Great bustard Otis tarda habitat selection in relation to agricultural use in southern Portugal

Authors: Moreira, Francisco, Morgado, Rui, and Arthur, Stephen

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Great bustard *Otis tarda* habitat selection in relation to agricultural use in southern Portugal

Francisco Moreira, Rui Morgado & Stephen Arthur

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We investigated habitat selection patterns of the great bustard *Otis tarda* in a dynamic agricultural landscape in southern Portugal. Combining data from 26 bustard counts with habitat mapping, we used resource selection functions to characterise habitat selection in two areas with different agricultural uses. Selection patterns were compared among areas, seasons (breeding, post-breeding and winter), and flock types (male, female and mixed) during the breeding season. Seasonal differences in selection patterns generally parallelled changes in estimated food availability. Stubbles (i.e. recently harvested fields) and stream margins were preferentially selected by all bustards during the post-breeding period, whereas cereal and fallow fields were selected during winter. During the breeding season, males selected fallow fields more than other habitat types, whereas females selected cereal fields. Habitat selection seemed to be influenced by habitat availability, with birds showing stronger selection for preferred habitats in the areas where they were less available. Great bustards used different habitat types throughout the agricultural year, and we recommend that habitat management promotes a rotational crop system that includes cereal and fallow fields.

Key words: agriculture, crops, great bustard, habitat management, habitat selection, Otis tarda, resource selection functions

Francisco Moreira & Rui Morgado, Centro de Ecologia Aplicada "Prof. Baeta Neves", Instituto Superior de Agronomia, Tapada da Ajuda, P-1349-017 Lisboa, Portugal - e-mail addresses: fmoreira@isa.utl.pt (Francisco Moreira); ruimorgado@isa.utl.pt (Rui Morgado)
Stephen Arthur, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701, USA - e-mail: steve_arthur@fishgame.state.ak.us

Corresponding author: Francisco Moreira

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In recent decades, many European landscapes created by traditional farming practices have changed due to agricultural intensification, afforestation or abandonment (e.g. Potter 1997). The extensive cereal crops of the Iberian Peninsula (also known as cereal steppes) are among the farming systems affected by these changes. Large-scale changes in land use present a threat to populations of several bird species (Suárez, Naveso & De Juana 1997), including the globally threatened great bustard *Otis tarda*. The great bustard occurs across Europe mostly in fragmented and declining populations (Tucker & Heath 1994). More than half of the world population is concentrated on the Iberian Peninsula (Alonso & Alonso 1996).

Previous studies of great bustards on the Iberian Peninsula suggest a complex pattern of habitat selection that varies according to agricultural practices and season of the year. Habitat selection in these areas is likely determined by food availability and breeding behaviour, because different habitats are used for feeding, male display and female nesting (e.g. Alonso & Alonso 1990, Helmich 1991).

We characterised habitat selection patterns of great bustards at two different lek areas in southern Portugal. Lek areas are crucial for the conservation of the species because males aggregate in these areas every spring to perform breeding displays to attract females (Morales, Alonso, Martin & Alonso 1996). Lek areas comprise a few hundred hectares and are regularly used over many years (e.g. Lane, Alonso & Martín 2001). The agricultural cycle creates a highly dynamic landscape due to activities such as sowing, ploughing and harvesting, and we investigated how frequent changes in habitat availability due to these activities affected habitat selection patterns in the areas. Furthermore, variation in agricultural use between the two areas allowed us to test for potential differences in habitat selection due to spatial differences in habitat availability.

Methods

Study areas

Our study was conducted in Castro Verde (ca 37°43'N, 7°57'W), a 65,000-ha cereal steppe where most of the Portuguese population of great bustards is concentrated (ca 800 birds). The traditional agricultural system is based on extensive cultivation of cereals in a rotation scheme, resulting in a mosaic of cereal fields, ploughed land, stubbles (recently harvested cereal fields) and fallow land. Both stubbles and fallow land are used for livestock grazing, particularly by sheep *Ovis aries* (Delgado & Moreira 2000). Two study areas including the main bustard leks were defined: Entradas (3,086 ha) and São Marcos (4,616 ha; Fig. 1). The areas were located about 6 km apart, and the majority of the land between them consisted of habitat unsuitable for great bustards (shrublands, woodlands and a river valley). Agricultural use differed between areas; Entradas had more productive soils and thus a larger area devoted to cereal cultivation and less fallow land, whereas in São Marcos the dominant land use was fallow land. During the study, the total number of individuals in the two areas ranged within 92-322 (Morgado & Moreira 2000).

