

Not Only Habitat But Also Sex: Factors Affecting Spatial Distribution of Little Bustard *Tetrax tetrax* Families

Author(s): Rocío Tarjuelo , María Paula Delgado , Gerard Bota , Manuel B. Morales , Juan Traba , Anna Ponjoan , Israel Hervás & Santi Mañosa

Source: Acta Ornithologica, 48(1):119-128. 2013.

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

DOI: <http://dx.doi.org/10.3161/000164513X670070>

URL: <http://www.bioone.org/doi/full/10.3161/000164513X670070>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Not only habitat but also sex: Factors affecting spatial distribution of Little Bustard *Tetrax tetrax* families

Rocío TARJUELO¹, María Paula DELGADO¹, Gerard BOTA², Manuel B. MORALES¹, Juan TRABA¹, Anna PONJOAN³, Israel HERVÁS¹ & Santi MAÑOSA³

¹Terrestrial Ecology Group (TEG), Department of Ecology, Universidad Autónoma de Madrid, E-28049, Madrid, SPAIN, e-mail: rocio.tarjuelo@gmail.com

²Biodiversity and Animal Conservation Lab (BAC-Lab), Forest Sciences Center of Catalonia, Crta. Sant Llorenç, km 2, 25280 Solsona, Catalonia, SPAIN

³Department of Animal Biology and Institute for Biodiversity Research (IRBio), Faculty of Biology, University of Barcelona, Avinguda Diagonal, 643, 08028 Barcelona, Catalonia, SPAIN

Tarjuelo R., Delgado M. P., Bota G., Morales M. B., Traba J., Ponjoan A., Hervás I., Mañosa S. 2013. Not only habitat but also sex: Factors affecting spatial distribution of Little Bustard *Tetrax tetrax* families. *Acta Ornithol.* 48: 119–128. DOI 10.3161/000164513X670070

Abstract. Species distribution patterns are determined not only by habitat preferences but also by biotic factors. Particularly, the presence of conspecifics may yield different types of benefits and costs for the individuals involved. This study analyses the spatial distribution of Little Bustard families during the breeding season in relation to the distribution of male core areas in three Spanish populations of the species. A compositional analysis is used to evaluate habitat selection and the habitat types most preferred by females with offspring. Spatial analyses were performed to evaluate the proximity of Little Bustard families to male core areas and male displaying sites. The habitat selection pattern was similar between regions, with semi-permanent vegetation and stubbles as most preferred habitats while others, such as ploughed land, were avoided. Families were located closer to male core areas than expected by chance and were spatially associated to male displaying sites. Little Bustard females may obtain different benefits from this spatial association such as access to more food resources and chances for second matings after a clutch loss. Also in stubbles, the capture of prey by chicks would be easier and semi-permanent habitats would serve as shelter. These results highlight the importance of intraspecific interactions in the definition of the habitat selection pattern of females and families. This study shows how spatial point pattern analysis may be a useful tool for integrating landscape and behavioural ecology.

Key words: Little Bustard, conspecific attraction, farmland conservation, habitat use, spatial point pattern analysis, habitat selection

Received — Oct. 2012, accepted — May 2013

INTRODUCTION

Habitat selection is one of the most important processes used to explain and predict the spatial distribution of species at different scales (Guisan & Zimmermann 2000, Suárez-Seoane et al. 2002, Guisan & Thuiller 2005), although biotic interactions may modify the distribution patterns based on pure habitat requirements (Rosenzweig 1981, Pearson & Dawson 2003, Araújo & Luoto 2007). In some cases, aggregated spatial distribution of conspecifics can be explained as a result of resource clustering (Cornulier & Bretagnolle 2006), but individuals can also obtain direct benefits from settling near conspecifics (Stamps 1988, Reed & Dobson 1993, Danchin et al. 1998). The presence of

conspecifics can be a cue to habitat quality (Boulinier et al. 1996, Beauchamp et al. 1997, Danchin et al. 1998, Serrano et al. 2001, Ward & Schlossberg 2004) facilitating its assessment, which is often a difficult and time-consuming process (Slagsvold 1986). Furthermore, individuals may display a clumped distribution pattern as an antipredatory strategy (Perry & Andersen 2003, Kullmann et al. 2008) or to gather valuable information about mates during the breeding season (Höglund & Alatalo 1995, Melles et al. 2009). Thus, it seems necessary to take into account both the landscape configuration and the behavioural traits of the species to describe spatial distribution patterns. However, studies that integrate behavioural ecology with landscape ecology are scarce

due to the difficulties to integrate the different spatial scales involved in these approaches (Lima & Zollner 1996, Melles et al. 2009).

The Little Bustard, *Tetrax tetrax*, is a medium sized Palearctic steppe bird whose distribution ranges from Morocco and the Iberian Peninsula to Central Asia (Del Hoyo et al. 1996). The populations of this species have suffered a drastic decline throughout its range mainly due to agricultural intensification (Goriup 1994). Nowadays, the Iberian Peninsula holds more than half of the world's population (García de la Morena et al. 2006). The species occupies areas of extensive grassland or cereal farmland, characterized by a varying degree of heterogeneity of land uses depending on the prevailing landscape type (Morales et al. 2005a, Silva et al. 2010). Habitat selection patterns of Little Bustard males have been well studied (Martínez 1994, Jiguet et al. 2000, Morales et al. 2005a, Delgado et al. 2010, Ponjoan et al. 2012), showing a marked preference for fallows and legume crops, which can ensure conspicuousness during the sexual display thanks to the low vegetation height, but also a high availability of food (Martínez 1998, Morales et al. 2008). However, the knowledge of the biology and habitat selection patterns of females is scarce (but see Salamolard & Moreau 1999, Morales et al. 2008, Lapiedra et al. 2011), largely because of their extremely secretive behaviour during the breeding season, which makes female observation difficult to obtain. Contrary to male preferences, females seem to select habitats with higher vegetation cover and greater amounts of litter and green weeds which may provide shelter and food for themselves and their offspring (Salamolard & Moreau 1999, Morales et al. 2008). Understanding the ecology of females, particularly those aspects related with breeding success, is essential to ensure the viability of Little Bustard populations (Morales et al. 2005b, Delgado et al. 2009).

