



Nest-site selection by Great Bustards *Otis tarda* suggests a trade-off between concealment and visibility

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Great Bustards *Otis tarda* have expanded their habitat range from historical occupancy of natural steppes to arable farmland, where the species initially benefited from favourable feeding conditions. More recently, the species has suffered severe declines due partly to agricultural intensification. Nest losses and juvenile mortality are amongst the factors most seriously affecting survival probabilities of many populations of this endangered species, suggesting that management of nesting habitats would bring conservation benefits. We studied nest-site selection in a Great Bustard population of central Spain by radiotracking 42 females for periods of between 1 and 4 years. Females selected nest-sites in fallows or cereal fields, in areas of low patch-type diversity, far from human infrastructure, and with good horizontal visibility. These results suggest that females look for shelter, but also need to have good visibility while incubating, and they support the hypothesis that nest selection is a trade-off between concealment and visibility. We interpret both preferences as adaptations to reduce predation pressure, one of the main causes of nest failure in this species. Nests were placed on slopes significantly orientated to the southeast, which suggests that females also seek sites protected from the cold north-westerly winds that are prevalent in the study area. To reduce nest destruction, harvesting should be delayed as long as possible and habitat conservation measures should not be restricted to lek sites but also include nesting areas, which are frequently located far from leks.

Keywords: farmland birds, nest predation, nesting habitat, visual field.

The Great Bustard *Otis tarda* is a ground-dwelling steppe bird inhabiting lowlands, river valleys and open country areas of the Palaearctic region (del Hoyo *et al.* 1996). Its range probably reached its maximum extent during the 18th century due to human clearance of forest areas, allowing the species to spread from natural steppes to arable land (Glutz *et al.* 1973, Cramp & Simmons 1980, Klafs 1985). During the 20th century, the species suffered dramatic declines and today it is considered Globally Threatened (BirdLife International

2000). It seems that hunting, agricultural intensification and habitat fragmentation due to human activity have played a decisive role in these declines (Heredia *et al.* 1996). The Spanish population has recovered since 1980, when a hunting ban was established, and is now apparently stable at 27 500–30 000 birds (around 60% of the world population; Palacín & Alonso 2008), with slight increases in some regions and decreases in marginal areas. The species is still threatened by habitat fragmentation in most Spanish regions due to agricultural change and built development (Palacín *et al.* 2004). In our study area in central Spain, numbers are currently stable, but populations

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remain threatened by urban expansion, changes in farming practices and some probable negative consequences of conspecific aggregation, a process by which birds are concentrating at high-quality areas and disappearing from others where habitat has deteriorated (Alonso *et al.* 2003, 2004, Martín 2008). Population viability analyses have revealed that nest losses and juvenile mortality are crucial parameters affecting the survival probabilities of small populations (Streich *et al.* 1996, Lane & Alonso 2001, Martín 2008). A field study in northern Spain recorded 57% pre-fledging chick mortality, attributed to both destruction by agricultural machinery and predation (Ena *et al.* 1987). The main predators identified were corvids and Red Foxes *Vulpes vulpes*, followed by various raptor species. In central Spain, up to 39% of clutches are lost before hatching, due to predation, disturbance and inclement weather (Magaña 2007). Recent studies have shown that predator control measures have contributed towards the stabilization of endangered Great Bustard populations in central Europe (Farago *et al.* 2001, Langgemach & Bellebaum 2005). Thus, management of the nesting habitat seems to be an effective measure in improving the conservation status of the species. However, few studies have been carried out on its nesting habitat preferences. Some studies have reported that Great Bustards select cereal fields and pasture land as nesting habitat (Farago 1986, 1987, Petrick 1996, Morgado & Moreira 2000). In dry cereal farmland, these are the habitats with the densest vegetation in spring, suggesting that Bustards are seeking to conceal their nest, as they probably did in natural steppes before adapting to farmland habitat. Because nest predation is the primary source of reproductive failure in many species (Ricklefs 1969, Martin 1988, 1992), birds are expected to select nest locations that minimize nest predation risk (Martin 1988, Hass 1998, Sieving & Willson 1998, Forstmeier & Weiss 2004, Miller *et al.* 2007). Nest-site selection may be particularly important in ground-nesting birds, whose nests are usually subject to particularly high rates of predation (Suárez *et al.* 1993, Goodrich & Buskirk 1995, Yanes & Suárez 1995, Amar *et al.* 2004, Jackson *et al.* 2004, Whittingham & Evans 2004, Langgemach & Bellebaum 2005, Isaksson *et al.* 2007). Nest concealment is a common adaptation that usually reduces predation risk (Martin 1992). However, a well-concealed nest may prevent incubating adults from having a good view of their