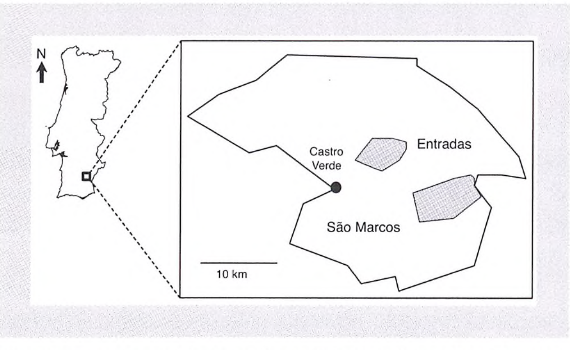

Figure 1. The Castro Verde region and the locations of the Entradas and São Marcos study areas.

Sampling seasons

We assessed habitat selection by great bustards during three seasons: winter (November-February), breeding (March-May) and post-breeding (June-October). During winter, great bustards gather in large mixed flocks and wander among suitable feeding sites. During the breeding season, flocks break up and birds concentrate around lek sites. After copulation, males progressively abandon the lek sites and gather in flocks, while females nest solitarily. During post-breeding, hens and juveniles join with males and other females in varying sized flocks (e.g. Hidalgo de Trucios & Carranza 1990, Morgado & Moreira 2000).

Bustard counts

Great bustards were counted in repeated surveys from November 1996 to October 1997 (Hidalgo de Trucios & Carranza 1990, Hellmich 1991). The study areas were travelled by automobile along fixed routes (38 km in Entradas and 57 km in São Marcos), at speeds of 10-30 km/hour. Along each route, bustards were counted from strategic observation points. The two areas were surveyed on two consecutive days (one area each day). Counts were not conducted in the middle of the day during spring and summer, because bustards are less active and more difficult to observe than in the morning and evening. Counts were made twice per month during December-February and June-August, once per month during September-November, and 3-4 times per month during March-May (to obtain more data during the breeding period). This yielded a total of 26 counts. When a flock was found, its size (including solitary birds), location and habitat type were recorded on a 1:25,000-scale map. Additionally, three types of flocks were identified during the breeding season: adult male, adult female and mixed flocks. Other flock types (e.g. females with chicks) were not included in the analyses. Outside the breeding season we were not confident in our ability to separate birds by age and sex class, and thus, combined all data for analysis.

Measuring habitat availability

Study areas were subdivided into agricultural parcels drawn on 1:25,000-scale maps. Habitat availability in the two areas was initially determined by travelling through the areas and noting land use in each parcel with the help of aerial photography obtained during November 1996. Habitat availability maps were updated by repeating this procedure at monthly intervals. The area of each habitat type was measured with a planimeter. For each bustard count we estimated habitat availability from the land use map for the corresponding month.

We defined seven habitat types: cereal fields, stubbles, fallow land (including stubbles from the previous year), ploughed fields, stream margins (areas within 5 m of river and lake shorelines), olive groves (including areas within 5 m of the grove, where olives could be found), and legume fields (in São Marcos). Cereal fields were sown in autumn and winter and most were harvested in summer. The few non-harvested cereal and legume fields remaining in summer were classified as fallow land beginning in July, as they had low vegetation and were used as pastures. Ploughed fields were classified as fallow land when they had developed a significant herbaceous vegetation cover (two months after ploughing).

Data analysis

We used selection ratios (Manly, McDonald & Thomas 1993, Arthur, Manly, McDonald & Garner 1996) to assess the relative frequency of habitat use by bustards. Because habitat availability often changed between flock counts, even within a season, we determined the ratios using a modification of Arthur et al.'s (1996) method. Our sampling unit was an observation of a flock of great bustards (≥ 1 individual). For each observation, we calculated a set of selection ratios as 1/(% availability) for the habitat type that was used and 0 for the remaining available types. Observations of bustards seen during each season were then used to derive maximum likelihood estimates of seasonal selection ratios (conceptually equivalent to the mean ratio of use to availability for the season). Estimating selection ratios required that the selection ratio for one habitat be set equal to 1.0, and selection for other habitat types estimated in relation to this reference habitat. Thus, we modified Equation (1) of Arthur et al. (1996) so that the selection ratios were estimated as:

$$\hat{w}_k = \frac{\sum_{i=1}^{D} o_{ik}}{\sum_{i=1}^{D} \frac{A_{ik}}{\sum_{j=1}^{H} A_{ij}\hat{w}_j}} \quad ,$$

where H = the number of habitat types, $\hat{w}_k$ is the selection ratio for a specific habitat type (k) from the set j = 1 to H, O_{ik} is the proportion of observations in habitat type k for observation i (either 0 or 1), A_{ik} is the proportional availability of that habitat on the day the observation was obtained, and D is the number of observations used to estimate the ratio. This equation is solved by iteration. For the first iteration, all $\hat{w}_j$ are set equal to 1.0, and new values are calculated for each $\hat{w}_k$ except the reference habitat, which is held constant at 1.0. These values are then substituted for the corresponding $\hat{w}_j$ for the next iteration, and the process is repeated until calculated values of $\hat{w}_k$ equal the corresponding $\hat{w}_j$ for all j. The magnitudes of the selection ratios indicate the intensity of selection for each type, relative to the reference type. We used fallow fields as the reference habitat, because this type was common in both areas and was used by all groups of bustards during all seasons. Thus, selection ratios > 1 indicate habitats with greater use (relative to availability) than fallow fields, whereas ratios < 1 indicate habitats with less use.

To determine if habitat use differed (relative to availability), we used a likelihood-ratio test (Manly et al. 1993, Arthur et al. 1996) to compare a (null) model that assumed equal use of all habitats and a model that allowed habitat use to differ. If the test suggested that the selection model provided a better fit to the data, then we concluded that habitat use was selective (i.e. non-random). We used a similar approach to determine if patterns of selection differed between areas or among groups of bustards. The likelihood-ratio was used to determine if a better fit was obtained by modelling each area or flock type separately, versus a model that pooled all data (Arthur et al. 1996).

To determine which habitat types were selected differently, we calculated the variance/covariance matrix for each set of selection ratios and tested the significance of differences between pairs of selection ratios using a z-test (Manly 1985: 406, Arthur et al. 1996: Appendix A). Selection ratios for habitats that were not used (ratio = 0) were assumed to differ from ratios for which the 95% confidence interval (CI) excluded 0, but not from habitats for which the 95% CI included 0. Significance of all statistical tests was set at $P < 0.05$.

Because patterns of habitat selection might differ among seasons and between study areas or sexes, we first determined patterns of habitat selection separately for bustards grouped by study area, season and flock type. This step comprised 10 separate likelihood-ratio tests: one for each study area during post-breeding and winter, and one for each of three flock types in each area during the breeding season. These tests included all habitat types that were available in each area during each season.

We then used two likelihood-ratio tests (one for each area) to determine if selection patterns differed among the three flock types during the breeding season. Finally, we used five likelihood-ratio tests to compare selection ratios between areas (one comparison each for winter and post-breeding and one comparison for each flock type during breeding). We used the z-test for each season and flock type to compare pairs of selection ratios for a specific habitat type between flocks or areas. In all of these comparisons, the models included only habitat types that were both available to and used by all groups. The primary effect of this restriction was to eliminate rare habitats. In the few cases where rare habitats were both available and used, they were discarded from the analyses because the variances of the resulting selection ratios were quite large, and tests including these types would have low power. All statistical analyses were performed using an EXCEL spreadsheet.

Results

Habitat availability

Availability of habitat types varied during the study (Fig. 2). Four habitat types (fallow land, cereal, stubble and ploughed fields) occupied more than 95% of the total area in both Entradas and São Marcos. However, 70% of agricultural land in São Marcos was fallow compared to 40% fallow land in Entradas.

