. Land use at these sites is primarily cereal cultivation, with smaller areas given over to olive groves, vineyards and other minor crops. Most cereal is grown in a traditional 2-year rotation system (Suárez, Naveso & de Juana 1997). In the first year winter cereals are cultivated between October and July. The resulting stubble is usually left until the spring of the second year, when it is ploughed. Before the cycle begins again these areas may be ploughed on two or three further occasions. Variations on this cycle do exist in the region. In some instances fields may be fallowed for 2 or more years, while in others irrigation systems have been introduced permitting annual cropping. The timing of these processes varies and the 2-year cycle is not necessarily synchronized between or within farms. Consequently a dynamic mosaic of ploughed, cereal and stubble habitats is created over the region.

Great bustards are polygynous and in spring males gather at traditional display sites or leks that are later visited by females who solicit copulations. Data for 11 leks in Madrid Province showed that locations were remarkably stable over a period of 10 years (J.C. Alonso *et al.*, unpublished data). For the rest of the year, flocks containing both male and female adult birds are very rare, though first or occasionally second year males are often present with their mothers in predominantly female flocks.

Until recently great bustards in Iberia were considered sedentary in the vicinity of leks, but recent work on radio-marked birds in north-western Spain has demonstrated that partial migrations of adults occurs, and some prior understanding of these is helpful when considering census data. In the case of males, there was strong interannual fidelity to lek sites in spring, but 69% of individuals moved on to non-breeding areas up to 20 km away (Morales *et al.* 2000). Adult females also behaved as partial migrants, with some remaining near the leks while others moved on to chick-rearing and wintering areas at distances of 15 km (Alonso, Morales & Alonso 2000). Juvenile dispersal was male-biased, and dispersing males were found up to 65 km from their natal site, but females usually < 5 km (Alonso *et al.* 1998). Young females generally returned and established as adults at leks closest to natal nests but males always established at more distant leks.

An ongoing study of the movements of radio-marked juvenile and adult birds in the region of this study is revealing similar movement patterns, although distances travelled tend to be greater (J.C. Alonso *et al.*, unpublished data). Both adult and juvenile males may move between sites or, in many cases, temporarily away from the region. Adult and juvenile females tend to make shorter excursions within sites or between nearby sites.

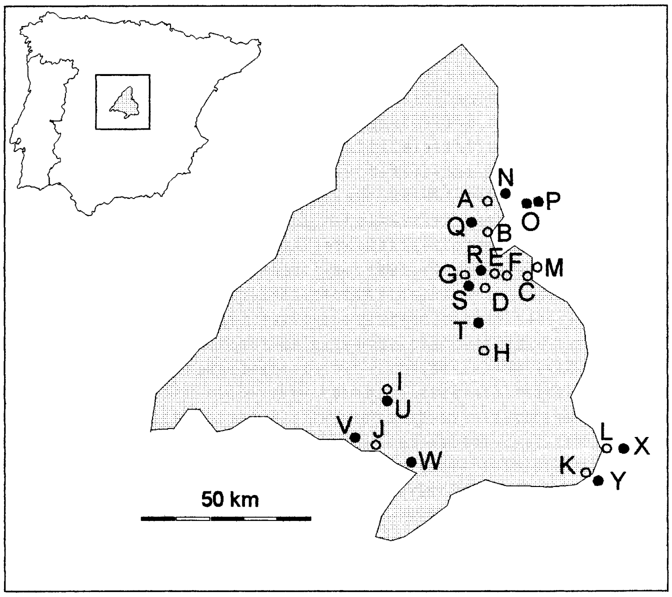

Fig. 1. Approximate locations of the centres of 25 distinct agro-steppe sites in Madrid Province (shaded area) and Castilla La Mancha, central Spain. Open circles mark preferred great bustard sites which include a lek (n = 13), whereas closed circles are potential sites of apparently suitable habitat (n = 12) but not known to be occupied by the species at the start of this study. 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 (East); K, Estremera-Fuentidueña de Tajo; L, Driebes; M, Quer; N, El Casar; O, Galápagos; P, El Palomar; Q, El Grullero; R, Daganzo-Valdeolmos; S, Paracuellos de Jarama; T, Loeches; U, Valdemoro-San Martín de la Vega; V, Torrejón de Velasco (West); W, Ciempozuelos; X, Illana; Y, Belinchón.

Methods

March censuses between 1988 and 1997 established the existence of 13 cereal steppe sites that included great bustard leks (Fig. 1, sites A to M; Alonso & Alonso 1990). Censuses at other times of the year confirmed that the species was always present in these areas. From June to August 1997 we searched the region for areas of apparently suitable cereal steppe that we believed could hold great bustards, but where the species was not known to occur. Our criteria for these areas were that they should be flat or gently undulating cereal-growing areas of at least 10 km^2 and that they should be similarly distributed within the region as the lek sites. Twelve areas were identified (Fig. 1, sites N to Y), although one of these (site Q) was slightly smaller, being 8 km^2. Subsequent analyses of satellite images from these areas, using time-series AVHRR-NDVI (normalized difference vegetation indices), confirmed independently that great bustards could be expected at these sites (P.E. Osborne, J.C. Alonso & R.G. Bryant, unpublished manuscript). The boundaries of all areas were delimited by various human-made or natural features such as urbanized areas and busy roads, or rivers and ridges of high uncultivated hills. The permanently occupied lek areas and apparently suitable areas are henceforth termed 'preferred' and 'potential' sites, respectively. The areas occupied by the 13 preferred sites ranged from 7 to 43 km^2 (mean ± SD, 26 ± 9·5 km^2) and in the potential sites the areas were from 8 to 26 km^2 (16 ± 5·2 km^2).