The Little Bustard shows sexual dimorphism and males provide no parental care to offspring (Cramp & Simmons 1980). The mating system has been described as an exploded lek (Jiguet et al. 2000), in which resources may influence settlement of male loosely aggregated territories (Traba et al. 2008), to which females are attracted and in which they may nest (Jiguet et al. 2000, Morales et al. 2013). In nidifugous species, such as the Little Bustard, female decisions at the moment of nesting should be the result of a trade-off between finding mating and nesting areas but also suitable

places for rearing fledglings (Blomqvist & Johansson 2008). However, to our knowledge, there are no studies that analyze the spatial distribution of Little Bustard families in relation to male display sites.

The aims of this study are (1) to analyze the habitat selection pattern of Little Bustard families during the breeding season; (2) to explore the role played by intraspecific relationships, namely the presence of males, to determine their spatial distribution.

METHODS

Study area

The study was conducted in three areas located in central and northeast Spain dominated by a cereal pseudo-steppe landscape. Two sites were located in the Ebro Valley in Catalonia: Bellmunt (41°47'N, 0°57'E) and Belianes (41°35'N, 0°59'E) and the other one in the Spanish southern plateau, in Ciudad Real province (38°57'N, 3°56'E) (Table 1). The regions are all under dry Mediterranean climate, with annual precipitation means around 400 mm. These three study sites are included within important areas for the conservation of steppe birds in Spain (Traba et al. 2007).

The three study areas present very little natural vegetation cover due to changes in land use for agriculture and are dominated by cereal crops (more than 50% of their surface). In summer, dry cereal and legume crops become stubble fields (ST) after harvesting. Ploughed areas (PL), dry woody cultures (DWC, including olive groves, vineyards and almond tree orchards), same-year fallows (hereafter called simply fallows, F) and fallows older than two years and low height scrublands (both classified as natural vegetation, NV) were present in every study site. Other minor substrates (OTHERS) were fruit tree orchards, pastures and urban areas. In order to determine the availability of the different habitat types, land-use maps were drawn by assigning to each field one of the previous habitat types for each study area.

Little Bustard surveys

Little Bustard male surveys were carried out between April and May 2008, corresponding with the period of maximum sexual display activity of males in Spain (Cramp & Simmons 1980). Surveys consisted of car routes using the existing rural

track and road network, which is dense in the three areas, completely covering each site, along which survey points separated by 500 m were established. Observation time at each point was 10 min, during which all Little Bustard males detected within telescope reach were recorded. Males detected acoustically were searched for by telescope in order to determine their actual position, so that virtually all active males present were finally detected visually. One survey was made in each study area with two car-teams surveying simultaneously. Each survey was made within the first three hours after daybreak and the three hours before sunset, these being the period when males are more active and thus, easier to detect (see, for example, Morales et al. 2008 and Delgado et al. 2009 for the same survey methodology). All the individuals were mapped and finally, maps were revised to detect potential double counts. Family surveys were carried out 7–31 July 2008, following the same procedure described for males. In this case, the number of fledglings was recorded and those observations with at least one Little Bustard fledgling were designated as family. The detectability of families might differ among substrate types given the secretive behaviour of females and chicks. However, cereal and leguminous crops were already harvested when surveys were carried out, allowing a nearly complete detection of families on stubbles (the dominant habitat). Special survey effort was made in the case of fallows and other habitat types with higher vegetation, which were carefully scanned for families. Productivity was measured as the number of fledgling per female.

Analysis of habitat selection

Family habitat selection was assessed by means of a compositional analysis for each area (Aitchison 1986, Aebischer et al. 1993). This analysis compares the log-ratios of the used and the available habitats, avoiding misinterpretations owing to the lack of independence among the proportions of different types of substrates found inside family home ranges. Using arbitrary study area boundaries to obtain the different substrates' availability may lead to biases due to the fact that individuals were only monitored in part of their distribution range, or to substrate composition dissimilarities between the predefined boundaries of the study area and the real distribution of the organisms (Aebischer et al. 1993). Thus, a Minimum Convex Polygon (MCP) was drawn using the geo-references of all male and family locations. Then,

availability of each substrate type was determined by extracting the information on land use maps for the MCP.

In order to establish family home range, each family observation was assigned a circular buffer with a 600 m radius. This buffer provides an area approaching the average Little Bustard family home range during the rearing period as estimated from radio-tracking by Lapiedra et al. (2011). This analysis was repeated for buffers of 400 and 800 m radius in order to determine whether results were sensitive to radius choice. Since similar results were obtained, hereafter only results of 600 m radius buffer are presented. The proportions of habitat types used by families were obtained by superimposing the defined home range of the families on maps of land use. Since compositional analysis requires that home range areas contain all available habitats, those habitat types not included within the home range were assigned proportion values of 0.00003, this being one order of magnitude lower than the minimum value found different from zero inside the family buffers (Aebischer et al. 1993, Bingham & Brennan 2004, Delgado et al. 2010). Compositional analysis was conducted in two stages. First, the existence of a selection pattern other than random was tested by using Wilks' lambda (λ) statistic (Aebischer et al. 1993). Then, if the habitat selection pattern differed from random, the order of preference of each habitat type was calculated by constructing a matrix of means of the differences in the log-ratios of the proportions of the used and available habitats for all the individuals. A positive value shows that the habitat is selected, whereas a negative one indicates habitat avoidance. For each habitat its *t*-value was calculated, indicating whether its use differed significantly from random. Finally, all habitats were ranked according to the number of positive values that they contributed to the matrix (Aebischer et al. 1993).