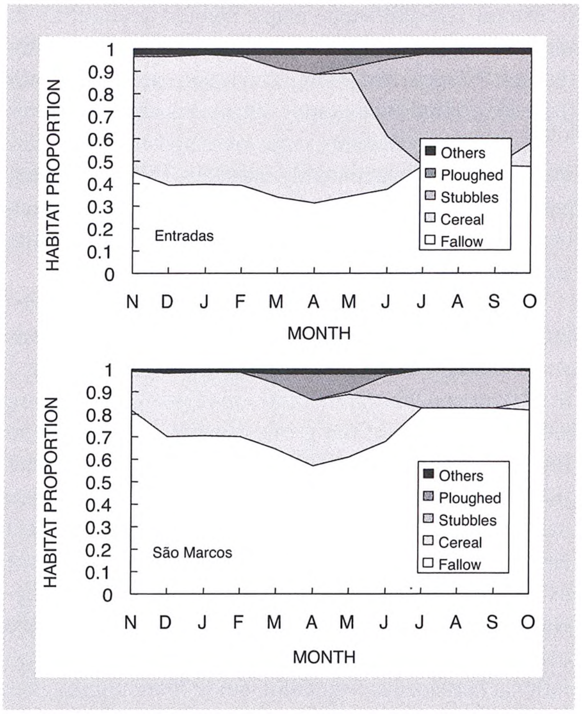

Figure 2. Monthly variations in habitat availability expressed as the proportion of the total area for great bustards in the study areas Entradas and São Marcos in Castro Verde during 1996-1997.

Habitat selection tests

For seven of 10 combinations of area, season and flock type, the selection model provided a better fit to the data than the non-selection null model (likelihood-ratio test:

Table 1. Selection ratios (w) and results of statistical comparisons between ratios for habitats used by great bustards in Entradas. N = number of great bustard flocks; na = habitat not available.

Season, flock type		Habitat type							Deviance test[a]		
		Fallow	Cereal	Stubbles	Ploughed	Olive	Legumes	Margins	Difference	df	P
Winter	w	1	0.61	na	7.29	10.78	na	0	32.23	3	<0.0001
	N	14	12		1	9					
	SD		0.22		7.54	4.48					
	Group[b]	A	A		A,B,C	B		C			
Breeding ♂♂	w	1	0.31	0	0.35	0	na	0	7.86	2	0.020
	N	15	8	0	1	0		0			
	SD		0.14		0.36						
	Group[b]	A	B	C	A,B,C	C		C			
Breeding ♀♀	w	1	0.39	0	0.36	0	na	0	5.72	2	0.056
	N	15	10	0	1	0		0			
	SD		0.16		0.37						
	Group[b]	A	B	C	A,B,C	C		C			
Breeding ♂♀	w	1	0.24	0	1.31	0	na	9.22	13.43	3	0.004
	N	12	5	0	3	0		1			
	SD		0.14		0.85			9.61			
	Group[b]	A	B	B	A,B	B		A,B			
Post-breeding	w	1	0.37	1.22	0	1.02	na	12.22	12.73	4	0.013
	N	37	2	45	0	2		3			
	SD		0.50	0.10		0.73		7.22			
	Group[b]	B	A,B,C	A	C	A,B,C		A,B,C			

[a] Deviance test comparing models that assume random use versus selective use of habitat types for each season and flock type.

[b] Ratios with the same letter did not differ (pairwise z-tests: P > 0.05). Values of 0 indicate habitats that were not used. Ratios differed from unused habitats if the 95% C.I. did not include 0.

Table 2. Selection ratios (w) and results of statistical comparisons between ratios for habitats used by great bustards in São Marcos. N = number of great bustard flocks; na = habitat not available.

Season, flock type		Habitat type							Deviance test[a]		
		Fallow	Cereal	Stubbles	Ploughed	Olive	Legumes	Margins	Difference	df	P
Winter	w	1	1.79	na	0	16.79	0	0	5.23	2	0.073
	N	14	10		0	1	0	0			
	SD		0.74			17.29					
	Group[b]	A	A		B	A,B	B	B			
Breeding ♂♂	w	1	0.29	0	0.11	0	0	3.15	24.19	3	<0.0001
	N	64	9	0	1	0	0	1			
	SD		0.10		0.10			3.18			
	Group[b]	A	B	C	B,C	C	C	A,B,C			
Breeding ♀♀	w	1	3.10	0	0.27	0	4.21	7.22	31.88	4	<0.0001
	N	28	41	0	1	0	3	1			
	SD		0.76		0.26		2.56	7.35			
	Group[b]	B	A	C	C	C	A,B,C	A,B,C			
Breeding ♂♀	w	1	0.91	0	0.28	0	0	6.27	4.50	3	0.212
	N	33	14	0	1	0	0	1			
	SD		0.28		0.28			6.37			
	Group										
Post-breeding	w	1	0.92	2.06	0	0	2.53	8.85	25.81	4	<0.0001
	N	117	9	45	0	0	2	4			
	SD		0.33	0.36			1.83	4.46			
	Group[b]	B	B	A	C	C	A,B,C	A,B,C			

[a] Deviance test comparing models that assume random use versus selective use of habitat types for each season and flock type.

