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Habitat selection and density-dependent relationships in spatial occupancy by male Little Bustards *Tetrax tetrax*

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This study analyses habitat selection by male Little Bustards *Tetrax tetrax* of a central Spanish population within their display sites during two consecutive breeding seasons. The areas of sexual display sites were determined by applying minimum convex polygons (MCP) to locations of individual males throughout the 2001 and 2002 breeding seasons. Habitat selection was addressed by means of a compositional analysis. The effects of variables related to phenology and to the density of conspecifics were examined, assuming an ideal free distribution of organisms. The spatial distribution of display areas was also analysed. During both years male Little Bustards showed a significant preference for old and same-year fallows, these offering both shelter and food. Contrary to what was expected, individuals did not select lower quality habitats when conspecific density increased or when areas were occupied earlier, suggesting that the population was not saturated. Display sites were not clumped, showing that in this population the Little Bustard may not employ a lek mating system, even though certain requirements of an exploded lek system – the inclusion in territories of particular habitat types that females could potentially use – were met. Our results emphasise the importance of agrarian substrates in determining occupation by this species, a finding with direct implications for the conservation of populations given that the agrarian landscape is on a sufficiently large scale for management measures to be introduced.

Key words: compositional analysis, exploded lek, ideal free distribution, point pattern analysis, sexual exhibition areas, Spain

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Population size, geographical distribution range and local density of a species are influenced in parallel by both physical variables and biotic factors (Brown 1984), which operate on various spatial and temporal scales, some more important than others according to scale (Pulliam 2000, Chase & Leibold 2003, Guisan & Thuiller 2005, Soberón 2007). Thus, abiotic, and essentially climatic factors are the most important on a large scale (Pearson & Dawson 2003, Thuiller *et al.* 2004). Other factors such as resource availability (Morris & Davidson 2000, Luoto *et al.* 2007) or biotic interactions (Fretwell & Lucas 1970, Morris 1999) come into play at small or intermediate scales, defining the realised niche of the species concerned. Such a realised niche is modulated in terms of a species' habitat preferences, with both ecological and evolutionary factors involved as possible selection factors (Rosenzweig 1981, Morris 2003). Evolutionary limitations will include those related to phylogeny and to certain life history strategies (e.g. reproductive, trophic etc.), whereas ecological limitations include those arising from the context into which the species fits, such as those associated with social organisation and the utilisation of resources, whether trophic or spatial (Fretwell & Lucas 1970, Morris 1999, Luoto *et al.* 2007). Under natural conditions individuals tend to maximise their biological efficiency via habitat selection which should be reflected, given equal competitive ability, in a non-random distribution of individuals within the landscape that they occupy (an Ideal Free Distribution, IFD; Fretwell & Lucas 1970, Rosenzweig 1981). In accordance with an IFD, favoured sites will be those that offer shelter and food, although other considerations, such as the need for suitable sites for sexual display, should be taken into account during the selection process (Morales & Traba 2009).

The Little Bustard *Tetrax tetrax* is a medium-sized steppe species, a member of the *Otididae* family. It has a Palearctic distribution, ranging from the Iberian Peninsula and Morocco to western China (del Hoyo *et al.* 1996). Its chief breeding populations are in Iberia, which holds half the global population (García de la Morena *et al.* 2006). Despite its original habitat being natural herbaceous steppes (Cramp & Simmons 1980), in Western Europe the species preferentially occupies cereal croplands and pastures (García de la Morena *et al.* 2006). Habitat selection and land use by Little Bustards have been studied on different spatial scales. These have revealed the importance of arthropod availability (Jiguet *et al.* 2002, Traba *et al.* 2008) and local vegetal structure during the breeding season, with some differences between the two sexes regarding the latter (Morales *et al.* 2008). Large-scale studies are chiefly descriptions of habitat use, obtained by spot observations (Wolff *et al.* 2001, 2002, Morales *et al.* 2005, Suárez-Seoane *et al.* 2008). Such studies indicate the species' preference for heterogeneous landscapes with high substrate diversity and the presence of fallow areas. Such areas are undergoing considerable change due in part to agricultural intensification, which is regarded as one of the chief causes of the decline of the Little Bustard population and the reduction in its area of distribution (Wolff *et al.* 2001, 2002, Morales *et al.* 2005, 2006, García *et al.* 2007).