SUBSTRATE SELECTION

Usage

Seven censuses of all preferred and potential sites were conducted. Two were made in autumn (September 1997 and 1998), two in winter (December 1997 and 1998) and two in spring (March 1998 and 1999). These times coincided with three important periods of the agricultural cycle: post-harvest, post-sowing and ploughing of winter stubbles, respectively. A census was also attempted in May 1998 (pre-harvest period), but a large and unknown percentage of the population was missed, probably because the birds were occupying tall cereal crops, and the results are not presented.

Each census was conducted by two teams of two people operating from four-wheel drive vehicles with binoculars and telescopes (× 20–60). Predetermined transects, totalling 425 km in the 25 sites, were driven such that each site was scanned for great bustards in a similar manner and intensity. As far as possible the same transects were used throughout the study; however, some became impassable after rain causing route alterations to be made from time to time. Censuses began at dawn and ended at dusk, although in September and March we stopped during the midday period (10:00–15:00 GMT) because great bustards often sit down during hot weather and become difficult to see. On each occasion a total of 530 km^2 was censused, which took from 7 to 40 days to complete depending on weather and logistic constraints.

When a great bustard flock was located, each bird was sexed, males were aged (≤ 1 years, 1 ≤ 2 years, otherwise adult) and the flock then categorized as 'male' (all males or, extremely rarely, all males with a single female, which we considered a very temporary association), 'female' (all birds female or females with ≤ second-year males) or 'mixed' (females with at least one adult male). The substrate on which the flock occurred was assigned to one of 13 categories: ploughed; stubble; germinated cereal (usually winter-sown wheat *Triticum aestivum* L. or barley *Hordeum vulgare* L.); fallow; grassland (often fenced areas for cattle); uncultivated land (stony ground with broom *Retama sphaerocarpa* L. a major feature); grapevine *Vitis vinifera* L.; olives *Olea europaea* L.; sunflower *Helianthus annuus* L.; legume (usually *Vicia sativa* L. grown as a fodder crop with barley); dry river course; border; and track. Additional categories available, but not used, were maize *Zea mays* L., vegetables and copse. Occasionally, a larger flock occupied two types of substrate, in which case it was considered as two flocks.

Availability

During each census the proportion of surface area occupied by each substrate category was estimated. As transects were driven, substrate type was recorded for each field or habitat patch encountered immediately to the left and right of the vehicle. For each site, the proportion in each substrate was calculated by dividing the substrate total by the number of patches counted. As more than 5000 fields and patches were recorded over the 25 sites per census, we assumed that each occupied an equal surface area (Alonso & Alonso 1990; Tella, Torre & Sánchez 1996; Blanco, Tella & Torre 1998; Lane *et al*. 1999). When large distances need to be covered, this method has the advantage of being quick and convenient in the field and records rarer substrate types. It has the disadvantage that substrates that tend always to occur in smaller plots, such as vines or olives, will be overestimated, although as these occupied a small proportion of the surface area in the 25 sites the error was unlikely to be great. Nevertheless, we checked the reliability of the method in a 13-km^2 zone of area A. Here we visited all fields and habitat patches and assigned each to the appropriate category. The area of each field was taken from 1 : 10 000 maps so that proportions of surface occupied by each category could be determined precisely. These data were comparable with those obtained from the transects and a chi-squared test indicated no difference between the methods ($\chi^2 = 4{\cdot}37$; d.f. = 6; $P = 0{\cdot}626$).

Analyses

For each census, we compared substrate usage with abundance using with the chi-squared statistic. When this was significant ($P < 0{\cdot}05$) we constructed Bonferroni 95% confidence intervals around the used sample proportion for each habitat (Neu, Byers & Peek 1974; Byers, Steinhorst & Krausman 1984). If the proportion available of a habitat fell either above the upper or below the lower confidence intervals, then we determined that the habitat was either avoided or selected, respectively. For these analyses, availability data were excluded from sites in which no great bustard flocks were observed. In all tests it was necessary to combine some of the habitat categories because many low 'expected' values would have otherwise biased the resulting chi-square value. Grapevine, olives, sunflower, legume, maize and vegetable were combined to form 'minor crops', while uncultivated land, grassland, track, copse and dry river course formed 'uncultivated', and finally borders were combined with fallow.

Numbers of flocks rather than individuals were used in these analyses because birds in flocks cannot be regarded as independent of one another. However, biased results might occur if relationships exist between flock size and substrate. That is, if flocks in ploughed fields, for example, always tended to be smaller than those elsewhere. For each census we therefore conducted one-way ANOVAS to test the null hypothesis that mean flock size is the same in all habitats, and found $P > 0{\cdot}05$ in all cases.

INFLUENCE OF HUMAN-MADE FEATURES ON FLOCK LOCATION

The influence of human-made environmental features on the location of great bustard flocks within sites was assessed by comparing flock positions with representative points (Sutherland & Crockford 1993). The flocks were plotted on 1 : 50 000 maps and distances were measured to the nearest urbanized area, metalled road, farm track, building and overhead electric cable. The representative points were the 1-km grid square cross-overs that fell within site boundaries. Because the maps were not always up to date, ground truthing was necessary at all sites to ensure that distances to these features was accurate. Distances of < 50 m were measured to the nearest 10 m, otherwise measurements were to the nearest 50 m.

MANOVA was used to assess differences following $\log_{10}$ (mean + 1) transformation. Only cross-overs from sites in which great bustards were observed were included ($n = 419$ cross-overs). Preliminary analyses revealed no differences between male and female flocks ($F_{5,604} = 1{\cdot}289$; Wilks' $\lambda = 0{\cdot}989$; $P > 0{\cdot}05$) or between years and seasons (respectively $F_{5,629} = 1{\cdot}689$; Wilks' $\lambda = 0{\cdot}989$; $P > 0{\cdot}05$; and $F_{10,1258} = 1{\cdot}289$; Wilks' $\lambda = 0{\cdot}973$; $P > 0{\cdot}05$) in distances to these features, so data for all censuses were pooled ($n = 637$ flocks). The minimum interval between censuses was 3 months, which we assumed was sufficiently long for observations of flocks to be considered independent.