[b] Ratios with the same letter did not differ (pairwise z-tests: P > 0.05). Values of 0 indicate habitats that were not used. Ratios differed from unused habitats if the 95% C.I. did not include 0.

P < 0.05; Tables 1 and 2). For models winter/São Marcos and breeding/Entradas/females, there was weak evidence of non-random habitat use, although they were not statistically significant (P = 0.07 and P = 0.06, respectively). Only one model (breeding/São Marcos/mixed) provided no evidence of habitat selection (P = 0.21). In spite of the variability of the estimates of individual selection ratios, several significant differences were evident. During winter, olives were selected more than fallow and cereal, which were selected more than stream margins in Entradas. In São Marcos, selection of olives was not significantly different from the selection of other types. Selection of cereal and fallow land was greater than selection of ploughed land, legumes and stream margins in São Marcos. During the breeding season, males selected fallow fields significantly more than cereals, stubbles and olives in both areas, and cereals were selected more than stubbles and olives. Females and mixed flocks also selected fallows more than cereals during the breeding season in Entradas, but in São Marcos, females selected cereals more than fallows. During the post-breeding season, stubbles were selected more than fallows, which were selected more than ploughed land in both areas.

Table 3. Habitat selection ratios and comparisons of selection models among three flock types in Entradas and São Marcos during the breeding season. Selection ratios on the same row with the same superscript letter were not significantly different (z-test: P > 0.05). Likelihood-ratio test compares a null model (NM), which pools across habitat or flock types, with a model that allows selection (SM) to differ among habitat or flock types.

	Selection ratio			Variance		Likelihood-ratio test				
	Fallow	Cereal	Ploughed	Cereal	Ploughed	NM	SM	Difference	df	P
Entradas										
Pooled	1^{a}	0.320^{b}	$0.629^{a,b}$	0.007	0.089	140.40	119.86	20.54	2	<0.001
Males	1^{a}	0.310^{b}	$0.349^{a,b}$	0.018	0.131	46.18	38.31	7.86	2	0.020
Females	1^{a}	0.392^{b}	$0.358^{a,b}$	0.026	0.137	47.03	41.31	5.72	2	0.057
Mixed	1^{a}	0.241^{b}	$1.304^{a,b}$	0.016	0.712	47.20	37.42	9.78	2	0.008
Comparison among flocks						119.86	117.04	2.82	4	0.589
São Marcos:										
Pooled	1^{a}	1.084^{a}	0.184^{b}	0.028	0.012	289.79	273.47	16.32	2	<0.001
Males	1^{a}	0.296^{b}	0.113^{b}	0.011	0.013	89.59	66.72	22.87	2	<0.001
Females	1^{a}	3.097^{b}	0.261^{c}	0.577	0.071	131.87	103.52	28.35	2	<0.001
Mixed	1^{a}	$0.908^{a,b}$	0.278^{b}	0.084	0.080	68.32	65.90	2.42	2	0.298
Comparison among flocks*						273.47	236.14	37.33	4	<0.001

* Pairwise comparisons between flock types. For cereal: males versus females, z = -3.65, P < 0.001; males versus mixed, z = -1.99, P = 0.05; females versus mixed, z = 2.69, P = 0.01. For ploughed, there were no significant differences between flock types.

Table 4. Habitat selection ratios and comparisons of selection models between the areas Entradas and São Marcos for three flock types during the breeding season. Selection ratios on the same row with the same superscript letter were not significantly different (z-test: $P > 0.05$). Likelihood-ratio test compares a null model (NM), which pools across habitat types or study areas, with a model that allows selection (SM) to differ among habitat types or study areas. Values of z and P in habitat columns compare selection ratios for that habitat between study areas.