Little Bustard habitat selection studies to date largely rely on spot observations (but see Jiguet *et al.* 2000). The present study raises this aspect from a different approach, identifying the composition of substrate types that male Little Bustards include within their sexual display areas, and investigating whether they represent a differential selection from those available in the study area (Johnson 1980, Aebischer *et al.* 1993, Beasly *et al.* 2007). For these purposes we studied the display sites used by individual males during two consecutive breeding seasons, which also served to show whether the selection pattern was consistent between years. In addition, and based on the males' preferences for particular substrate types, the following predictions were tested. According to the IFD theory (Fretwell & Lucas 1970) favourable habitats should be the first to be occupied when a population is establishing, with suboptimal habitats becoming occupied as population density increases. Thus male Little Bustards should tend to establish territories in poorer-quality habitats, in terms of the availability of favoured habitat types, as the density of conspecifics increases or when they establish territories late in the season. In this event, male display sites should be spatially associated with preferred habitats. Alternatively, if their mating system is taken to be an exploded lek (Höglund & Alatalo 1995, Jiguet *et al.* 2000, 2002, Morales *et al.* 2001), male territories would be expected to be relatively clumped, independently of the distribution of preferred habitat types.

Establishing the pattern of habitat selection within display sites in Little Bustard should provide more information on the species' preferences by taking account of all or most of the substrate types that individuals use. The relative ease with which habitat management measures could be applied on the scale of the agricultural landscape makes such information especially relevant to managing and conserving the species.

METHODS

Study area

The study was carried out at Valdetorres del Jarama (40°40'N, 3°25'W, 700 m a.s.l., 1,500 ha), a cereal-growing area in central Spain in the Jarama and Henares Steppes' Special Protection Area for birds, one of the most important areas for steppe birds in the Iberian Peninsula (Traba *et al.* 2007). This area is a plain with 80% cover of cereal crops, ploughed areas and same-year fallows (called fallows throughout this manuscript). The remainder is covered by fallow areas older than two years and set-aside land (called old fallows throughout this manuscript) and, to a much smaller extent, by vineyards and scrub. The mean field size (± SD) was 1.68 ± 3.5 ha. Little bustards are present in Valdetorres del Jarama only during the breeding season, migrating to spend the winter in the southern half of Iberia, mainly in irrigated areas (García de la Morena *et al.* 2006).

Male Little Bustards surveys

The fieldwork was carried out between 30 March and 30 June in 2001 and 2002, corresponding with the period of maximum reproductive activity of the species in central Spain (Cramp & Simmons 1980). Surveys consisted of transects made by car throughout the study area, making use of available roads and tracks. Stops were made every 500 m at which all detected males were recorded. Each survey was made in one day, taking place within three hours after daybreak and, if necessary, within three hours before sunset, these being the periods when the males are most active and most easily detectable (Schulz 1985). Individual males were identified on basis of their plumage characteristics (Arroyo & Bretagnolle 1999, Jiguet *et al.* 2000). The same routes were followed weekly during the breeding season, ensuring uniform sampling. Eleven and 13 such surveys were carried out during 2001 and 2002, respectively. Some additional observations were also incorporated, these being uniformly distributed across the study area, thus avoiding any sampling bias (see also Morales *et al.* 2008, Traba *et al.* 2008, Delgado *et al.* 2009). The exact position of each male was plotted on a map of the study area, indicating the substrate on which it was found.

Sexual display areas

There were 31 individually identified males in 2001 and 29 in 2002. The mean number of observations per male was 6.5 ± 3.6 in 2001 and 6.8 ± 4.4 in 2002. Only males for which we had at least four locations were included in the analysis of display sites. The sample size in 2001 was thus 21 individuals, about 64% of the maximum number of males censused in the study area that year (Delgado *et al.* 2009), with a mean of 7.9 ± 3.3 plots per individual. The sample size in 2002 was 24 individuals, about 83% of the maximum censused in the study area that year (Delgado *et al.* 2009), with a mean of 8.3 ± 3.9 plots per individual. The length of stay, in weeks, of each male was calculated from the first and last dates on which it was detected.