surroundings. Götmark *et al.* (1995) suggested that this might hinder early detection of approaching predators, and in colonial birds also hinder some useful forms of conspecific communication. Thus, nest location may reflect a trade-off between concealment and visibility (see also Spencer 2002, Amat & Masero 2004, Forstmeier & Weiss 2004).

Here we analyse nest-site selection by Great Bustards in relation to topography, land use and field diversity, the numbers, and distribution of birds in the lek areas and human infrastructures in central Spain. Although numerous studies have examined habitat selection of this species (Alonso & Alonso 1990, Hidalgo de Trucios & Carranza 1990, Hellmich 1991, Martínez 1991a,b, Redondo & Tortosa 1994, Pescador & Peris 1996, Onrubia *et al.* 1998, Morgado & Moreira 2000, Lane *et al.* 2001, Osborne *et al.* 2001, Suárez-Seoane *et al.* 2002, Fonseca 2004, Moreira *et al.* 2004), this is the first to assess habitat preferences of nesting females using a multivariate approach. The aims were to quantify the factors determining nest-site selection in the Great Bustard, to develop a multivariate model to evaluate habitat patches as potential nesting areas and to assess whether nest-site selection in Great Bustards supports the trade-off hypothesis proposed by Götmark *et al.* (1995).

METHODS

Study area

The study was conducted in the Important Bird Area 074 (Talamanca-Camarma) and its surroundings (40°40'N, 3°25'W, between Madrid and Guadalajara provinces, see Fig. 1). This area holds a population of approximately 1100 Great Bustards (Alonso *et al.* 2003). To measure variables for analysis we selected an area of 769 km² that included all nest-sites that were located through radiotracking (see below). The terrain is flat to slightly undulating, with a mean elevation of 740 ± 83 m asl. It is primarily dedicated to cereal cultivation (mainly wheat *Triticum aestivum* and barley *Hordeum* spp.), with smaller fields of legumes *Vicia* spp., olive *Olea europaea* groves and grapevines *Vitis vinifera*. Most cereal is grown in a traditional 2-year rotation system (Suárez *et al.* 1997), which creates a dynamic mosaic of ploughed land, cereal and stubble patches across the region (see details in Lane *et al.* 2001, Alonso *et al.* 2003). Cereal fields are harvested during