	Selection ratio			Variance		Likelihood-ratio test				
	Fallow	Cereal	Ploughed	Cereal	Ploughed	NM	SM	Difference	df	P
Females										
Pooled	1^{a}	1.630^{a}	0.164^{b}	0.134	0.028	163.45	150.39	13.06	2	0.001
Entradas	1^{a}	0.392^{b}	$0.359^{a,b}$	0.026	0.137	47.03	41.31	5.72	2	0.057
São Marcos	1^{a}	3.097^{b}	0.261^{c}	0.576	0.07	131.87	103.52	28.35	2	<0.001
Comparison between areas						150.39	144.83	5.56	2	0.062
z		-3.48	0.21							
P		<0.001	0.830							
Males										
Pooled	1^{a}	0.299^{b}	0.171^{b}	0.007	0.015	135.77	105.61	30.16	2	<0.001
Entradas	1^{a}	$0.310^{a,b}$	0.349^{b}	0.018	0.130	46.18	38.31	7.86	2	0.02
São Marcos	1^{a}	0.296^{b}	0.114^{b}	0.011	0.013	89.59	66.72	22.87	2	<0.001
Comparison between areas						105.61	105.03	0.58	2	0.75
Mixed flocks										
Pooled	1^{a}	0.579^{b}	$0.707^{a,b}$	0.027	0.138	115.52	111.54	3.98	2	0.136
Entradas	1^{a}	0.241^{b}	$1.303^{a,b}$	0.016	0.712	47.20	37.42	9.78	2	0.008
São Marcos	1^{a}	$0.908^{a,b}$	0.277^{b}	0.084	0.008	68.32	65.90	2.42	2	0.298
Comparison between areas						111.54	103.32	8.22	2	0.016
z		-2.10	1.29							
P		0.035	0.227							

Habitat selection patterns during the breeding season

During the breeding season, only fallows, cereal fields and ploughed fields were used by all flock types in both areas (Table 3). The likelihood-ratio test indicated a significant difference in selection pattern among flock types in São Marcos ($P < 0.001$). This difference was due to the selection of cereal fields, which differed significantly among all flock types (paired z-tests: $P < 0.05$). Females selected cereal fields over fallows, mixed flocks selected the three habitat types equally, and males selected fallows over cereal fields. Selection of ploughed land (compared to fallows) was similar among flock types ($P > 0.05$). For Entradas, both the likelihood-ratio test ($P = 0.589$) and the z-tests ($P \geq 0.30$) showed a similar pattern of habitat selection by the three flock types.

Habitat selection patterns in the two study areas

Because there was evidence that selection during the breeding season differed among flock types in São Marcos, we compared areas separately for each flock type (Table 4). For males, selection did not differ between areas (likelihood-ratio test: $P = 0.75$; all z-tests: $P > 0.5$). There was a different pattern of habitat selection between areas among females and mixed flocks, with cereal fields being more strongly selected in São

Table 5. Habitat selection ratios and comparisons of selection models between the areas Entradas and São Marcos during the post-breeding and winter seasons. Selection ratios on the same row with the same superscript letter were not significantly different (z-test, $P > 0.05$). Likelihood-ratio test compares a null model (NM), which pools across habitat types or study areas, with a model that allows selection (SM) to differ among habitat types or study areas. Values of z and P in habitat columns compare selection ratios for that habitat between study areas.

	Selection ratio			Variance		Likelihood-ratio test				
	Fallow	Cereal	Stubbles	Cereal	Stubbles	NM	SM	Difference	df	P
Post breeding										
Pooled	1^{a}	0.441^{b}	0.813^{a}	0.023	0.023	394.67	405.44	10.78	2	0.005
Entradas	1^{a}	0.365^{b}	1.217^{a}	0.075	0.073	129.65	125.88	3.77	2	0.152
São Marcos	1^{a}	0.930^{a}	2.064^{b}	0.116	0.131	265.01	249.58	15.44	2	<0.001
Comparison between areas						405.44	375.46	29.98	2	<0.001
z		-1.29	-1.87							
P		0.20	0.06							
Winter										
Pooled	1^{a}	1.003^{a}		0.089		74.50	74.50	0	1	0.992
Entradas	1^{a}	0.616^{a}		0.005		39.12	37.60	1.52	1	0.218
São Marcos	1^{a}	1.793^{a}		0.553		35.38	33.49	1.89	1	0.169
Comparison between areas						74.50	71.09	4.41	1	0.06
z		-1.50								
P		0.13								

Marcos (likelihood-ratio tests: $P \leq 0.06$; z-tests comparing selection for cereal fields: $P < 0.005$). There was strong evidence of a different pattern of selection for fallows, cereal fields and stubbles between areas (likelihood-ratio test: $P < 0.001$) during post-breeding (Table 5). This pattern may have been due to stubbles being more strongly selected in São Marcos, although this difference was not significant ($P = 0.06$). During winter, only cereal fields and fallow land were used in both areas (see Table 5). Neither the likelihood-ratio test ($P = 0.06$) nor the z-test ($P = 0.13$) indicated a significant difference in selection between areas.