Spatial distribution pattern

The fixed kernel method with least-square cross-validation (Worton 1989, Seaman & Powell 1996) was used to define the distribution of Little Bustard males during the period of sexual display from individual observations in each study area. This method has been frequently employed for estimating home ranges since it describes a territory in terms of a probabilistic model and is free of parametric assumptions of the data (Worton 1989). Core areas (areas intensively used by animals) of displaying males were delineated by the

“change in gradient” technique (Harris et al. 1990), analysing the number of males accumulation curve between consecutives isopleths. The core area was defined by the surface enclosed within the isopleth in which a first decline in the slope of the number of males accumulation curve was observed. Finally, core areas of the Ciudad Real population enclosed the territory within the 40% isopleth and core areas of the Bellmunt and Belianes populations were defined by the territory enclosed within the 50%. The area enclosed by the isopleths does not need to be continuous in space (Harris et al. 1990).

To analyse the spatial distribution of Little Bustard families in relation to male core areas several variables were calculated for each family observation: 1) The distance from the family observation to the closest male core area centroid, 2) the probability of male presence in the point where the family was sighted (calculated by means of the kernel function), 3) the mean of male presence probability inside the predefined family home range, 4) the maximum of male presence probability inside the predefined family home range and 5) the coefficient of variation of male presence probability inside the predefined family home range. In order to determine whether the spatial distribution of Little Bustard families follows a random pattern, 100 series of n random points (being n the number of families detected in the corresponding study area) were generated within each study area. The same variables calculated for the families were also calculated for each random point. The mean of the overall random points represents the mean of a randomly distributed population. A Hotelling’s t -test was used to test the hypothesis of different means between families and the theoretical reference value of a randomly distributed population for each study area (Carrascal et al. 2008).

A bivariate Ripley’s K function analysis was conducted with data from each study area to assess whether a spatial association between the location of males and females exists and at what scales it occurs (Wiegand & Moloney 2004). This function analyses the spatial association between two different types of points and detects scale dependent changes in the spatial pattern. The null hypothesis of independence between the male and female point patterns was evaluated. Ripley’s L function, a transformation of K function into a linear one, was used since it stabilizes the variance and makes the results easier to interpret (Ripley 1981). Since the spatial aggregation

between males and females could arise from a coincidental habitat selection pattern, we used a bivariate Ripley’s K function to analyze the degree of spatial aggregation between females and the field’s centroids of their preferred habitats, identified in the previous compositional analysis.

Compositional analysis and kernel smoothing parameters were performed using the package “adehabitat” (Calenge 2006) for the R software v.2.14 (R Development Core Team 2010), while the ArcGis 9.3 program (ESRI 2007) was employed to calculate kernels. Spatial variables were calculated in R software v.2.14, Hotelling t -tests were performed by the package “ICSNP” (Nordhausen et al. 2012) and Ripley’s functions were performed by the package “ads” (Pelissier & Goreaud 2010), both for the R software v.2.14.

RESULTS

Different male, family and fledgling densities were found between study areas (Table 1). Bellmunt and Belianes showed similar values of male density although the highest family and fledgling density were found in Belianes. Ciudad Real was the locality with the lowest male, family and fledgling densities.

Habitat selection pattern

The availability of the different habitats differed between study areas, although stubbles remained as the most abundant habitat in all localities (Fig. 1). The compositional analysis showed that habitat selection by Little Bustard families differed significantly from random in all study areas (Bellmunt: $\lambda = 0.0596$, $p < 0.001$; Belianes: $\lambda = 0.3575$, $p < 0.001$; Ciudad Real: $\lambda = 0.1048$, $p = 0.046$). In the three study sites there was a positive selection of stubbles and semi-permanent vegetation habitats (being fallows in Ciudad Real

Table 1. Description of study area with corresponding densities of males, families and fledglings (in 2008). Productivity (measured as the number of fledglings per female) and the number of families are also given.

	Study area		
	Bellmunt	Belianes	Ciudad Real
Area (ha)	1794	1839	10698
Number of families	12	34	5
Number of males/100 ha	4.24	4.02	2.34
Number of families/100 ha	0.67	1.85	0.05
Number of fledglings/100 ha	1.23	2.39	0.09
Productivity	2.44	1.30	1.11