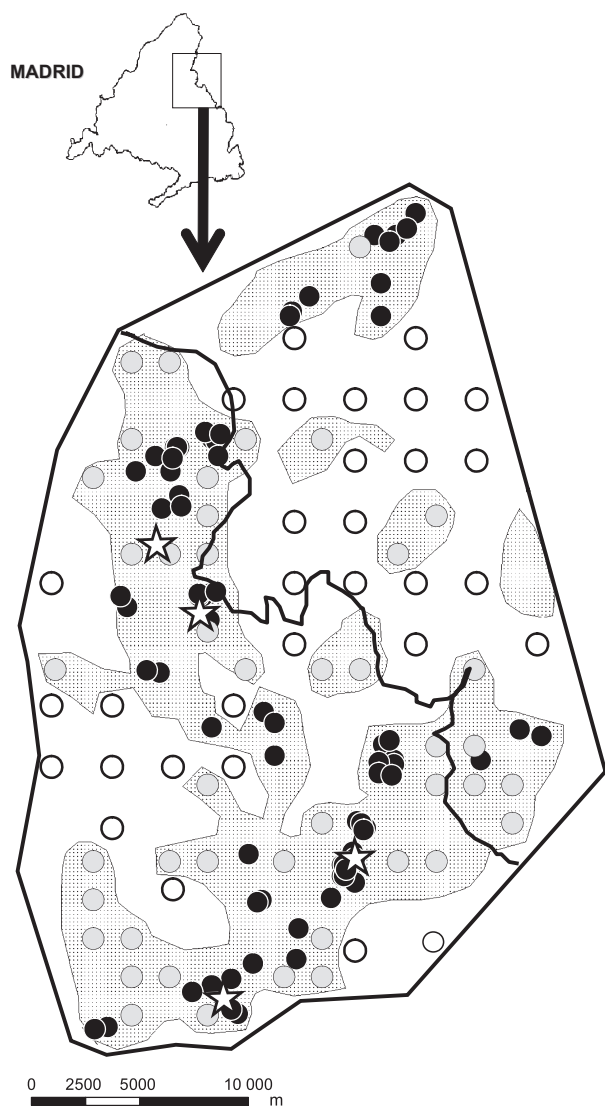


Figure 1. Map of the study area showing its location in Madrid region (central Spain), nest-sites (black dots), control sites (shaded dots = C1, open dots = C2) and centres of the four leks where the females were captured (stars). Shaded patches show the areas used by the birds through the year, as obtained from 29 complete censuses of the study area performed between 1995 and 2003 (seven in spring, 22 in other seasons). $n = 42$ nest-sites 44 C1 sites and 30 C2 sites.

late June to early July. Stubbles and fallows are also used for sheep grazing.

Locating nests

From 1998 to 2003, we radiotracked 42 female Great Bustards using Telonics TR2-TS1 telemetry receivers. Four birds were captured by chasing them down when they were 3–10 weeks old and

still dependent on their mothers, and 38 using rocket-nets when they were fully grown. All birds were marked with both PVC wing-tags and backpack-mounted radio-transmitters (TW3 $2 \times$ AA units, 60 g; Biotrack Ltd, Wareham, UK) using an elastic band as harness, and located by triangulation (White & Garrott 1990) and by subsequent visual observation with a 20–60 \times telescope at least once per month throughout their lives. When the birds moved outside the range usually covered by ground tracking, E-24 Beechcraft aeroplanes from the Spanish Air Force were used to locate them from the air. During the nesting period (May–June) we increased the tracking frequency and checked all radiotagged individuals on average every 6 days (range = 2–9 days, $sd = \pm 2$) but generally we did not establish visual contact with females to avoid flushing them from the nest. Instead, the position of the birds was determined through triangulation of two or more bearings taken from the edges of the field where the female was found, and approaching at least once to within approximately 50 m of the bird. When a female was located in the same place over two or more consecutive weeks we assumed it was nesting and considered the average of those locations as its nest-site. Four locations in the same place were interpreted as a successful nesting attempt (eggs hatched), and two or three locations as unsuccessful (not hatched), as incubation may last up to 28 days (Glutz *et al.* 1973). Given our several years of experience of radiotracking Great Bustards in this area, the reliability of directional antennas in flat terrain and the short triangulation distance, we believe our error in locating a nest-site was not more than *c.* 5 m, a much smaller distance than the size of the pixels or circles used to define habitat variables (see below). All analyses were carried out exclusively with first clutches, so the few replacement clutches found ($n = 4$) were excluded.

Control sites

We compared the characteristics of nest-sites with those of two different sets of control sites. The first set (C1) consisted of 44 points uniformly distributed across the habitat used by the Great Bustards within the study region (Fig. 1). However, these control sites could include or be close to some sites actually used by non-marked females for nesting. The only way to select a control sample of sites