Discussion

Habitat selection patterns during the breeding season

The pattern of habitat selection by great bustards in Castro Verde may have differed from other locations in the Iberian Peninsula because habitats varied as a result of different agricultural systems (e.g. Alonso & Alonso 1990, Hellmich 1991, Lane et al. 2001). For example, in northwestern and central Spain (Villafafila, Salamanca, Leon and Madrid) cereal and leguminous crops (mainly lucerne *Medicago sativa*) are far more abundant than natural pastures (similar to fallow land), which occupy < 10% of the agricultural area (Alonso & Alonso 1990, Martínez 1991, Pescador & Peris 1996). In these northern regions, lucerne is available throughout the year and is strongly preferred by great bustards (Alonso & Alonso 1990, Martínez 1991, Peris, Corrales, Gonzalez & Velasco 1992). Leguminous crops in Castro Verde are rare, not available during all seasons, and exclude lucerne. Roadside borders are also an important habitat in northern regions, particularly during summer when this habitat supports a high arthropod biomass (e.g. Alonso & Alonso 1990). Edges of roads and fields were not considered a separate habitat type in Castro Verde because habitat characteristics change abruptly at field edges and the borders between roads, and adjacent fields do not represent distinct habitats. In southern Spain, the agricultural landscape is similar to Castro Verde, with a high proportion of fallow land and an absence of lucerne. The pattern of habitat selection in this region (Hidalgo de Trucios & Carranza 1990, Hellmich 1991) is more similar to the one in Castro Verde.

Olive groves do not occur in most areas where great bustards have been studied, although Lane et al. (2001) mentioned the potential importance of this habitat in the Madrid area. In southern Spain (Andalucia) great bustards were observed adjacent to an olive grove and fed on olives during winter (Redondo & Tortosa 1994). Use of olive groves by great bustards likely depends on availability and patch characteristics such as size and tree density. The use of stream margins has not been described elsewhere except in the Caceres region during July-September (Hidalgo de Trucios & Carranza 1990).

As in previous studies, our results suggest that food abundance and breeding behaviour are important determinants of habitat selection patterns in Castro Verde. During post-breeding, selection was strongest for stubble fields and stream margins. During this season, great bustards feed on arthropods, seeds and plants (Palacios, Garzón & CastroViejo 1975, Lane, Alonso, Alonso & Naveso 1999). Stream margins provide both food and water (e.g. Borralho, Rito, Rego, Simões & Vaz Pinto 1998) and lack trees or tall shrubs which constitute unsuitable habitat. Both seeds and arthropods, particularly grasshoppers, are abundant in stubble fields, which serve as excellent foraging areas (Telleria, Santos, Alvarez & Sáez-Royuela 1988, Hellmich 1991, Díaz & Telleria 1994, Delgado 1997).

During winter, we identified olive groves, cereal and fallow fields as preferred habitats. The winter diet of bustards is mainly green plant material and seeds (e.g. Lane et al. 1999). Other studies reported use of olive groves by bustards (Redondo & Tortosa 1994, Lane et al. 2001), and bustard droppings in our study areas frequently contained olive seeds. Furthermore, other studies have shown that seeds and seedlings are typically abundant in cereal fields (e.g. Pescador & Peris 1998) and fallow fields (including stubbles from the previous summer; Díaz & Telleria 1994, Alonso, Alonso & Bautista 1994).

Our results also indicated that during the breeding season males showed stronger selection for fallow fields than for all other habitat types. This habitat is suitable for breeding displays because it has abundant food and short vegetation providing good visibility (Hellmich 1991). Females might be expected to show stronger selection for cereal fields because they were preferred nesting habitat in Castro Verde (Morgado & Moreira 2000), but this pattern was only observed in São Marcos. However, females may have been less detectable in the larger areas of cereal fields in Entradas, if they hid in taller vegetation. Alternatively, the intensity of selection for a preferred habitat may be partly a function of the availability of that habitat type.

Is habitat selection influenced by availability?

Mysterud & Ims (1998) suggested that the relative use of a particular habitat might change as availability changes. One consequence of this would be that conventional analyses of habitat selection would indicate preference for a necessary habitat if it were rare, but not if it were common (Mysterud & Ims 1998). Differences in habitat selection patterns by great bustards in our study were consistent with differences in habitat availability. Selection ratios for preferred habitats were generally higher in areas where they were less abundant. Outside of the breeding season, bustards are more abundant in Entradas than in São Marcos (Morgado & Moreira 2000). Entradas probably is more important as a feeding area (larger proportion of cereal fields) and constitutes a secondary breeding ground compared to São Marcos. Further, seasonal movement of birds is likely to occur between these two (and other) areas. Birds that stayed in São Marcos during post-breeding and winter showed stronger selection for the comparatively scarcer habitats that provide food (cereal and stubble fields). The same pattern was evident during the breeding season when the most important nesting habitat (cereal fields) was more strongly selected by females in the area where it was scarcer. In this latter situation, detectability could have contributed to the observed result, but this was unlikely to occur during post-breeding and winter, when the vegetation in the cereal and stubble fields was very low.