The Minimum Convex Polygon method (MCP; Mohr 1947) was used to determine the extent of the display sites of each individual, obtained by joining the outermost of all its plot positions. This procedure has been widely used when describing territories due to its simplicity and non-parametric nature (Aebischer *et al.* 1993, Gilbert *et al.* 2005, Gray *et al.* 2009). The MCP is greatly affected by peripheral plots and may overestimate territory size by including areas which an individual seldom visits (Barg *et al.* 2005). In our study the plots were made during the males' peak courtship period and so may not represent the full territory of each individual (Anich *et al.* 2009), but they do guarantee that sufficiently observations were made to represent the individual sexual display sites. The MCP is a more inclusive method than others, incorporating all the habitat types visited by an individual. Moreover, it does not require independent observations since it is not based on a statistical calculation (contrarily to kernel areas or harmonic means), which avoids potential problems arising from possible temporal autocorrelations (Aebischer *et al.* 1993). The MCPs were constructed using the Animal Movement facility of Hawth's Tools (Beyer 2004) for ArcMap 9.2. A generalised linear model (GLM) was used to compare the areas of display sites between the two years, controlling for the number of plots used in constructing each MCP. Nearest-neighbour distances (Clark & Evans 1954) were used to analyse the spatial distribution of territories in the study area each year. This involved the calculation of the relationship between the nearest-neighbour distance between the central points of the MCPs and the expected distance in a theoretical population with a random spatial distribution (*R* index; Clarks & Evans 1954). *R* index values below 1 indicate increasing levels of clumping, and vice-versa. The z-statistic was used to test for significance of the deviation from random relative to a normal distribution. The proportions of each substrate type within the display sites were obtained by superimposing the MCPs on maps of land-use in 2001 and 2002. The land-use maps were obtained by systematic surveys of the study area during which each field was assigned to a specific type of land use. These habitat types were: cereal crops, fallow areas, old fallows, ploughed land and vineyards.

Analysis of habitat selection

Habitat selection was assessed by means of a compositional analysis (Aitchison 1982, Aebischer *et al.* 1993). This method has been employed previously in studies of habitat use by radiomarked individuals in which the area of territory use is determined (Duriez *et al.* 2004, Gilbert *et al.* 2005, Beasly *et al.* 2007, Gray *et al.* 2009), but it has never previously been applied to studies of Little Bustards. The analysis compares log ratios of utilised habitats with those available, thus avoiding biases that may arise from the lack of independence of the proportions of different substrate types in the habitat used. Furthermore, it employs the individual as the sampling unit, thus avoiding problems of autocorrelation and pseudoreplication, which typically affect data derived from animal censuses (Aebischer *et al.* 1993).

Nearly all habitat analysis methods require a measure of habitat availability with which to compare habitat use by individuals, a measure that is normally derived from an arbitrarily defined study area. Using a predefined study area as a measure of habitat availability may bias estimates of habitat selection if the animals are monitored in only part of their range and if habitat composition differs between the study area and the home range areas (Aebischer *et al.* 1993). This problem was avoided by calculating a Minimum Convex Polygon (MCP) including all the plots of all the individuals for each year of the study. The available proportions of each type of substrate were thus obtained for each study year by superimposing these total MCPs on maps of land use, as explained above.

The logarithmic transformations carried out in the compositional analysis require that the MCP for each animal should include all the available habitat types (Aebischer *et al.* 1993). The present study only considered the four principal substrate types represented in the study area: cereal crops (C), ploughed areas (P), fallows (F) and old fallows (OF). Vineyards were not included in the analysis since they had a marginal presence in the study area: less than 0.5% of the total area, and they were not used by Little Bustards in either year. Males used the four substrate types during both years but not all of them were represented in all the display areas. Aebischer *et al.* (1993) recommend substituting the zeros corresponding with unutilised habitat types with a very small number other than zero. Bingham & Brennan (2004) suggest substituting a figure between 0.003 and 0.007 in order to minimise Type 1 errors in the compositional analyses, so the zeros were replaced by 0.003 in the present case (see Beasley *et al.* 2007 for a similar approximation).

The analysis was conducted in two stages. The existence of habitat selection other than random was first examined using Wilks' Lambda (λ) statistic. The order of preference of each habitat type was next determined by constructing a matrix of means of the differences in the log-ratios for utilisation and availability for all the individuals (selection indices). Such indices were positive or negative according to whether a substrate was chosen or rejected respectively. The habitat types were then ranked according to the sum of the total number of positive values that they contributed to the matrix. The value of t, which measures the significance of the deviation in the use of each habitat type relative to random, was also obtained for each substrate (Aebischer *et al.* 1993).

In order to determine whether the selection indices obtained via the compositional analysis for each substrate type differed significantly from each other, a generalised linear model (GLM) for each year of the study was constructed, with the selection index as the dependent variable and substrate type as factor, considering each display site as a separate observation. In addition, a second GLM with selection indices for each habitat type as dependent variables and study year as factor was employed to verify that the general pattern of habitat selection within these areas was similar during both study years.