where we knew for sure that Great Bustards were definitely not nesting would have been to perform regular searches walking through the whole area and flushing all incubating females. However, we did not consider this method in order not to disturb the nesting birds. Therefore, to confirm the patterns found through comparison with C1 sites, we also used a second set of control sites (C2), which consisted of 30 points distributed across areas not regularly used by the birds and, as such, almost surely not including any nesting site (Fig. 1). We distinguished between areas used and not used by means of Great Bustard locations obtained during 29 complete censuses of the study area performed between 1995 and 2003 (seven in spring, 22 in other seasons; Alonso *et al.* 2003, unpubl. data). During these censuses, we surveyed the whole study area including all known lek sites, their immediate surroundings, and other areas with suitable habitat. Each census was conducted by two or three teams of two people operating from four-wheel drive vehicles with binoculars and telescopes. We delineated the area used by Bustards by joining all locations of birds obtained during the censuses through a minimum convex polygon. The areas between were defined as non-used areas. This double-control design allowed us to compare nest-site features with features of sites where Great Bustards are present during the rest of the year and with those from which Great Bustards are normally absent. We could therefore identify the specific nest-site characteristics selected by nesting females independently of whether the habitat is used or not used by the species for other activities.

Habitat variables

We analysed four groups of explanatory variables that might influence nest-site selection (Table 1). The first group described the topography of the study area and comprised seven variables extracted from a digital terrain model (DTM) with a spatial resolution of 25 m (25 × 25 m pixels, ~0.06 ha; Geographic Database on Land Use of the Comunidad de Madrid Consejería de Obras Públicas, Urbanismo y Transportes). The models of slope, orientation and roughness are derivatives of the DTM. The orientation and slope variables were created using the IDRISI32 (Clark Labs 2000) orientation and slope functions, respectively (Eastman 2003). The visual field of incubating females was estimated from a DTM with a spatial resolution of

25 m (25 × 25 m pixels, ~0.06 ha; Geographic Database on Land Use of the Comunidad de Madrid, Consejería de Obras Públicas, Urbanismo y Transportes). The DTM allows one to choose the height from which one wishes to measure visual field. We chose the height of 1 m because this was similar to the height of a standing female with stretched neck scanning for predators from the nest. This is also clearly higher than the average height of cereal during incubation (50–80 cm between mid April and late May, own unpubl. data), and thus we thought that a female could scan for predators above the cereal plants. The second group of explanatory variables reflected land use and habitat diversity. We considered the following land-cover types: ploughed, cereal, fallow (fields uncultivated for several years, with natural herbaceous vegetation), grassland, other used substrates (vineyards, olive groves, legumes, uncultivated land), and substrates not used by the Bustards during other seasons (river courses, paved roads, tracks, buildings, woodlands). Number of fields, and proportion, diversity and interspersion of land-cover types were measured in a circle of 500 m radius around focal points (nest-site or control site) from aerial photographs and digital maps (1:10 000). To define diversity we used the Shannon–Weaver index, $H = -\sum(P_i \ln P_i)$, where P_i is the proportion of area covered by each land-cover type. Interspersion was defined as the number of land-cover type changes counted along both a north–south axis and a west–east axis within the 500-m-radius circle. A third group of variables was included to take account of the influence of human-made features, by measuring the minimum distance from nest-sites or control points to buildings, roads and power lines and the area occupied by such human-made features around the focal point. A final group of variables accounts for various local population characteristics around the focal points describing the distribution and abundance of conspecifics and the distance to the lek centre. These variables were taken from Great Bustard numbers and locations obtained during the 29 censuses performed between 1995 and 2003 (see above). Agricultural use data were collected on an annual basis and the appropriate year selected for analysis. As for social factors, we used overall means through the study period, as lek centres were extremely stable, and bird numbers and distribution at each lek remained quite steady through the years.

Table 1. Predictor variables used to characterize the habitat at Great Bustard nests and control sites. Level indicates whether the variable was measured from a 25 × 25 m pixel or in a circle of 500 m radius around nest or control locations.