HABITAT DIFFERENCES BETWEEN PREFERRED AND POTENTIAL SITES

Standard discriminant analysis (Afifi & Clark 1996), followed by the jack-knife procedure to test robustness, was used to assess whether our set of variables discriminated between the preferred and potential sites in a biologically meaningful way. Six analyses were performed, one per census, in each of which 15 variables were entered. The first six, describing distances to the five human-made features and the mean gradient for each site, were the same in all models. However, the nine variables comprising the percentages of six substrate categories, the Shannon indices of diversity (*H*) and evenness (*J*; calculated from all 15 substrate types; Begon, Harper & Townsend 1986) and mean distance between successive field boundaries (a crude estimate of field size) were unique to each model. Transformed means ($\log_{10}$ mean + 1) from the cross-overs for each site determined distances to the human-made features and arcsine square root-transformed data were used for the six substrate categories. Mean gradient for a site was obtained from values at grid square cross-overs. These were estimated trigonometrically from the shortest possible line that joined successive 20-m contours and also passed through a cross-over.

Results

DISTRIBUTION, SIZE AND NUMBER OF FLOCKS ENCOUNTERED

Great bustard flocks were always observed in the 13 preferred sites with the exception of site F in December 1997 and site C in December 1998 (Fig. 1). These sites were close together and great bustard movements between them were known to occur. In four of the potential sites (U, W, X, Y) great bustards were never seen, in three more (N, O, S) flocks were seen during one census only, at sites P and T they were seen twice, and at V and R on five occasions, but always in small numbers. Site Q was exceptional in the potential category in that a small female flock was seen in all six censuses, but it did not hold a lek and these birds were not present in follow-up surveys in April 1997–99. Although great bustards were seen in potential areas, flock density km^{-2} was negligible and

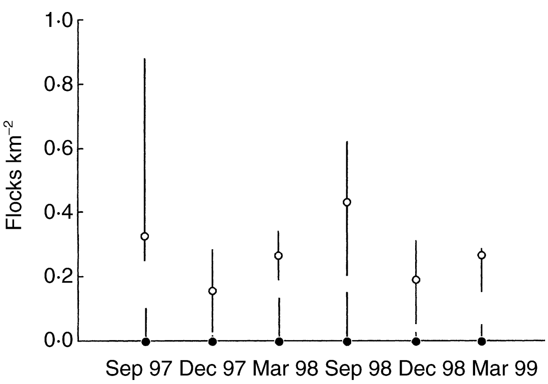

Fig. 2. Density of great bustard flocks in preferred (open circles) and potential (closed circles) sites. Medians are plotted with 25 and 75 percentile sites for six censuses. In each case $P < 0{\cdot}001$ (*U*-tests).

in all cases significantly lower than in preferred areas (Fig. 2). Birds in potential areas were probably making seasonal or dispersal movements.

Flock sizes differed between seasons but followed a similar pattern between years (Table 1). More, smaller, flocks were observed each September when females were brood-rearing, compared with other seasons when birds aggregated in larger flocks. Most males > 1 year old were absent from this region in September (unpublished locations of radio-marked birds) and comparatively few male flocks were seen in either year at this time. Some males had returned by December and all were present at their leks by March. This pattern was also consistent between years. Mixed flocks were unusual throughout the study and accounted for only 4% of those seen.

SUBSTRATE SELECTION

Consistent patterns in substrate selection were apparent both between seasons and years (Fig. 3). Stubble fields were always used significantly more often than expected, with the exception of December 1997 when statistical significance was not reached but the same trend was apparent. In contrast, ploughed and uncultivated areas were always used less often, if at all. In the case of ploughed substrates formal significance was not reached in December of either year, but the trends were still against selection. Germinated cereals were used in proportion to availability in December, but less often in March. Fallowed areas and minor crops occupied little surface area and were generally used in proportion to availability.

INFLUENCE OF HUMAN-MADE FEATURES ON FLOCK LOCATION

Examination of the histograms in Fig. 4 shows data for the representative points to be positively skewed in the cases of roads, tracks, buildings and electric cables, but that for the flocks to be less so, indicating a tendency to avoid these features. Overall, the distribution of the great bustard flocks differed significantly compared with the representative points with respect to the five human-made features considered (Wilks' $\lambda = 0{\cdot}935$, $F_{5,1050} = 14{\cdot}7$, $P < 0{\cdot}0001$). A posteriori Tukey-tests showed that transformed mean distances of flocks were significantly greater from all these features than means of the representative points ($P < 0{\cdot}007$ in all cases).

HABITAT DIFFERENCES BETWEEN PREFERRED AND POTENTIAL SITES

None of the five human-made features nor the gradient, nor any substrate category in December 1997, September 1998 or March 1999, differed statistically between the preferred and potential great bustard sites (Table 2). Of the remaining analyses only three

Table 1. Number and size of great bustard flocks during six surveys in central Spain

Census	Male	Female*	Mixed†	Total	Flock size (mean ± SD)
September 1997	7	184	1	192	3·7 ± 4·3
December 1997	14	54	1	69	11·0 ± 11·3
March 1998	26	66	8	100	11·4 ± 12·3
September 1998	16	132	3	151	5·1 ± 4·5
December 1998	21	39	5	65	15·9 ± 15·5
March 1999	29	43	8	80	15·8 ± 18·7
Totals	113	518	26	657‡	

*Defined as all females, or females with ≤ 2-year males.
†Females with at least one adult male.
‡An additional 50 flocks were seen in flight during the study, but were omitted from all analyses.