We also attempted to test the hypotheses derived from the IFD hypothesis, regarding differences in habitat quality between the display areas in relation to conspecific density and phenological variables for each year of the study. This employed a regression analysis taking the extent of preferred habitat types within the display areas (a measure of habitat quality) as the dependent variable and the following factors as independent ones: the date on which territories were established, the density of conspecifics in the study area on those dates and the lengths of stay of males in their territories. Finally, we took assessed the existence of spatial association between the locations of male display sites and habitat types favourable to them. The degree of grouping of fields that offered the substrate types selected by Little Bustards, identified via the compositional analysis, was first tested by a nearest-neighbour analysis between field centroids. We then analysed the degree of spatial aggregation between the display sites and the fields that offered the selected habitat types by means of a bivariate Ripley's K function analysis (Wiegand & Moloney 2004) between the centroids of display areas and of those fields. This analysis is a variant of the univariate Ripley's K function in which the spatial relationship between two different types of events is based on the distribution of distances of type 1 events (in this case the display area centroids) with respect to type 2 events (centroids of fields with favourable habitat types) within circles of different radius centred on a fixed number of type 2 points chosen at random, in order to detect the existence of aggregation at different scales. We employed the function $L(r)$, a transformation of K into a linear function, which is more readily interpretable since the expected value of L for a random distribution is zero (Wiegand & Moloney 2004).

The analyses employed the STATISTICA 6.0 (StatSoft 2002), Resource Selection Analysis Software for Windows (Leban 1999) and PASSaGE 2 beta (Rosenberg 2009) statistical packages. All means are given with their standard error (SE).

RESULTS

Display sites

Figure 1 shows the locations within the study area of the display sites of each individual male in 2001 and 2002. The mean length of occupancy of display sites by male Little Bustards was close to seven weeks in both

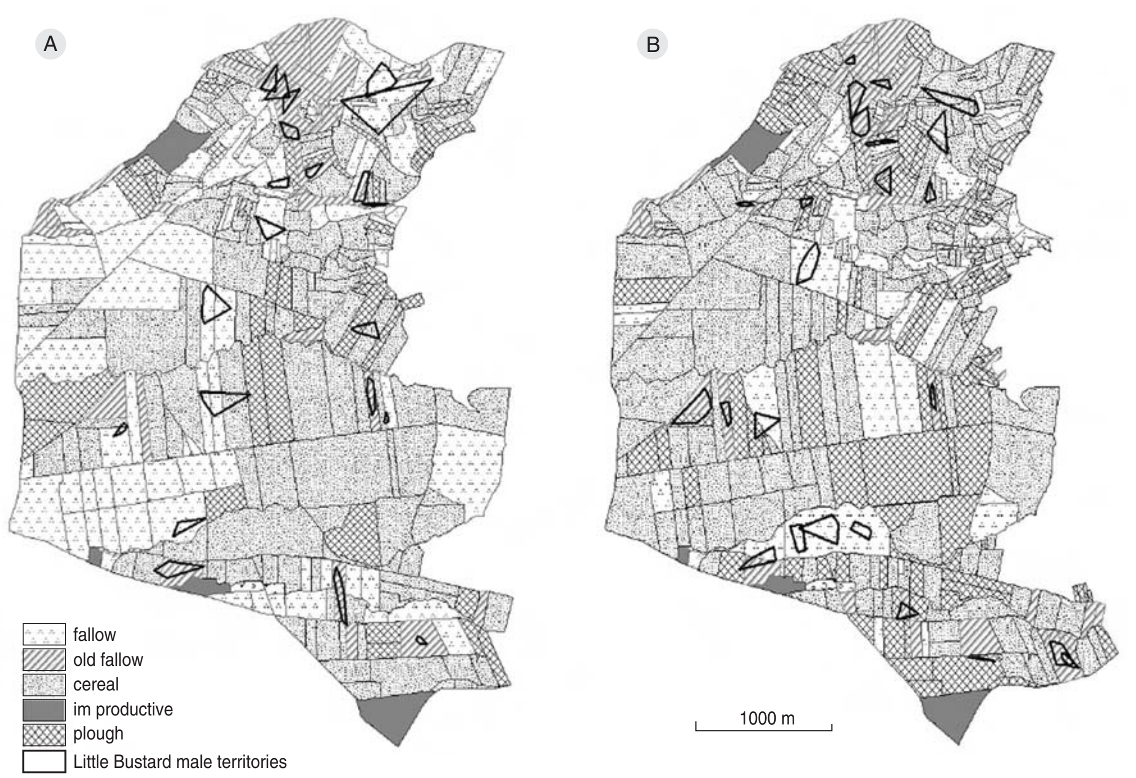

Figure 1. Agrarian substrate composition in 2001 (A) and 2002 (B) and Minimum Convex Polygons (MCP) for each individually identified male (sexual display areas).