Assumptions and limitations of the data

Estimation of selection ratios and resource selection functions require that resource units be sampled randomly and independently (Manly et al. 1993). We tried to maintain independence between observations by considering flocks as the sampling unit, instead of individuals. This reduced the sample size, particularly during winter, when great bustards gather in large flocks (Morgado & Moreira 2000). Even so, flocks might be attracted to each other, especially during the breeding season. If this were the case, estimates of selection indices could still be meaningful but standard errors might not indicate the true variation in the population (Manly et al. 1993). Females nesting in cereal fields could have been overlooked. Thus, we may have underestimated selection indices for this habitat type during the breeding season.

Another important assumption is that individuals (or flocks) have unrestricted and equal access to all available resource units. We believe this was true because the dispersal capabilities and home ranges of great bustards (e.g. Alonso, Alonso, Martin & Morales 1995, Alonso, Morales & Alonso 2000, Morales, Alonso, Alonso & Martin 2000) are large in comparison to the dimensions of our study areas.

Other studies (e.g. Hellmich 1991, Lane et al. 2001) have shown that some variables not considered in our study, such as man-made features (villages, roads, tracks and buildings), hunting, agricultural activities and livestock, might influence habitat selection by great bustards.

Conservation implications

Our results showed that patterns of habitat selection by great bustards change throughout the year, probably in response to changing patterns of food availability and the need for specific habitat features for nesting and breeding displays. Thus, a mosaic of habitat types seems essential for maintaining this population. In this context, both agricultural intensification and land abandonment are expected to be detrimental for great bustards, as they will simplify landscape composition and lead to a loss of necessary habitats (Fig. 3). The mosaic results from a low-profitability rotational crop system that can only be maintained by providing financial support to farmers, usually through agri-environmental policies. The priority for habitat management in our study areas should be to maintain habitat types suitable for displaying males (fallow fields, in particular), because the occurrence of lek grounds is the main reason for their high conservation value. Our results also suggest that cereal fields near lek areas are important for nesting females and should be promoted. Although great bustards used olive groves during winter, we do not recommend that

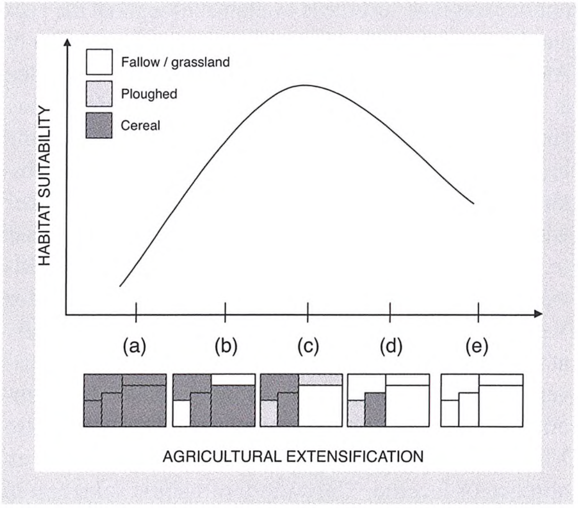

Figure 3. Hypothetical model of habitat suitability for great bustards as a function of agricultural landscape structure across a gradient of agricultural extensification in southern Portugal. Habitat suitability is lowest in intensively farmed land (a), maximum in a mosaic landscape dominated by fallow land (c) and decreases again in a landscape dominated by grassland and no crop farming (e). Departing from an ideal situation (c), both agricultural intensification (towards a) and agricultural abandonment (towards e, accompanied by shrub encroachment) will be detrimental for great bustards.

olive groves be planted in our study areas because olive groves are unsuitable habitat during the breeding season. Winter habitats are probably less limiting than lek grounds for this specific population. Lastly, further studies should aim to clarify habitat use-availability relationships and evaluate the potential importance of regional variation in land use types. If this relationship holds, then important habitats for great bustards should be promoted in regions where they are scarce.

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