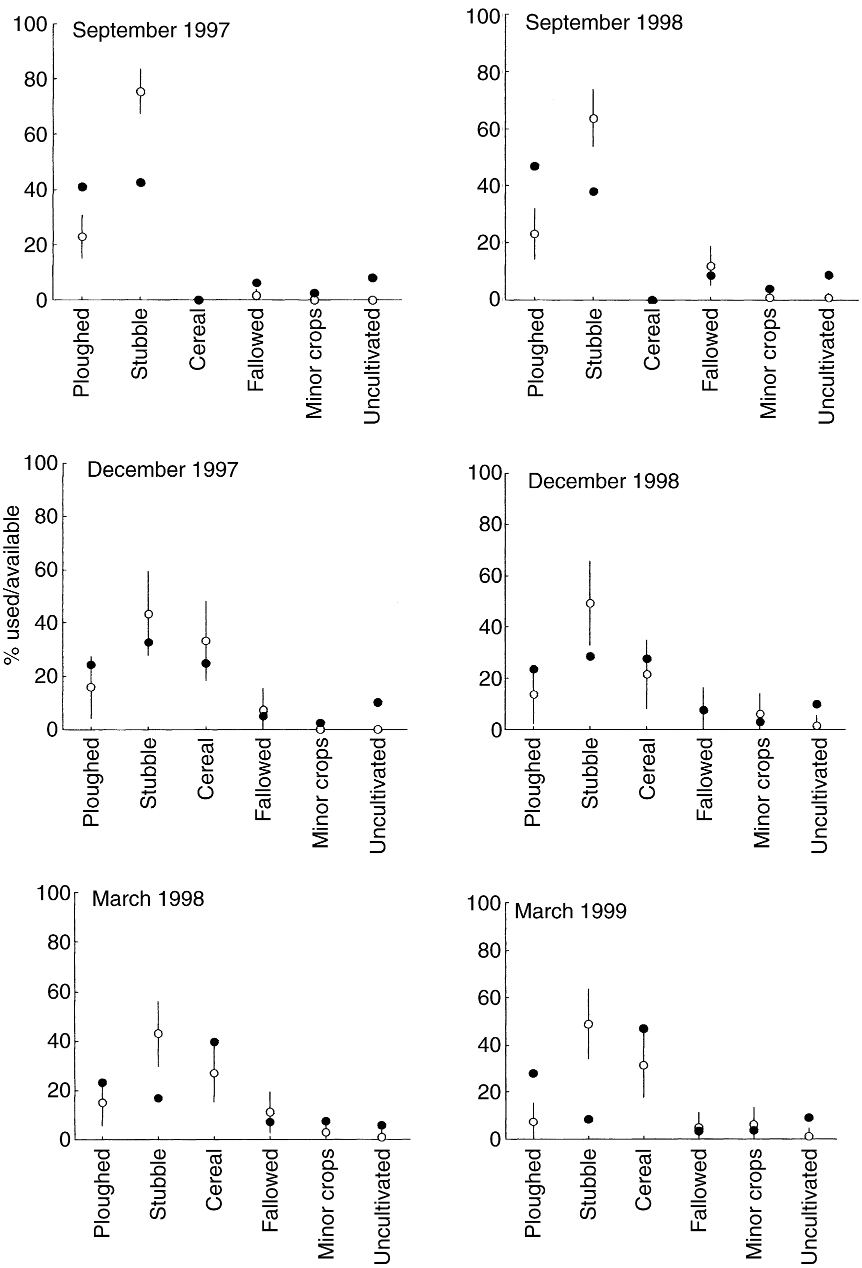

Fig. 3. Use (open circles ± 95% confidence limit) and availability (closed circles) of six substrates between September 1997 and March 1999. For each census the null hypothesis that flocks occurred in substrates in proportion to their availability was rejected ($P < 0{\cdot}05$). The uncultivated category comprises uncultivated lands, as well as grasslands, tracks, woodland and dried rivers, and minor crops includes grapes, olives, sunflower, legumes, maize and vegetables.

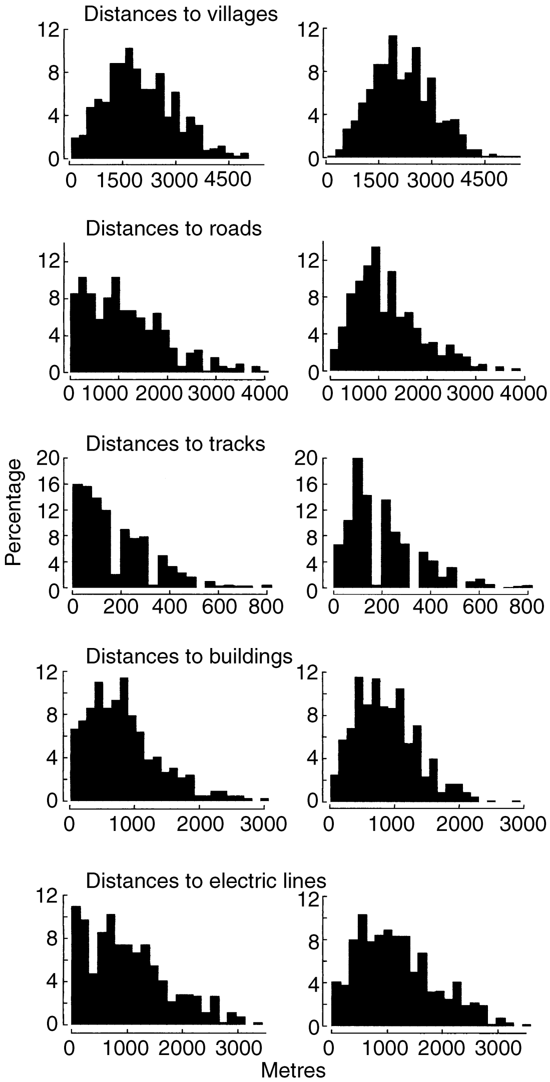

Fig. 4. Frequency distributions showing distances (m) of 419 representative points (left column) and 619 great bustard flocks (right column) to five human-made features. Note different scales.