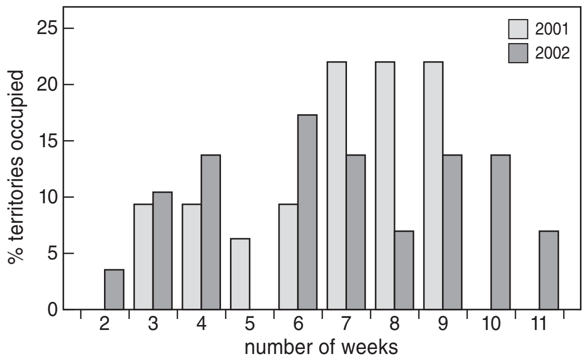

Figure 2. Territory occupation length (in weeks) at Valdetorres del Jarama. (week 1: 25–31 March ; week 2: 1–7 April; etc.).

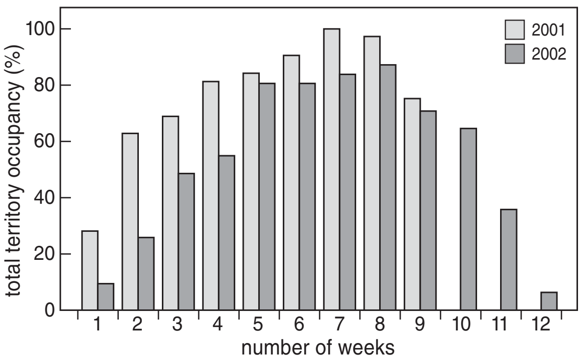

Figure 3. Weekly progression of territory occupation at Valdetorres del Jarama (week 1: 25–31 March ; week 2: 1–7 April; etc.).

years (mean: 2001 = 6.8 ± 2; 2002 = 6.9 ± 2.7). In 2001 ~70% of sites were occupied for 7–9 weeks. In 2002 ~30% were occupied for 6–7 weeks and ~20% were ocupied for 8–9 weeks (Fig. 2). Figure 3 shows the weekly progression of site occupation during both study years. Maximum occupancy was reached in week seven (6–12 May) in 2001 and in week eight (13–19 May) in 2002.

The mean sizes of the display sites obtained by MCP calculations were 1.73 ± 2.18 ha in 2001 and 1.49 ± 1.12 ha in 2002. Although there was a significant relationship between the number of plots and display area size ($F_{1,42} = 18.54$; $P = 0.00$), there were no significant differences between years after controlling for the number of plots used in determining each display area ($F_{1,42} = 0.62$; $P = 0.43$).

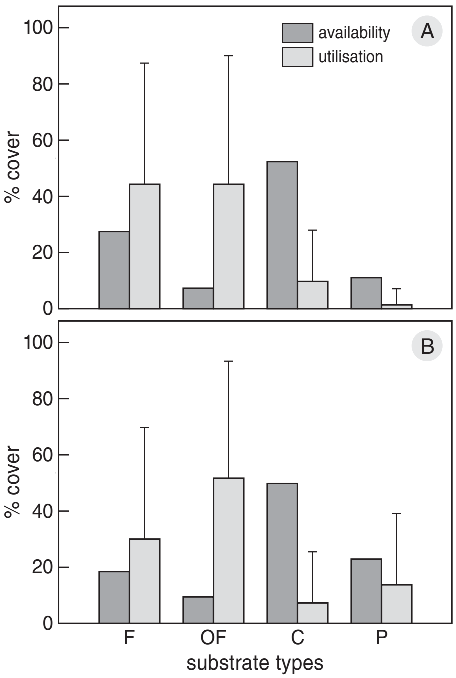

Figure 4. A comparison between the total percentage of each substrate type within all MCPs combined and the mean percentages (+ SD) for male Little Bustard territories in (A) 2001 and (B) 2002. (F: fallows; OF: old fallows; C: cereal crops; P: ploughed land).

Habitat selection

The availability of old fallows and cereal crops in the study area remained relatively constant between 2001 and 2002 (Fig. 4). The extent of fallows declined in 2002 when that of ploughed land increased.