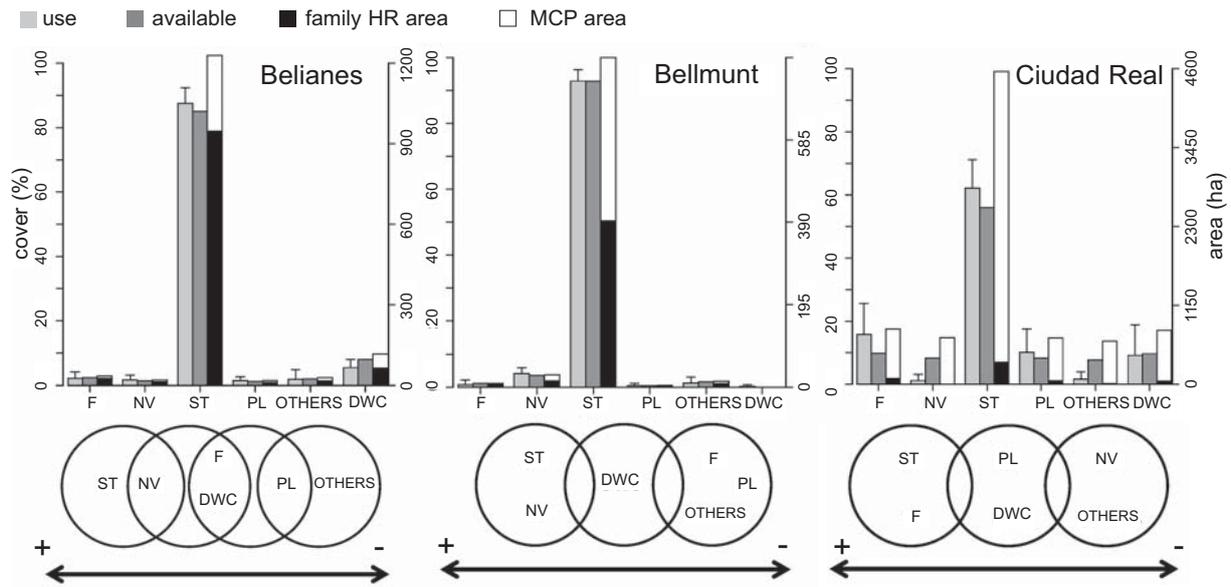


Fig. 1. Proportion of available substrates within the total MCP and the mean proportion and standard deviation of the substrates within the assigned home range of the families in three study areas. F — fallows; NV — natural vegetation; ST — stubbles; PL — ploughed areas; DWC — dry woody cultures; OTHERS — pastures, fruit tree growing and urban areas. Also the area of each habitat type inside the MCP and the area of the overall family home range surface are provided. Below each graphic a diagram with the interpretation of the Compositional Analysis is provided complementing results showed in Table 2. Habitats within the same circle do not differ significantly in their use by Little Bustard families. Arrows represent a gradient from most preferred (+) to less preferred (-) habitats.

and natural vegetation in Bellmunt and Belianes, Table 2). Ploughed lands and “Others” tended to be avoided inside Little Bustard family home ranges (Fig. 1).

Spatial distribution pattern

Families showed distances to male core areas significantly lower than expected by chance in all study areas (Table 3). The probability of male

Table 2. Rank matrix of substrates based on the comparison between the proportion of available habitat within the total Minimum Convex Polygon (minimum area enclosing all the Little Bustard observations) and the proportion inside the home range of the families in three study areas. Each element in the matrix represents the mean differences between usage and availability replaced by its sign. Triple sign indicates significant deviation from random with $p < 0.05$. The rank reflects substrate preference based on the sum of positive values in each row, where high values indicate a greater preference for that substrate. Substrate abbreviations see Fig. 1.

Study site	Substrate type (usage/available)	F	NV	ST	PL	DWC	OTHERS	Rank
Bellmunt	F		---	---	-	-	-	0
	NV	+++		+	+++	+	+++	5
	ST	+++	-		+++	+	+++	4
	PL	+	---	---		-	-	1
	DWC	+	-	-	+		-	2
	OTHERS	+	---	---	+	+		3
Belianes	F		-	---	+	+	+++	3
	NV	+		-	+++	+	+++	4
	ST	+++	+		+++	+++	+++	5
	PL	-	---	---		-	+	1
	DWC	-	-	---	+		+++	2
	OTHERS	---	---	---	-	---		0
Ciudad Real	F		+++	+	+	+	+++	5
	NV	---		---	-	-	-	0
	ST	-	+++		+	+	+++	4
	PL	-	+	-		+	+	3
	DWC	-	+	-	-		+	2
	OTHERS	---	+	---	-	-		1

presence in a point where a family was located was significantly higher than the theoretical value of a randomly distributed population in Bellmunt and Belianes but did not differ from random in Ciudad Real. However, the same trend was found in the three study sites, with values of male presence higher than expected by chance. The coefficient of variation of male presence probability inside family home range areas presented significant differences in all study areas, taking values lower than expected from random. Likewise, the mean and maximum of male presence probability inside the family home ranges were significantly different from random in Bellmunt and Belianes, with values higher than reference ones. Thus, family observations were found closer to areas which had higher probability of male presence during the mating period and this probability showed less variation inside family home ranges than expected by chance.

Family locations were spatially aggregated with displaying male locations in all study areas (Fig. 2). Regarding the spatial relationship between families and their preferred habitat types shown by the compositional analysis, stubble field centroids and Little Bustard broods were significantly aggregated (Fig. 2). Little Bustard families and natural vegetation centroids were independ-

ently distributed in Bellmunt and Belianes (Fig. 2), although almost the entire area of this habitat fell within the family home ranges (Fig. 1). However, in Ciudad Real families were aggregated with fallow field centroids (Fig. 2) but there were still large patches of unused fallows within the Minimum Convex Polygon (the minimum area enclosing all the Little Bustard observations, Fig. 1).

DISCUSSION

Our study shows that in different Spanish Little Bustard populations, females do not establish their home ranges at random, preferring stubbles and habitats which offer higher vegetation density at low to medium heights, such as fallows and natural vegetation, which is consistent with results from previous studies (Jiguet et al. 2002, Morales et al. 2008, Lapiedra et al. 2011). In addition, Little Bustard broods were spatially aggregated with male display core areas which may bring benefits during the rearing period.

We found very low productivity values of Little Bustard in the three study areas, which is consistent with information obtained from radio tagging studies conducted on some of them

Table 3. Spatial distribution of Little Bustard families in relation to the male core areas for each study site (Mean, standard deviation and Hotelling t-test results, see methods for details). For each variable, the mean value of the families was compared with a reference value obtained from 100 series of n random points (being n the number of families detected in each study area. Bellmunt: 12 families; Belianes: 34 families; Ciudad Real: 5 families).