Table 2. Means (± SD) of variables describing preferred and potential great bustard sites during six censuses, in central Spain. Differences were assessed by *t*-tests where* denotes $P < 0{\cdot}05$†

Variable‡	Preferred areas (n = 13)	Potential areas (n = 12)
To village (m)	1970 ± 590	1840 ± 540
To road (m)	1100 ± 410	1370 ± 750
To track (m)	180 ± 50	170 ± 50
To building (m)	840 ± 230	820 ± 370
To cable (m)	1050 ± 390	880 ± 400
Slope (degrees)	2·9 ± 1·2	3·0 ± 1·8
September 1997		
% plough	44 ± 12	36 ± 10
% stubble	39·3 ± 12·1	42 ± 15
% fallow*	5·7 ± 3·7	10 ± 5
% cereal	0·3 ± 1·1	0 ± 0
% minor crops	2·7 ± 3·8	5 ± 6
% uncultivated	8·3 ± 6·1	8 ± 9
Diversity index, H	0·503 ± 0·082	0·54 ± 0·10
Evenness index, J	0·685 ± 0·096	0·71 ± 0·10
Field width (m)	240 ± 140	210 ± 90
December 1997		
% plough	26 ± 15	25 ± 17
% stubble	33 ± 13	33 ± 15
% fallow	4 ± 3	5 ± 6
% cereal	23 ± 17	17 ± 13
% minor crops	3 ± 3	3 ± 4
% uncultivated	11 ± 9	17 ± 17
Diversity index, H	0·62 ± 0·06	0·62 ± 0·07
Evenness index, J	0·72 ± 0·08	0·75 ± 0·09
Field width (m)	230 ± 110	220 ± 90
March 1998		
% plough*	22 ± 4	28 ± 9
% stubble	17 ± 11	15 ± 13
% fallow	8 ± 4·9	8 ± 8
% cereal	41 ± 10	35 ± 12
% minor crops	5 ± 6	4 ± 6
% uncultivated	7 ± 4	10 ± 11
Diversity index, H	0·66 ± 0·08	0·64 ± 0·10
Evenness index, J	0·73 ± 0·09	0·73 ± 0·08
Field width (m)	210 ± 70	210 ± 90
September 1998		
% plough	41 ± 10	41 ± 9
% stubble	38 ± 10	33 ± 9
% fallow	9 ± 4	11 ± 10
% cereal	0 ± 0·0	0 ± 0·0
% minor crops	4 ± 4	4 ± 6
% uncultivated	8 ± 5	11 ± 7
Diversity index, H	0·54 ± 0·06	0·56 ± 0·08
Evenness index, J	0·69 ± 0·11	0·71 ± 0·07
Field width (m)	220 ± 100	210 ± 80
December 1998		
% plough	24 ± 18	26 ± 25
% stubble*	29 ± 10	21 ± 9
% fallow	7 ± 5	7 ± 6
% cereal	29 ± 15	33 ± 21
% minor crops	3 ± 4	2 ± 2
% uncultivated	8 ± 5	11 ± 7
Diversity index, H	0·62 ± 0·07	0·58 ± 0·09
Evenness index, J	0·72 ± 0·06	0·70 ± 0·10
Field width (m)	230 ± 120	180 ± 59
March 1999		
% plough	28 ± 11	23 ± 8
% stubble	9 ± 4	9 ± 4
% fallow	4 ± 3	4 ± 4
% cereal	46 ± 11	51 ± 11
% minor crops	4 ± 5	3 ± 6
% uncultivated	9 ± 6	11 ± 10
Diversity index, H	0·60 ± 0·07	0·57 ± 0·11
Evenness index, J	0·64 ± 0·15	0·65 ± 0·17
Field width (m)	220 ± 90	230 ± 140

†After Bonferroni adjustment these *t*-tests were no longer significant ($P > 0{\cdot}008$).
‡For analyses percentages were arcsine square root-transformed and distances to human-made features log (mean + 1)-transformed.

were significant, which demonstrated differences in percentages of fallow, ploughed land and stubble between preferred and potential areas in September 1997, March 1998 and December 1998, respectively. However, when a Bonferroni adjustment was made to account for the number of *t*-tests within each census these few differences no longer reached statistical significance ($P > 0{\cdot}008$).

None of the six discriminant analyses were able to classify the preferred and potential sites convincingly. Wilks' lambda *P*-values ranged from 0·15 to 0·95, indicating no differences between the mean vectors of preferred and potential sites. Correct classifications by the jack-knife procedure were low, ranging from 36% to 56%.

Discussion

We examined habitat selection patterns of great bustards in central Spain over 2 years. Substrate selection patterns were similar in each year. Great bustards always selected stubble fields, and always avoided ploughed and uncultivated land. Cereal was used less often than expected in March, but in proportion to availability in December. Minor habitats and fallowed land were used occasionally, usually in proportion to availability. Human-made features, such as overhead cables and roads, were avoided. None of these variables could be used to explain why great bustards were generally absent from some apparently suitable steppe areas.

SUBSTRATE SELECTION

Despite their large size, great bustards can be remarkably difficult to locate during hot midday periods, when they tend to sit down. Consequently surveys were restricted to morning and evening periods, when the birds were walking, feeding and generally easier to see. Thus substrate selection here reflects feeding sites and may not be representative of midday resting sites. Although we suspect that habitat differences in substrate selection of feeding and resting areas are not great, at least the importance of olive groves may have been underestimated as they may be used occasionally by birds seeking midday shade. At site L a flock of male great bustards was seen on several occasions walking out of an olive grove in the late afternoon to feed on areas of stubble.