Group	Variable	Level	Range of values	Description
Topography	Altitude (m)	Pixel	600–1500	Altitude above sea level
	Slope	Pixel	0–100	% Maximum difference in altitude around the pixel among four directions: N, W, E and S
	Orientation	Pixel	0–360	Orientation of maximum downward slope
	Roughness (%)	Pixel	0–100	Variability in slopes of all neighbour pixels to nest or control site (derivative of the slope)
	Distance to water course (m)	Pixel	0–2085	Distance to the nearest watercourse
	Closest obstacle (m)	Pixel	50–195	Distance to the nearest visual obstacle (hollow, cliff, etc.)
	Visual field (ha)	Pixel	2–542	Unobstructed visual area from a point located at 1 m height above nest or control up to 2000 m maximum radius
Land use and habitat diversity	Patch type (%)	Circle	0–100	Percentage surface area of each substrate type (see types identified in Methods)
	Number of fields	Circle	5–236	Number of fields in the circle
	Diversity	Circle	0–1.47	Shannon–Weaver diversity index (combining number and surface area of fields)
	Interspersion	Circle	3–21	Number of changes in land use along two main axes (N–S and W–E)
Human-made features	Buildings (m)	Pixel	0–3225	Distance to the nearest building
	Roads (m)	Pixel	0–3183	Distance to the nearest paved road
	Power lines (m)	Pixel	25–11 857	Distance to the nearest high-voltage power line
	Surface area of human infrastructures (%)	Circle	0–100	Percentage area occupied by these and other human infrastructures (tracks, gravel pits, etc.)
Social features	Distance to lek centre (km)	Pixel	0.20–17.95	Distance to the nearest lek centre (lek centre was the average location of the male flock at display time, 1 March–15 April)
	Distance to lek centroid (km)	Pixel	1.12–33.07	Distance to the centroid of the three nearest leks
	Mean flock size in spring	Circle	0–34	Mean number of birds per flock in spring
	Mean flock size other seasons	Circle	0–48	Mean number of birds per flock in other seasons
	Number of flocks in spring	Circle	0.00–3.14	Mean number of flocks in spring
	Number of flocks other seasons	Circle	0.00–1.77	Mean number of flocks in other seasons

We used a 500-m radius because this is approximately the maximum distance covered by chicks during their first weeks after hatching (own unpubl. data), so these circles are indicative of the environmental characteristics of both the nesting and the early chick-rearing period. As control focal points we selected the top left corner of 25 × 25 m pixels of the DTM used to extract the values of the variables (see below). We used the samples of pixels separated by 1.75 km (C1) or 2.80 km (C2), excluding all sites located in urban areas.

To prevent overlapping of nest-site and control circles we discarded control points that were less than 1 km from the nearest nest-site. All variables were measured using the software ARCGIS 9 (Environmental Systems Research Institute Inc. 2005) or IDRISI32 (Clark Labs 2000).

Data analyses

Land-cover selection

From the land-cover availability and usage data, we calculated habitat selection indices (Ivlev selection index (ISI), Ivlev 1961) as $ISI = (r_i - p_i)/(r_i + p_i)$ where r_i is the usage frequency of patch type i and p_i is the availability of the same patch type. Values of ISI vary between -1 (patch type avoided) and $+1$ (maximum positive selection of the patch type). Values equal or close to zero indicate no preference for the corresponding patch type.

Factors affecting nest-site selection and nesting success

Variables were log-transformed (continuous variables) or arcsine-transformed (percentages). Mean values for the different variables collected at

nest-sites and control points were first compared through univariate analysis using Student's *t*-tests. To avoid pseudoreplication, for females with multiple nest locations we averaged the environmental characteristics of their nests on consecutive years and used one data point for each female in the analysis of nest-site selection. As females remained as a rule very faithful to their nest-site in consecutive years (see below), averaging features from various years for some females probably caused a negligible reduction in variance and was useful to capture a more precise characterization of the nest-site preferred by each female. However, to corroborate the results, we repeated the analyses using only first-year nest locations for each female. The statistical significance of the mean vector indicating 'Orientation' was tested by the Rayleigh test (Batschelet 1981), and later nest and controls were compared using the Mardia–Watson–Wheeler test (Batschelet 1981). All variables were then entered into a General Discriminant Analysis (GDA), following a forward stepwise process, with values $F = 4$ and $F = 3.9$, respectively, to enter and remove. As a first step, GDAs were performed for each of the four groups of predictor variables (topography, land use and habitat diversity, human-made features, and social characteristics), and later all habitat variables were analysed together. To assess whether nesting success was affected by nest-site selection, we compared the fate of nests (dependent variable, hatched vs. not hatched) with all variables of Table 1 showing significance in the GDA (independent variables), through logistic regression analysis (Hosmer & Lemeshow 1989, Shaffer 2004). Finally, we used chi-square tests to compare nest fate among land-cover types. Data were analysed using STATISTICA version 6.0 (StatSoft 2001).