Study site		Mean	SD	Reference value	t	d.f.	P
Bellmunt	Distance to the closest male core area centroid (m)	658.76	222.05	1211.53	74.37	11	0.0000
	Probability of male presence at the family observation point	0.1130	0.1189	0.0283	6.08	11	0.0313
	Home range mean raster value	0.0672	0.0437	0.0264	10.45	11	0.0079
	Home range max raster value	0.1713	0.0903	0.0981	7.87	11	0.0171
	CV of the home range	0.6946	0.1828	1.3620	159.95	11	0.0000
Belianes	Distance to the closest male core area centroid (m)	875.33	412.91	1087.50	8.98	33	0.0052
	Probability of male presence at the family observation point	0.0327	0.0209	0.0174	18.11	33	0.0002
	Home range mean raster value	0.0281	0.0153	0.0169	18.19	33	0.0002
	Home range max raster value	0.0588	0.0218	0.0402	24.81	33	0.0000
	CV of the home range	0.5754	0.2506	1.0973	147.51	33	0.0000
Ciudad Real	Distance to the closest male core area centroid (m)	853.94	261.29	1297.23	14.39	4	0.0192
	Probability of male presence at the family observation point	0.0084	0.0042	0.0043	4.82	4	0.0931
	Home range mean raster value	0.0083	0.0051	0.0043	3.5	4	0.1558
	Home range max raster value	0.0213	0.0109	0.0112	4.34	4	0.1056
	CV of the home range	0.7014	0.2949	1.0942	8.87	4	0.0408

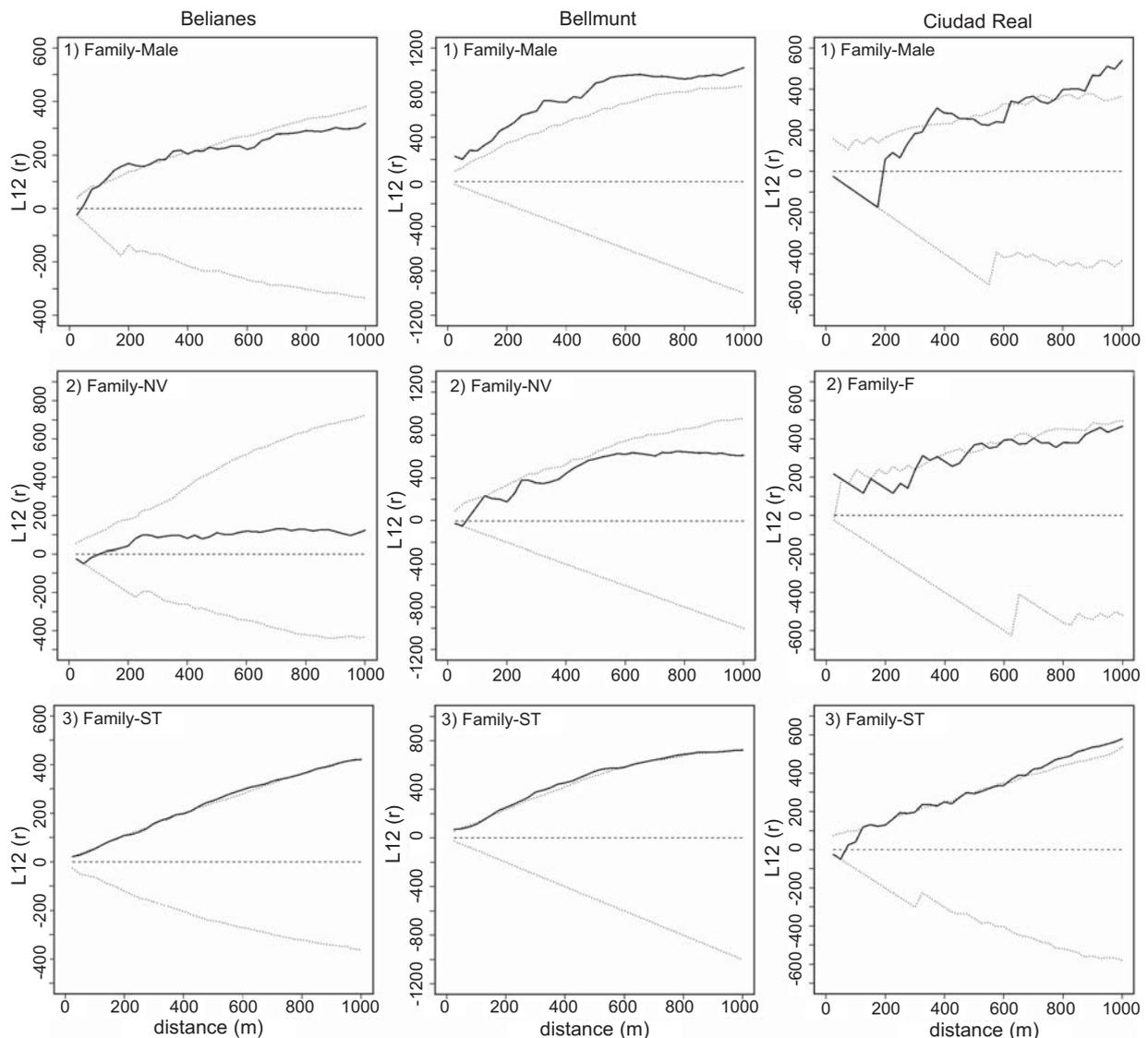


Fig. 2. Analysis of Ripley's bivariate function $L(r)$ for evaluating spatial correlation between 1) family observations and male observations for Belianes, Bellmunt and Ciudad Real; 2) family observations and centroids of natural vegetation fields (NV) for Belianes and Bellmunt and families and centroids of fallow fields (F) for Ciudad Real; 3) family and centroids of stubble fields (ST) for the three study areas. The solid line represents the observed function, the broken line represents the expected function under spatial complete randomness and dotted lines indicate 95% confidence limits resulting from the randomisation of the distribution pattern. The spatial pattern is random when the observed $L(r)$ falls within the confidence limits, uniform if it occurs below them and clumped if it occurs above them.