Stubbles were consistently selected during the study, regardless of season. They are likely to be an important source of the arable weeds that occur in the diet throughout the year, and may also be rich in invertebrates and spilled grains that are eaten during the summer and autumn (Lane *et al*. 1999). Other studies have also suggested that stubble fields are important feeding grounds for this species (Ena, Lucio & Purroy 1985; Hidalgo & Carranza 1990). Apart from great bustards, stubbles are known to be preferred by other steppe birds, suggesting their maintenance will be of key importance to the conservation of steppe birds generally (Suárez, Naveso & de Juana 1997). Elsewhere, the massive declines of farmland birds in Britain during the last three decades have probably resulted in part from the large reductions in the amount of overwinter stubble (Fuller *et al*. 1995; Bradbury *et al*. 2000; Chamberlain *et al*. 2000). Unfortunately, in our region irrigation technology was introduced over parts of sites C and F during 1998 and annual cereal cropping and hence loss of winter stubbles will now occur in these areas.

Although our method was suitable for determining selection or avoidance of the more common substrates, the importance of two minor habitats may have been underestimated as feeding habitats. In the second year of the study a small number of fields (in sites C, E, F, H) were sown with legume crops (*Vicia sativa* L.) and great bustards were observed in these crops at three sites (C, F, H). However, sufficient flocks were not present in the censuses to permit legume to be considered as a single category in the chi-square analyses (expected values too low) and so legume was lumped into minor crops, which as a group was never selected. Elsewhere several authors have commented on strong selection of areas sown with another legume crop, alfalfa, which when available can dominate the diet (Alonso & Alonso 1990; Peris *et al*. 1992; Lane *et al*. 1999).

Olives, also included in the category of minor crops, may also be underestimated as a feeding site as birds could be missed more easily in groves than in open areas. In March 1998 the gizzard of a dead male (probably predated by a dog or fox) found at site L was full of olive stones. Redondo & Tortosa (1994) considered olive groves an important feeding habitat for a marginal population in southern Spain, noting that droppings were often packed with olive stones.

Uncultivated areas were strongly avoided by great bustards, suggesting that abandoning steppe areas or initiating pine *Pinus* spp. plantations would be detrimental. Unfortunately Suárez, Naveso & de Juana (1997) consider such changes likely in the more marginal steppe areas in the next decade. Indeed, during this study we noticed these changes occurring in our region, albeit on a small scale for the moment. A small pine plantation is present at site K, as are areas of abandoned land at sites J and U.

Our methodology was inappropriate for the period prior to harvest. Although we did conduct a census in May 1998 we counted only 239 females compared with 850 in March. At this time nesting females may be especially elusive, impossible to observe, and so hopelessly bias selection analyses. It is probable, although not confirmed, that ripening cereal is the most important nesting habitat for the species and it should be considered an important habitat even though it was sometimes less preferred at other times of the year. It will be necessary to radio-tag adult females to assess nest site selection quantitatively and to determine the potential impacts of timing of harvest and irrigation practices on nesting success.

INFLUENCE OF HUMAN-MADE FEATURES ON FLOCK LOCATION

Villages, roads, tracks and buildings were generally avoided, presumably because of disturbance associated with such features. Locations of flocks on the ground also tended to be further from powerlines than representative points. However, for birds in flight overhead cables are a notable threat and collisions resulting in death occur predictably although infrequently in our region. In September 1997 two adult males and one female were found dead beneath a newly erected powerline at site G. Similar observations have been reported elsewhere in Europe and Morocco (Alonso, Alonso & Muñoz-Pulido 1994; Hellmich 1999). Alonso, Alonso & Muñoz-Pulido (1994) found that attaching red PVC spirals at 10-m intervals along the groundwires reduced all bird collision incidents by 60% at a site in south-western Spain.

DIFFERENCES BETWEEN PREFERRED AND POTENTIAL SITES

We were unable to detect habitat features that could persuasively explain the transient, low density, occurrence of great bustards or their complete absence at the potential sites. To all intents and purposes land management was similar, as was the extent of human-made features, and during surveys in potential sites we frequently encountered other steppe birds, including little bustard *Tetrax tetrax* L., stone curlew *Burhinus oedicnemus* L., black-bellied sandgrouse *Pterocles orientalis* L. and calandra lark *Melanocorypha calandra* L. Moreover, in a parallel study in which 90·1% of occupied 1·1-km pixels were correctly classified using remotely sensed images (normalized difference vegetation indices extracted from AVHRR data) as a predictor, most of the potential sites (N, O, P, Q, R, T, U, W, X, Y) also contained pixels in which great bustard occurrence probabilities approached one (P.E. Osborne, R.G. Bryant & J.C. Alonso, unpublished data).

Of course it can be argued that some other, unmeasured, variables might explain distribution patterns between occupied and potential sites. Examples include disturbance related to (legal) hunting activity or differences in application rates of agricultural chemicals, but we think these are unlikely. Given that land management is so similar, chemical use probably is also, and some form of hunting, mainly for red-legged partridges *Alectoris rufa* L. and hares *Lepus granatensis* L., occurs at all 25 sites.

Our assertion is that habitat availability is not limiting distribution, in which case an alternative explanation is required. Recent reviews have highlighted the role of conspecific attraction in determining distribution. Here the crux of the arguments is that dispersing individuals are attracted to already occupied areas, and habitat suitability is judged on the presence of conspecifics (Smith & Peacock 1989; Reed & Dobson 1993; Danchin & Wagner 1997). Recently we tested some of the predictions of the conspecific attraction hypotheses with great bustard census data collected over a decade in Madrid (J.C. Alonso *et al.*, unpublished data). As predicted, sites with large populations of great bustards in 1988 increased over the following 10 years, while smaller ones decreased, even accounting for the confounding effects of differential productivity between large and small sites. Also, the locations of the 11 leks monitored (in sites A–K) were stable and no new leks were established, giving rise to 'traditional' occupation of sites regardless of the suitability of nearby areas. Due to their lek breeding system and strong breeding site philopatry, great bustards seem to have a poor capability to colonize new areas, and dispersing individuals probably use the presence of conspecifics as cues when choosing where to settle, rather than habitat cues. These results indicate that settlement patterns in the great bustard are critically influenced by the prevailing distribution of the species.