The compositional analysis showed that Little Bustards preferred fallows and old fallows (Fig. 4). Thus habitat selection within the display sites differed significantly from random with respect to what was available within the study area (2001: $\lambda = 0.511$; $\chi^2 = 14.09$; $P < 0.05$; 2002: $\lambda = 0.358$; $\chi^2 = 24.64$; $P < 0.01$).

Table 1 shows the results of the compositional analyses for 2001 and 2002 respectively. The number of positive elements in each row determines the order of preference of the corresponding habitat type. In both years, old fallows received most positive values and cereal crops most negative values. Thus the rank order of habitat selection for both 2001 and 2002 was OF > F > P > C. There were significant differences in selection of different habitat types both in 2001 ($F_{3,\,80} = 9.02$; $P < 0.005$) and 2002 ($F_{3,92} = 15.58$; $P < 0.005$). There was no distinction between the usage of same-year and old fallows in 2001 (Table 2), which shows that the above rank order should not be interpreted strictly. Both ploughed areas and cereal crops were less used than fallows and old fallows by male Little Bustards in 2001 (Table 2). The same occurred in 2002, when

Table 1. Rank matrix of variables based on the comparison of habitat composition within male Little Bustard display sites (MCPs) with habitat availability in the study area in two years[a]. (F: Fallows; OF: Old fallows; C: Cereal crops; P: Ploughed land).

Year	Substrate type (use)	Substrate type (availability) F	OF	C	P	Rank[b]
2001	F		-	+++	+++	2
	OF	+		+++	+++	3
	C	---	---		-	0
	P	---	---	+		1
2002	F		---	+++	+	3
	OF	+++		+++	+++	4
	C	---	---		+	1
	P	-	---	+++		2

[a] Matrix cells correspond to mean differences between usage and availability replaced by their sign. Triple signs show a significant deviation from chance with $P < 0.05$.

[b] The rank equals the sum of positive values in each row. High rank values indicate greater preference for that habitat type.

Table 2. Results of Tukey's post-hoc tests for the GLMs analysing selection of different habitat types in both years (see Table 1 for variable abbreviations).

Substrate type (use)	2001				2002			
	F	OF	C	P	F	OF	C	P
F		0.458	0.021	0.050		0.006	0.013	0.293
OF	0.458		0.000	0.000	0.006		0.000	0.000
C	0.021	0.000		0.988	0.013	0.000		0.540
P	0.050	0.000	0.988		0.293	0.000	0.540	

selection of old fallows was significantly greater than that of both cereals and ploughed areas but also of fallows (Table 2).

The general habitat usage of male Little Bustard remained constant during both study years ($F_{3,41} = 0.29$; $P = 0.83$). The univariate analyses for each substrate type also showed no significant between-year differences in their selection patterns (in all tests $P > 0.3$).

The regression analyses which were used to examine the hypothesis of variation in habitat quality between display sites relative to different demographic and phenological variables, showed no significant effect in either year on the total area of selected habitat types (fallows and old fallows) of any of the other variables considered. These were: date when males occupied display sites (2001: $F_{1,19} = 0.68$, $P = 0.42$; 2002: $F_{1,22} = 0.26$, $P = 0.61$), length of stay ($F_{1,19} = 0.11$, $P = 0.7$; 2002: $F_{1,22} = 1.7$; $P = 0.2$) and density of males within the study area when display sites were established (2001: $F_{1,18} = 0.5$, $P = 0.48$; 2002: $F_{1,22} = 0.8$, $P = 0.37$).

Spatial distribution

The spatial distribution analyses showed that the centroids of the MCPs (the display areas) were not significantly clumped in either study year (2001: $R = 1.05$, $z = 0.44$, $P > 0.05$; 2002: $R = 0.97$, $z = -0.233$, $P > 0.05$). In both years also, fields that offered the substrates that male Little Bustards selected preferentially, i.e. fallows and old fallows, showed significant spatial aggregation, being higher in 2002 (2001: $R = 0.92$, $z = -1.84$, $P < 0.05$; 2002: $R = 0.79$, $z = -4.56$, $P < 0.01$). Finally, significant spatial aggregation was detected between the display site centroids and those of the fields that offered the selected substrates, both in 2001 and 2002 (Figs 5A and 5B, respectively).