RESULTS

Nest-site fidelity

Between 1998 and 2003, we located 76 nests of 42 marked females (19 females with single-year locations, 23 with multiple-year locations: 14 of these on two consecutive years, seven on three and two on four). Females tended to nest each year close to where they nested in the previous year (median distance between years = 220 m). The maximum distances between nest locations from consecutive years were 4.27, 19.21 and 24.53 km. The first

two corresponded to females moving from sites where they started their first-year nesting attempt late in the season and failed during the first incubation week (one of them was a 3-year-old female in her first nesting attempt) to sites where they were established for at least the following 2 years. The third female (unknown age) moved from a site where she failed before hatching, to a new site where she was killed by a predator during incubation. Excluding these cases, which were probably explained by a negative experience during the early incubation stages, the mean distance between nests of consecutive years was 0.74 km (sd = ± 0.56 , range = 0.10–2.28 km). Nests were located a mean of 4.5 km (sd ± 4.5 , Table 2) from lek centres, in areas of appropriate habitat between neighbouring leks, and were significantly closer to the lek centroids than controls (Fig. 1, Table 2).

Nesting habitat selection

The distribution of nests among land-cover types was markedly different from the proportions of these land-cover types available in the study area ($\chi^2 = 24.8$, $P < 0.001$), indicating that habitat use was non-random. Fallow fields and cereal fields were selected by females as nesting patches (Table 3). Ploughed fields were used less than would be expected by random distribution and all other land-cover types were wholly avoided for nesting.

Factors affecting nest location and nesting success

Univariate exploratory analysis showed several significant differences between the sites used by females to nest and the control sites (Table 2). The visual field was larger for nest-sites than for C1 sites and the slope of the nesting ground was significantly orientated towards the southeast ($148 \pm 65^\circ$, $P < 0.01$, Rayleigh test), in contrast to the slopes of C1 and C2 control sites, which did not show any preferred orientation. Nest-sites had larger surface area of cereal fields, lower diversity of patch types, lower surface area of human-made features and smaller distance to lek centroids than C1 sites. With respect to C2 sites, nest-sites were further from water courses, had larger surface area of cereal and ploughed fields, smaller surface area of human-made features, larger distance to buildings, and smaller distance to lek centres and centroids.

Table 2. Untransformed values of the environmental variables measured at Great Bustard nests ($n = 42$) and control sites (Control-1: areas used by the birds, $n = 44$; Control-2: areas not regularly used by the birds, $n = 30$), and results of univariate comparisons (Student's t -test).