MANAGEMENT IMPLICATIONS

Our contention that availability of steppe habitats is not a limiting factor for great bustards in the Madrid region has profound implications for the conservation of this globally endangered species, especially when two additional observations are considered. First, the phenomenon of conspecific attraction leads to consistent occupancy of traditional sites and severely restricts the species' capacity to establish at new lek sites or recolonize those that have gone extinct. Secondly, despite honourable intentions, expensive captive breeding and particularly reintroduction programmes have unfortunately failed (Martín *et al.* 1996). Thus, once great bustards are lost from an area they are unlikely to return. Maintaining suitable habitat in the areas where the birds occur will prove critical to the survival of this species, and with this in mind we make three recommendations.

First, a conservation priority should be to maintain the number of existing leks. For poorly known great bustard areas, censuses are needed to determine location and status of leks, as many are currently unknown beyond local communities. With collaboration from colleagues we have recently made some progress with this regard in Andalucía and Navarra in Spain, and in northern Morocco (Alonso *et al.* 2000; J.C. Alonso *et al.*, unpublished data).

Secondly, once site locations are established they should be monitored regularly and strict conservation measures applied. These must include maintenance or reintroduction of the 2-year rotation system and protection of sites from unsuitable infrastructure developments. Farmers can take advantage of financial incentives to maintain traditional practices under the Agri-Environment Programme (EU Regulation 2078/92), while designating great bustard sites as part of the Natura 2000 ecological network would accord them considerable protection from development as the Birds Directive (79/409) and Habitats Directive (92/43) are binding and enforceable (Pain & Dixon 1997; Beaufoy 1998). Unfortunately, relatively few farmers have taken advantage of the Agri-Environment Programme and most steppe areas are currently unprotected (Suárez, Naveso & de Juana 1997; Beaufoy 1998). Moreover, in Madrid four great bustard leks are under immediate threat from proposed or ongoing developments that include constructions of new powerlines, urbanized areas, an international airport and an amusement park. We also note that EU Afforestation payments (Regulation 2080/92) should not be granted for steppe areas where great bustards occur.

Finally, as the general worth of overwinter stubbles for great bustards (as well as other steppes birds) seems beyond refute, future research efforts should now be directed at determining the best ways to manage stubbles to increase their value as feeding habitat, rather than simply aiming to demonstrate selection. Experimental manipulation of fields and monitoring of subsequent use would be an ideal approach. Options could include those aimed at promoting the growth of arable weeds present in the diet, or undersowing cereals with a legume. Establishing a legume in the stubble field would benefit both great bustards and farmers, the former by enhancing winter food supply, and the latter by boosting soil nitrogen levels for subsequent crops. Ideally fields improved for great bustards should be away from sources of disturbance or danger, such as roads and powerlines.

Acknowledgements

We thank: Alberto Duque, Eva Fernandez, Antonio Gil, Elena Izquierdo, Manuel Morales, Marina Magaña, Enrique Martín, Carlos Palacín, Rafael Vaquerizo, and Pat Vázquez for their contributions to our field work; Luis Miguel Bautista and Luis M. Carrascal for discussing with us the merits of the many possible statistical techniques; Gerry Lane (Royal Agricultural College, UK) for suggesting undersowing cereals with a legume for great bustard management; and Gillian Kerby, Steve Ormerod, José Tella and an anonymous referee for their helpful comments. This project was funded by a Marie Curie Research Training Grant awarded to S.J. Lane under the Training and Mobility of Researchers Programme by the European Commission DG XII for Science, Research and Development. Additional funds from DGESIC (PB97–1252) were awarded to J.C. Alonso. C.A. Martin holds a predoctoral fellowship from the Community of Madrid.

References

Afifi, A.A. & Clark, V. (1996) *Computer-Aided Multivariate Analysis*, 3rd edn. Chapman & Hall, London, UK.

Alonso, J.C. & Alonso, J.A. (1990) *La población de Avutardas de la provincia de Madrid. Parámetros demográficos, selección de hábitat y distribución de la avutarda* Otis tarda *en tres regiones españoles*. ICONA, Madrid, Spain.

Alonso, J.C. & Alonso, J.A. (1996) The great bustard *Otis tarda* in Spain: present status, recent trends and an evaluation of earlier censuses. *Biological Conservation*, **77**, 79–86.

Alonso, J.C., Alonso, J.A. & Muñoz-Pulido, R. (1994) Mitigation of bird collisions with transmission lines through groundwire marking. *Biological Conservation*, **67**, 129–134.

Alonso, J.C., Lane, S.J., Dawson, R. & Idaghdour, Y. (2000) Great bustards in Morocco: status in spring 1999 and evidence of a decline in recent decades. *Oryx*, **34**, 141–146.

Alonso, J.C., Martín, E., Alonso, J.A. & Morales, M.B. (1998) Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. *Behavioral Ecology*, **9**, 243–252.

Alonso, J.C., Morales, M.B. & Alonso, J.A. (2000) Partial migration, and lek and nesting area fidelity in female great bustards. *Condor*, **102**, 127–136.

Beaufoy, G. (1998) The EU Habitats Directive in Spain: can it contribute effectively to the conservation of extensive agro-ecosystems? *Journal of Applied Ecology*, **35**, 974–978.