(Lapedra et al. 2011) and similar to that found in previous studies in other Spanish populations (Morales et al. 2007, own unpublished data). These low productivity values pose a serious threat to the subsistence of these populations since productivity has been highlighted as a key demographic parameter for the viability of Little Bustard populations (Morales et al. 2005b, Delgado et al. 2009). Moreover, the number of families found in these areas seems very low com-

pared to male densities, as reported in other populations of central Spain and France (Inchausti & Bretagnolle 2005, Delgado et al. 2009). If the sex ratio is biased towards males, the female shortage may add a further negative effect to the low productivity, increasing even more the extinction risk of the species in the study areas as shown by population viability analysis (Morales et al. 2005b).

Little Bustard families presented a similar habitat selection pattern in the three study

populations. Semi-permanent vegetation was one of the most preferred habitat types. Families selected fallows in Ciudad Real and old fallows and low height scrublands in Bellmunt and Belianes. These substrates are characterized by greater vegetation cover and height than stubbles, so they could work as concealment places from predators or bad weather conditions (Silva et al. 2004). In addition, semi-permanent vegetation harbours a greater amount of green weed cover and insect availability (Lapiedra et al. 2011) facilitating the access of females with offspring to food resources. Stubble fields, resulting from the harvest of cereal and leguminous crops, were also a selected habitat and comprise more than half of the available surface within the Little Bustard distribution range in the study areas during summer. At this period, stubbles remain as habitat basically providing food resources (Silva et al. 2007, Lapiedra et al. 2011). However, other habitat types are clearly avoided, such as pastures which are daily grazed by sheeps, fruit tree orchards and wooded patches, which is in accordance with previous studies (Salamolard & Moreau 1999, Wolff et al. 2001).

The spatial aggregation between Little Bustard families and the territories previously occupied by males may bring several benefits to females with offspring. If females remained and nested close to male territories as seen in previous studies (Jiguet et al. 2000, Morales et al. 2013), they would save energy by avoiding movements to distant places. During the rearing period, access to food resources could be crucial for determining female distribution. The diet of chicks consists of arthropods, mainly orthopterans and large beetles, at least until 3 weeks old (Cramp & Simmons 1980, Jiguet 2002). The territories of Little Bustard males hold more abundance of large beetles than areas outside them (Traba et al. 2008), though it has been shown that abundance of food resources inside male territories does not influence male attractiveness (Jiguet et al. 2002). However, females would have access to larger amounts of food by settling near or within the male core areas and this could increase the probability of chick survival and therefore the reproductive success of females. Moreover, this would be also a good strategy to acquire new mating opportunities after a clutch loss, especially in a species like the Little Bustard with a high rate of first clutch failure (Lapiedra et al. 2011).

Our results show that the distribution of Little Bustard families is associated to male display

locations even though some females with chicks move considerably far from the nesting site (Lapiedra et al. 2011). However, the spatial aggregation between families and Little Bustard male display locations could be due to a coincidental habitat selection pattern at landscape level. Although previous studies have shown that males and females have different microhabitat requirements, males requiring habitats that promote conspicuousness whilst females select habitats that guarantee concealment (Morales et al. 2008), at landscape level a variable degree of overlap in habitat selection may exist, especially in those regions affected by agricultural intensification. In Bellmunt and Belianes indeed, Little Bustard family home ranges harbour almost the entire available surface of semi-permanent vegetation areas (fallow and natural vegetation) (Fig. 1), which is also one of the habitat types most preferred by males for sexual displaying (Martínez 1994, Morales et al. 2005a, Delgado et al. 2010, Ponjoan et al. 2012). Thus, when the overall suitable habitat is saturated owing to its scarceness in the landscape, we cannot disentangle whether the association between brood ranging areas and male display sites is produced by its use by males or by coincident habitat preferences of both sexes. In Ciudad Real, however, Little Bustard broods are aggregated with fallow fields but, despite the large available surface of this habitat inside the MCP (Fig. 1), females with offspring still stay closer to male core displaying areas. Therefore, these results suggest that display locations of males could influence the decisions of females regarding the establishment of their brooding range.

CONCLUSION

The spatial aggregation between Little Bustard families and male territories found in this study reflect processes that operate at the individual level, although they may have effects on the population's dynamic and, therefore, important implications for conservation. The management aiming to enhance the species' population conditions should bear in mind not only male requirements but also the suitable habitat for females during the chick rearing season. In both cases, it seems necessary to maintain an extensive farmland model that ensures a mosaic landscape of different agrarian substrates, but keeping a certain proportion of fallows and natural vegetation areas. Finally, the studies based on spatial point

patterns may result a useful tool for integrating behaviour and landscape ecology given that they allow to evaluate the consequences of individual-level responses on population dynamics, such as habitat use or conspecific attraction, in this case mediated by mate choice, which could not be detected by exclusively a behavioural approach.