DISCUSSION

The analysis of habitat selection based on individuals' display sites, rather than on isolated observations, gives information on a broader spectrum of space use that takes into account movements by individuals in most of the areas that they prefer. Spot observations of individuals in most studies on use of space originate from radiotracking. Our study, however, used a method proposed by Arroyo & Bretagnolle (1999), identifying individual males on the basis of their nuptial plumage and other morphological characters, that has been used successfully in previous studies of Little Bustard (Jiguet *et al.* 2000, 2002). Radiotracking is a costly technique that entails risk for the captured individuals (Ponjoan *et al.* 2008), so the method used here provides a good alternative, especially during the reproductive period when males are most easily detected. The MCPs derived from spot observations of individuals identified in this way correspond with their display sites, which comprise part but not all of their territories (Anich *et al.* 2009). The mean sizes of such display areas in both study years were similar to those found in previous studies that recorded core usage areas (i.e. 2 ha; Petretti 1993), but they are smaller than those reporting total home ranges (i.e. 19 ha; Jiguet *et al.* 2000).

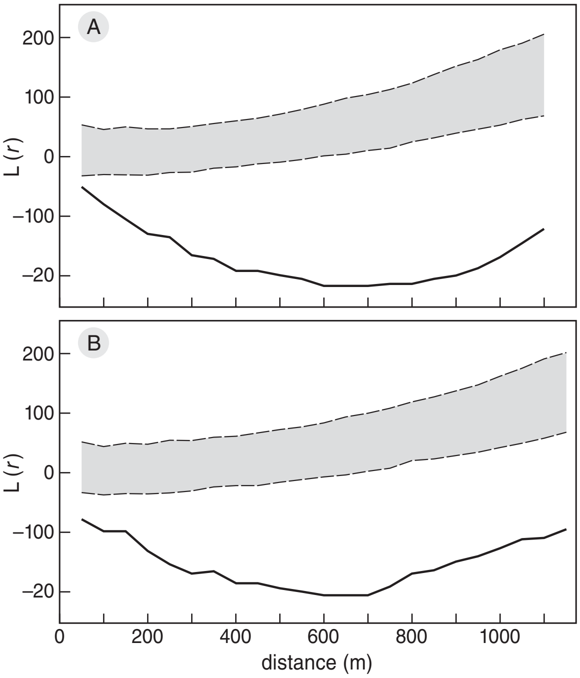

Figure 5. Results of the analyses of Ripley's bivariate function L(r) (solid line) of the distribution of the centroids of male Little Bustard territories with respect to the centroids of fields of same-year and old fallows (the substrate types that male Little Bustards preferentially select) in (A) 2001 and (B) 2002. The broken lines represent 95% confidence limits resulting from the randomisation of the distribution pattern (999 simulations). L(r) values within the 95% confidence limits indicate a random distribution. L(r) values less than zero indicate significant aggregation and values greater than zero indicate repulsion.

With respect to selection patterns, male Little Bustards included a larger than expected proportion of fallows and old fallows within their display sites, relative to their availability. In contrast, both cereal crops and ploughed areas were under-represented. This selection pattern was constant during both years, indicating fidelity to permanent and semi-permanent habitat types and also to areas which offered some degree of mosaic structure. In general, the observed habitat selection patterns matched those of earlier studies of the species (Jiguet *et al.* 2000, 2002, Wolff *et al.* 2001, Morales *et al.* 2005, 2006, García *et al.* 2007), but they contribute more reliable information through being based on display sites and not on spot observations. Male Little Bustards are associated with habitat types that offer both protection and food (Jiguet *et al.* 2000, Morales *et al.* 2005, 2006, 2008). During the breeding season in central Iberia they prefer areas with high substrate diversity (Morales *et al.* 2005): fallows and leguminous crops, as well as pastures offering high floristic and arthropod diversity. At this time males are courting females and defending their territories from other males, both activities that require being visible from some distance and which demand high energy expenditure (Jiguet 2001). They thus choose habitat types that offer a degree of protection against possible predators but which allow themselves to be seen by females and other males, and furthermore those in which abundant food is available (Jiguet *et al.* 2000, 2002, Wolff *et al.* 2001, Morales *et al.* 2005, 2008, Traba *et al.* 2008). Cereal crops are probably avoided in display sites since the vegetation is already too tall during the breeding season, reducing visibility. Ploughed land is also poorly represented in display sites since although it offers high visibility it may provide neither sufficient protection nor food resources (Morales *et al.* 2008, Morales & Traba 2009). As previous studies have revealed, the selection of relatively permanent habitat types may be associated with particular structural characteristics in their vegetation common to all of them (Martínez 1998, Moreira 1999). Morales *et al.* (2008) found that male Little Bustards tend to occupy areas with abundant detritus and with dense but low vegetation during the breeding season, these being characteristic of areas of natural vegetation and, in particular, of both fallows and old fallows. Such habitat types show greater interannual stability in vegetation structure, which explains why they were selected in both study years, although they depend on some management (e.g. grazing) that both prevents vegetation from growing too tall and the establishment of woody species.