Begon, M., Harper, J.L. & Townsend, C.R. (1986) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford, UK.

Blanco, G., Tella, J.L. & Torre, I. (1998) Traditional farming and key foraging habitats for chough *Pyrrhocorax pyrrhocorax* conservation in a Spanish pseudosteppe landscape. *Journal of Applied Ecology*, **35**, 232–239.

Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J. & Wilson, J.D. (2000) Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology*, **37**, 789–805.

Byers, C.R., Steinhorst, R.K. & Krausman, P.R. (1984) Clarification of a technique for analysis of utilization–availability data. *Journal of Wildlife Management*, **48**, 1050–1053.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771–788.

Chan, S. & Goroshko, A. (1998) *Action Plan for Conservation of the Great Bustard*. Asia Council, Birdlife International, Tokyo, Japan.

Collar, N.J., Crosby, M.J. & Stattersfield, A.J. (1994) *Birds to Watch. 2. The World List of Threatened Birds*. Birdlife International, Cambridge, UK.

Cramp, S. (1980) *Handbook of the Birds of Europe the Middle East and North Africa. 2. Hawks to Bustards*. Oxford University Press, Oxford, UK.

Danchin, E. & Wagner, R.H. (1997) The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution*, **12**, 342–346.

Ena, V., Lucio, A. & Purroy, F.J. (1985) The great bustard in León, Spain. *Bustard Studies*, **2**, 35–52.

Faragó, S. (1993) Development of great bustard populations in Hungary in the period 1987–90. *Folia Zoologica*, **42**, 221–236.

Faragó, S. (1996) Lage des Großtrappenbestandes in Ungarn und Ursachen für den bestandsrückgang. *Naturschutz und Landschaftspflege in Brandenburg*, **1/2**, 12–17.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.H., Baillie, S.R. & Carter, N. (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, **9**, 1425–1441.

Hellmich, J. (1999) *The Great Bustard in Morocco*. International Foundation for Conservation and Development of Wildlife, Inezgane, Morocco.

Hidalgo, S.J. & Carranza, J. (1990) *Ecología y comportamiento de la avutarda (*Otis tarda *L.)*. Universidad de Extremadura, Cáceres, Spain.

del Hoyo, J., Elliot, A. & Sargatal, J. (1996) *Handbook of the Birds of the World. 3. Hoatzin to Auks*. Lynx Edicions, Barcelona, Spain.

Johnsgard, J.A. (1991) *Bustards, Hemipodes and Sandgrouse*. Oxford University Press, Oxford, UK.

Kollar, H.P. (1996) Action plan for the great bustard (*Otis tarda*) in Europe. *Globally Threatened birds in Europe Action Plans* (eds D. Heredia, L. Rose & M. Painter), pp. 245–260. Council of Europe Publishing, Strasbourg, France.

Lane, S.J., Alonso, J.C., Alonso, J.A. & Naveso, M.A. (1999)

Seasonal changes in diet and diet selection of great bustards *Otis t. tarda* in north-west Spain. *Journal of Zoology*, **247**, 201–214.

Litzbarski, B. & Litzbarski, H. (1996) Zur Situation de Grosstrappe *Otis tarda* in Deutschland. *Vogelwelt*, **117**, 213–224.

Martín, E., Alonso, J.A., Alonso, J.C. & Morales, M. (1996) Evaluation of captive breeding as a method to conserve threatened great bustard (*Otis tarda*) populations. *Conservación de las aves estaparias y su hábitat* (eds J. Fernández & J. Sanz-Zuasti), pp. 131–136. Junta de Castilla y León, Valladolid, Spain.

Martínez, C. (1991) Patterns of distribution and habitat selection of a great bustard (*Otis tarda*) population in north-western Spain. *Ardeola*, **38**, 137–147.

Morales, M.B., Alonso, J.C., Alonso, J.A. & Martín, E. (2000) Migration patterns in male great bustards *Otis tarda* in Spain. *Auk*, **117**, 493–498.

Neu, C.W., Byers, C.R. & Peek, J.M. (1974) A technique for analysis of utilization–availability data. *Journal of Wildlife Management*, **38**, 541–545.

Nicolai, B. (1993) *Atlas der Brutvögel Ostdeutschlands*. Gustav Fischer, Stuttgart, Germany.

Pain, D.J. & Dixon, J. (1997) Why farming and birds in Europe? *Farming and Birds in Europe* (eds D. Pain & M.W. Pienkowski), pp. 1–24. Academic Press, London, UK.

Peris, S.J., Corrales, L., Gonzalez, N. & Velasco, J.C. (1992) Surveys of wintering great bustards *Otis tarda* in west-central Spain. *Biological Conservation*, **60**, 109–114.

Redondo, A. & Tortosa, F.S. (1994) Status and habitat use of a population of great bustards in southern Spain. *Avocetta*, **18**, 81–84.

Reed, J.M. & Dobson, A.P. (1993) Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution*, **8**, 253–256.

Smith, A.T. & Peacock, M.M. (1989) Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology*, **4**, 320–323.

Suárez, F., Naveso, M.A. & de Juana, E. (1997) Farming in the drylands of Spain: birds of the pseudosteppes. *Farming and Birds in Europe* (eds D. Pain & M.W. Pienkowski), pp. 297–330. Academic Press, London, UK.

Sutherland, W.J. & Crockford, N.J. (1993) Factors affecting the feeding distribution of red-breasted geese *Branta ruficollis* wintering in Romania. *Biological Conservation*, **63**, 61–65.

Tella, J.L., Torre, I. & Sánchez, C. (1996) Habitat availability and roost-site selection by the stone curlew *Burhinus oedicnemus* in an arid cultivated landscape (Los Monegros, NE Spain). *Revue d'Ecologie (Terre et Vie)*, **51**, 153–159.

Received 26 June 1999; revision received 7 August 2000