ACKNOWLEDGEMENTS

We wish to thank J. Caro, F. Casas, E. L. García, J. Viñuela and M. Pérez for their collaboration. Rocío Tarjuelo was supported by a PhD grant from the Spanish Minister of Education (FPU). Belianes and Bellmunt field work has benefited from the financial support from REGSEGA (Regs Sistema Segarra-Garrigues), Departament de Medi Ambient i Habitatge (Generalitat de Catalunya). Field work in Ciudad Real was partly supported by Aeropuerto de Ciudad Real, S. A. This paper is a contribution to projects CGL2004-06147-C02-01, CGL2004-06147-C02-02 and CGL2009-13029/BOS of the Spanish Ministry of Science, as well as to the REMEDINAL2 network of the CAM (S-2009/AMB/1783) and the Steppe-ahead project (Fundación General CSIC, Banco Santander and CSIC).

REFERENCES

- Aebischer N. J., Robertson P. A., Kenward R. E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Aitchison J. 1986. The statistical analysis of compositional data. Chapman and Hall, London.
- Araújo M. B., Luoto M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol. Biogeogr.* 16: 743–753.
- Beauchamp G., Belisle M., Giraldeau L. A. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *J. Anim. Ecol.* 66: 671–682.
- Bingham R. L., Brennan L. A. 2004. Comparison of type I error rates for statistical analyses of resource selection. *J. Wildl. Manage.* 68: 206–212.
- Blomqvist D., Johansson O. C. 1995. Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. *Ibis* 137: 550–558.
- Boulinier T., Danchin E., Monnat J.-Y., Doutrelant C., Cadiou B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *J. Avian Biol.* 27: 253–256.
- Bradbury J. W. 1981. The evolution of leks. In: Alexander R. D., Tinkle D. W. (eds). *Natural selection and social behaviour*. Chiron Press, New York, pp. 138–169.
- Calenge C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197: 516–519.
- Carrascal L. M., Palomino D., Seoane J., Alonso C. L. 2008. Habitat use and population density of the houbara bustard *Chlamydotis undulata* in Fuerteventura (Canary Islands). *Afr. J. Ecol.* 46: 291–302.
- Cornulier T., Bretagnolle V. 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. *Ecography* 29: 240–250.
- Cramp S., Simmons K. E. L. (eds) 1980. *The birds of the Western Palearctic*. Vol. II. Oxford Univ. Press.
- Danchin E., Boulinier T., Massot M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79: 2415–2428.
- Del Hoyo J., Elliott A., Sargatal J. 1996. *Handbook of the birds of the World*, Vol. III, Hoatzin to Auks. Lynx Edicions, Barcelona.
- Delgado M. P., Morales M. B., Traba J., García De La Morena E. L. 2009. Determining the effects of habitat management and climate on the population trends of a declining steppe bird. *Ibis* 151: 440–451.
- Delgado M. P., Traba J., García de la Morena E. L., Morales M. B. 2010. Habitat selection and density-dependent relationships in spatial occupancy by male Little Bustards *Tetrax tetrax*. *Ardea* 98: 185–194.
- ESRI. 2007. GIS and mapping software. <http://www.esri.com/>.
- García de la Morena E. L., Bota G., Ponjoan A., Morales M. B. 2006. [The Little Bustard in Spain. I National Census 2005]. SEO/BirdLife. Madrid.
- Goriup P. D. 1994. Little Bustard *Tetrax tetrax*. In: Tucker G. M., Heath M. F. (eds). *Birds in Europe: their Conservation Status*. Birdlife International, Cambridge, UK, pp. 236–237.
- Guisan A., Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8: 993–1009.
- Guisan A., Zimmermann N. E. 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135: 147–186.
- Harris S., Cresswell W. J., Forde P. G., Trehwella W. J., Woollard T., Wray S. 1990. Home-range analysis using radio-tracking data — a review of problems and techniques particularly as applied to the study of mammals. *Mammal. Rev.* 20: 97–123.
- Höglund J., Alatalo R. V. 1995. *Leks*. Princeton Univ. Press.
- Inchausti P., Bretagnolle V. 2005. Predicting short-term extinction risk for the declining Little Bustard (*Tetrax tetrax*) in intensive agricultural habitats. *Biol. Conserv.* 122: 375–384.
- Jiguet F. 2002. Arthropods in diet of Little Bustard *Tetrax tetrax* during the breeding season in western France. *Bird Study* 49: 105–109.
- Jiguet F., Arroyo B., Bretagnolle V. 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. *Behav. Process.* 51: 63–82.
- Jiguet F., Jaulin S., Arroyo B. 2002. Resource defence on exploded leks: do male little bustards, *T. tetrax*, control resources for females? *Anim. Behav.* 63: 899–905.
- Kullmann H., Thünken T., Baldauf S. A., Bakker T. C. M., Frommen J. G. 2008. Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. *Biol. Lett.* 4: 458–460.
- Lapiedra O., Ponjoan A., Gamero A., Bota G., Mañosa S. 2011. Brood ranging behaviour and breeding success of the threatened little bustard in an intensified cereal farmland area. *Biol. Conserv.* 144: 2882–2890.
- Lima S. L., Zollner P. A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* 11: 131–135.
- Martínez C. 1994. Habitat selection by the little bustard *Tetrax tetrax* in cultivated areas of central Spain. *Biol. Conserv.* 67: 125–128.