The analyses of the distribution patterns of the display sites employed only those males for which a MCP was obtained, which represented a high proportion of the breeding males in the study area in both years. The results may therefore be considered reliable and representative. The analyses show that there was no significant clumping of display sites in either year. Nevertheless, there was significant spatial aggregation of such sites with fields offering the habitat types preferentially selected by male Little Bustards (fallows and old fallows). This, together with the results obtained on differential habitat selection and the fact that the selection pattern did not differ between the two study years, may suggest that, at the spatial scale of the study area, males seek particular habitats prior to other factors, such us presence of other males. In the study area the spatial pattern of field use changes from one year to the next due to crop rotation (Fig. 1), although habitat availability remains relatively constant (Fig. 4). Thus, males may change position from year to year to find the habitats that meet their requirements and to avoid those unfavourable (Fig. 1).

Fields of both fallows and old fallows were significantly mutually clumped in both 2001 and 2002. The fact that the display sites are significantly spatially associated with such fields, but not with each other, may mean that the number of individuals present in the study area was not large enough for all the optimum areas to be occupied. In consequence, territories are distributed throughout the study area without clumping. This finding may also be supported by the fact that the extent of fallow areas within the display sites did not differ in relation to phenological variables as the arrival dates and lengths of stay of males in their territories, nor in relation to the density of conspecifics in the study area when the territories were established. According to the IFD hypothesis (Fretwell & Lucas 1970), favourable habitat types are the first to be occupied and competition for such habitat types increases as population density increases, leading to occupation of lower-quality, suboptimal areas once the most suitable have been occupied. The latter did not occur in our study area due to undersaturation.

Our results may have implications in defining the mating system of Little Bustards in the study population. In some European populations the Little Bustard shows an exploded lek mating system, in which males defend loosely aggregated territories that also contain food and other resources that females may potentially use (Höglund & Alatalo 1995, Jiguet *et al.* 2000, 2002, Morales *et al.* 2001). Our present findings show that the males in the study area significantly selected particular habitat types for their breeding territories. Also, Traba *et al.* (2008) have found that the territories of this same population offer greater amounts of valuable food resources, notably large carabid and tenebrionid beetles, than their surroundings. Both these results would support the existence of the exploded lek as the principal mating system in the study area. However, the fact that territories were not spatially aggregated suggests that, at least at the studied spatial scale, the Little Bustards in this population may not form leks, for which clumped territories are an essential requirement (Beehler & Foster 1988). The boundaries between polygyny with resource defence, an exploded lek or a lek involving active resource defence are sometimes hard to establish, since such factors as density, sex-ratio and habitat quality may influence (Höglund & Alatalo 1995, Ligon 1999). Thus, there is a great intra-specific variation within typical lekking species (Carranza *et al.* 1989, Jiguet *et al.* 2000, Morales *et al.* 2001).

Our results reveal that the distribution of male Little Bustards in the study population is driven largely by habitat preferences, prior to factors associated with its typical mating system. The preference of the Little Bustard for heterogeneous cultivated areas and permanent habitat types may have a direct consequence on the conservation of its populations since the agrarian landscape involves a large enough scale to introduce management measures. Knowledge of the mating system and its variability is equally essential in developing conservation measures, since these may be influenced by the ecological functioning of the population.

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SAMENVATTING

In midden-Spanje werd onderzocht in welke habitats mannetjes Kleine Trap baltsen. In de twee onderzoeksjaren bleken de mannetjes een voorkeur te hebben voor geploegd en vervolgens geëgd land. Het maakte niet uit of het land eerder in het voorjaar of in een voorgaand jaar was bewerkt. Wanneer de aantallen baltsende vogels toenamen, werd geen gebruik gemaakt van minder aantrekkelijke habitats. Dit wijst erop dat het gebied nog niet volledig gevuld was met territoria. De baltsplekken lagen niet dicht bij elkaar, dus er was geen sprake van een gezamenlijke baltsplaats (lek). De resultaten onderstrepen het belang van agrarisch gebied voor de Kleine Trap. Dit is een belangrijk gegeven omdat beschermingsmaatregelen op het agrarisch land (bestaande uit het handhaven van een traditionele bedrijfsvoering) op een voldoende grote schaal kunnen plaatsvinden. (DH)

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