Variable	Nests	Control-1	Control-2	Nests vs. C1	Nests vs. C2
	Mean \pm sd	Mean \pm sd	Mean \pm sd	P	P
Topography					
Altitude	728 \pm 76	708 \pm 66	717 \pm 74	ns	ns
Roughness	6.0 \pm 3.4	7.9 \pm 8.2	8.8 \pm 10.4	ns	ns
Slope	6.4 \pm 3.9	6.7 \pm 5.0	6.2 \pm 4.5	ns	ns
Orientation ^a	148 \pm 65	192 \pm 101 ^b	158 \pm 121 ^b	0.014	ns
Closest obstacle	81 \pm 20	90 \pm 28	73 \pm 21	ns	ns
Visual field	127 \pm 101	86 \pm 100	124 \pm 125	0.004	ns
Distance to water course	638 \pm 362	640 \pm 436	442 \pm 411	ns	0.039
Land-cover and farmland structure					
Cereal fields	41.8 \pm 20.5	29.5 \pm 23.4	26.8 \pm 23.3	0.007	0.002
Ploughed fields	33.7 \pm 22.3	33.7 \pm 22.6	17.9 \pm 21.0	ns	0.003
Fallow fields	1.1 \pm 1.9	1.8 \pm 3.7	1.2 \pm 2.5	ns	ns
Grassland	0.2 \pm 1.3	0.0 \pm 0.0	0.1 \pm 0.5	ns	ns
Other used patch types	14.1 \pm 17.8	21.9 \pm 24.2	22.2 \pm 24.8	ns	ns
Number of patches	52 \pm 39	59 \pm 48	77 \pm 61	ns	ns
Diversity	0.82 \pm 0.31	1.00 \pm 0.26	0.95 \pm 0.35	0.004	ns
Interspersion	9.6 \pm 2.4	10.6 \pm 3.5	10.1 \pm 3.5 ^c	ns	ns
Human features					
Buildings	1310 \pm 555	1252 \pm 760	874 \pm 793	ns	0.003
Roads	878 \pm 581	1017 \pm 767	874 \pm 793	ns	ns
Power lines	2341 \pm 2791	1874 \pm 2136	2225 \pm 1985	ns	ns
Surface area of human infrastructures	4.4 \pm 4.9	10.4 \pm 14.9	31.6 \pm 27.8	0.007	< 0.001
Social features					
Distance to lek centre	4.5 \pm 4.5	5.1 \pm 3.2	5.7 \pm 3.2	ns	0.026
Distance to lek centroid	7.1 \pm 5.4	15.7 \pm 6.6	13.2 \pm 8.1	< 0.001	< 0.001
Mean flock size in spring	7.5 \pm 7.9	5.6 \pm 8.6	^d	ns	
Mean flock size other seasons	4.5 \pm 4.0	6.2 \pm 9.5	^d	ns	
Number of flocks in spring	0.5 \pm 0.6	0.4 \pm 0.6	^d	ns	
Number of flocks other seasons	0.4 \pm 0.4	0.3 \pm 0.4	^d	ns	

^aSample sizes were 41, 39 and 28, respectively, for nests, C1 and C2 sites; the remaining sites were on flat terrain, i.e. with no orientation.

^bC1 and C2 samples showed no significant orientation.

^cSample size was 25 (five samples were located in non-agricultural areas where there were no patch changes).

^dC2 sites are sites with no Bustards.

Considering predictor variables by groups, there were significant differences between nest-sites and both C1 and C2 control sites (Tables 4 and 5). As with the univariate analyses, multivariate discriminant analysis showed that visual field, percentage surface area of cereal fields, diversity of patch types, surface area of human-made features and distance to lek centroids were the main factors determining differences between nest-sites and C1 sites. In the analysis including all habitat variables, the three most significant variables were surface area of cereal fields, diversity of patch types and visual field (Table 4). When comparing nest-sites with C2 sites, the discriminating variables were

distance to watercourses and lek centroids, surface areas of cereal and ploughed fields, number of fields and surface areas of human-made features. The analysis including all habitat variables retained four variables: surface area of human-made features, number of patches, visual field and surface area of other patch types (Table 5). The same significant variables were obtained from analyses for all habitat variables using nest locations only from the first year.

The analyses of nesting success showed no influence of habitat or social variables. None of the variables included in the logistic regression significantly affected the clutch fate (in all cases,

Table 3. Percentage availability and use of different land-cover types by nesting female Great Bustards, and Ivlev's selection index (ISI).

Patch type	Available	Used for nesting	ISI
Ploughed fields	38.05	15.79	-0.41
Cereal fields	39.61	76.32	0.32
Fallow fields	1.79	7.89	0.63
Grassland	0.10	0.00	-1.00
Other used patch types ^a	8.80	0.00	-1.00
Patch types not used by the birds in other seasons ^b	10.24	0.00	-1.00
Unidentified patches	1.41	0.00	-1.00

^aIncludes uncultivated land, legumes, vineyards and olive groves.

^bIncludes watercourses, woodlands, paved roads, tracks and buildings.

$P > 0.05$). Moreover, nests located in cereal or fallow fields, the two patch types selected as nesting substrate, did not differ in hatching success from nests located in ploughed fields ($\chi^2 = 0.14$, $P = 0.71$, $n = 76$ nesting attempts).