- Martínez C. 1998. [Microhabitat selection of Little Bustard *Tetrax tetrax* during breeding season] *Ardeola* 45: 73–76.
- Melles S., Badzinski D., Fortin M. J., Csillag F., Lindsay K. 2009. Disentangling habitat and social drivers of nesting patterns in songbirds. *Landscape Ecol.* 24: 519–531.
- Morales M. B., Bretagnolle V., Arroyo B. 2005b. Viability of the endangered Little Bustard *Tetrax tetrax* population of Western France. *Biodivers. Conserv.* 14: 3135–3150.
- Morales M. B., García J. T., Arroyo B. 2005a. Can landscape composition changes predict spatial and annual variation of little bustard male abundance? *Anim. Conserv.* 8: 167–174.
- Morales M. B., García de la Morena E. L., Delgado M. P., Traba J. 2007. Recent tendency and future viability of Little Bustard (*Tetrax tetrax*) in Comunidad de Madrid. In: de la Puente J., Pérez-Tris J., Juan M., Bermejo A. (eds). [Ornithological yearbook of Madrid 2006]. SEO-Monticola, pp. 40–55.
- Morales M. B., Traba J., Carriles E., Delgado M. P., García de la Morena E. L. 2008. Sexual differences in microhabitat selection of breeding little bustards *Tetrax tetrax*: Ecological segregation based on vegetation structure. *Acta Oecol.* 34: 345–353.
- Morales M. B., Traba J., Delgado M. P., García de la Morena E. L. 2013. The use of fallows by nesting Little Bustard *Tetrax tetrax* females: implications for conservation in mosaic cereal farmland. *Ardeola* 60: 85–97.
- Nordhausen K., Sirkia S., Oja H., Tyler D. E. 2012. ICSNP: Tools for Multivariate Nonparametrics. R package version 1.0-9. <http://CRAN.R-project.org/package=ICSNP>
- Pearson R. G., Dawson T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.* 12: 361–371.
- Pelissier R., Goreaud F. 2010. ads: Spatial point patterns analysis. R package version 1.2-10. <http://CRAN.R-project.org/package=ads>.
- Perry E. F., Andersen D. E. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. *Condor* 105: 756–770.
- Ponjoan A., Bota G., Mañosa S. 2012. Ranging behavior of little bustard males, *Tetrax tetrax*, in the lekking grounds. *Behav. Process.* 91: 35–40.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reed J. M., Dobson A. P. 1993. Behavioural constraints and conservation biology: Conspecific attraction and recruitment. *Trends Ecol. Evol.* 8: 253–256.
- Ripley B. D. 1981. *Spatial Statistics*. Wiley, New York.
- Rosenzweig M. L. 1981. A theory of habitat selection. *Ecology* 62: 327–335.
- Salamolard M., Moreau C. 1999. Habitat selection by Little Bustard *Tetrax tetrax* in a cultivated area of France. *Bird Study* 46: 25–33.
- Seaman D. E., Powell R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075–2085.
- Serrano D., Tella J. L., Forero M. G., Donazar J. A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *J. Anim. Ecol.* 70: 568–578.
- Silva J. P., Faria N., Catty T. 2007. Summer habitat selection and abundance of the threatened little bustard in Iberian agricultural landscapes. *Biol. Conserv.* 139: 186–194.
- Silva J. P., Palmeirim J. M., Moreira F. 2010. Higher breeding densities of the threatened little bustard *Tetrax tetrax* occur in larger grassland fields: Implications for conservation. *Biol. Conserv.* 143: 2553–2558.
- Silva J. P., Pinto M., Palmeirim J. M. 2004. Managing landscapes for the little bustard (*Tetrax tetrax*): lessons from the study of winter habitat selection. *Biol. Conserv.* 117: 521–528.
- Slagsvold T. 1986. Nest site settlement by the Pied Flycatcher: Does the female choose her mate for the quality of his house or himself? *Ornis. Scand.* 17: 210–220.
- Stamps J. A. 1988. Conspecific attraction and aggregation in territorial species. *Am. Nat.* 131: 329–347.
- Suárez-Seoane S., Osborne P. E., Alonso J. C. 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. *J. Appl. Ecol.* 39: 755–771.
- Traba J., García de la Morena E. L., Morales M. B., Suárez F. 2007. Determining high value areas for steppe birds in Spain: hot spots, complementarity and the efficiency of protected areas. *Biodivers. Conserv.* 16: 3255–3275.
- Traba J., Morales M., García de la Morena E. L., Delgado M. P., Krištín A. 2008. Selection of breeding territory by little bustard (*Tetrax tetrax*) males in Central Spain: the role of arthropod availability. *Ecol. Res.* 23: 615–622.
- Ward M. P., Schlossberg S. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conserv. Biol.* 18: 519–525.
- Wiegand T., Moloney K. A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104: 209–229.
- Wolff A., Paul J. P., Martin J. L., Bretagnolle V. 2001. The benefits of extensive agriculture to birds: the case of the little bustard. *J. Appl. Ecol.* 38: 963–975.
- Worton B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.

STRESZCZENIE

[Czynniki wpływające na rozmieszczenie grup rodzinnych strepeta]

W pracy analizowano wybiórczość siedliskową i rozmieszczenie przestrzenne rodzin (samic z młodymi) strepeta w odniesieniu do miejsc występowania samców (obserwowanych głównie w okresie toków). Badania prowadzono w trzech populacjach w Hiszpanii (Belianes, Bellmunt i Ciudad Real), które różniły się zagęszczeniem strepetów i liczbą wyprowadzanych piskląt (Tab. 1).

W poszczególnych populacjach grupy rodzinne preferowały podobne siedliska — tereny odłogowane i ścierniska (Fig. 1, Tab. 2). Samice z pisklętami stwierdzane były bliżej miejsc występowania samców i tokowisk niż wynikałoby to z losowego rozmieszczenia (Tab. 3, Fig. 2). Autorzy sugerują, że takie rozmieszczenie przestrzenne może wiązać się zarówno z dostępem do obfitujących zasobów pokarmowych, jak i dawać szansę samicom na lęgi powtarzane po ewentualnej stracie. Preferowanie ściernisk może wiązać się z łatwiejszym zdobywaniem pokarmu przez pisklęta, natomiast preferowanie odłogów — z dostępnością miejsc wykorzystywanych jako schronienie.