DISCUSSION

Great Bustard females selected fallows or cereal fields for nesting, in areas of low land-cover diversity, far from human infrastructures and with slopes orientated towards the southeast. Females also preferred sites with good horizontal visibility. These trends show a preference for shelter and

minimum human disturbance, but also suggest that females like to have some surveillance ability while incubating. Together they are likely to represent adaptations to reduce predation pressure. However, we were unable to find hatching success differences associated with any of the habitat characteristics selected by nesting females, possibly because our sample was not large enough to detect these nesting success effects. Among land-cover types found in cereal farmland in spring, fallows and cereal fields are indeed those with the densest vegetation cover and therefore offering the highest protection against predators. Their selection by nesting females confirms previous findings in other areas of the species' distribution range, where a preference of cereal fields for nesting was interpreted as a way to protect nests from predators (Alonso *et al.* 1995, Petrick 1996, Morgado & Moreira 2000, Farago *et al.* 2001, Watzke 2007). Predation is certainly one of the main causes of nest failure in this (Ena *et al.* 1987, Langgemach & Bellebaum 2005, Watzke 2007, own unpubl. data) and most other ground-nesting species (Ricklefs 1969, Baines 1990, Martin 1992, Willson *et al.* 2001, Whittingham & Evans 2004, Isaksson *et al.* 2007). Moreover, predation is probably the main factor causing annual female mortality rates to peak in Great Bustards during the nesting and early chick-rearing period (Martin 2008). During two decades of radiotracking Great Bustards in various study areas we have recorded several cases of females being killed by predators while incubating

Table 4. Significant predictor variables obtained from discriminant analyses between nest-sites ($n = 42$) and C1 sites ($n = 44$) using variables shown in Table 2. Separate analyses were performed for (a) topography, (b) farmland conditions, (c) human-made features, (d) social characteristics and (e) all habitat variables together.

Parameter	Wilks value	F	df	P	% Correctly classified	
					C1	Nest
(a) Topographic variables						
Visual field	0.904	8.89	1.84	0.004	63.64	66.67
(b) Farmland conditions						
Diversity	0.893	9.94	1.84	0.002	75.00	59.52
Area of cereal fields	0.903	8.88	1.84	0.004		
(c) Human-made features						
Area of human-made features	0.917	7.62	1.84	0.007	50.00	71.43
(d) Social characteristics						
Distance to lek centroid	0.612	53.19	1.84	< 0.001	77.27	66.67
(e) All habitat variables						
Area of cereal fields	0.900	9.11	1.84	0.003	79.55	73.81
Diversity	0.905	8.56	1.84	0.004		
Visual field	0.913	7.82	1.84	0.006		

Table 5. Significant predictor variables obtained from discriminant analyses between nest-sites ($n = 42$) and C2 sites ($n = 30$) using variables shown in Table 2. Separate analyses were performed for (a) topography, (b) farmland conditions, (c) human-made features, (d) social characteristics and (e) all habitat variables together.

Parameter	Wilks value	F	df	P	% Correctly classified	
					C2	Nest
(a) Topographic variables						
Distance to water course	0.941	4.41	1.70	0.039	13.33	92.86
(b) Farmland conditions						
Area of ploughed fields	0.772	20.08	1.65	< 0.001	70.00	88.09
Number of crop patches	0.820	14.88	1.65	< 0.001		
Area of cereal fields	0.834	13.51	1.65	< 0.001		
(c) Human features						
Area of human features	0.547	57.94	1.70	< 0.001	66.67	92.86
(d) Social characteristics						
Distance to lek centroid	0.829	14.42	1.70	< 0.001	50.00	80.95
(e) All habitat variables						
Area of human features	0.513	63.61	1.65	< 0.001	76.67	92.86
Number of crop patches	0.922	5.65	1.65	0.020		
Visual field	0.927	5.24	1.65	0.025		
Other used patch types	0.943	4.06	1.65	0.048		

(pers. obs.), and there must be a strong selection pressure for females to choose sites with dense, protective vegetation cover for nesting. By selecting sites within areas of low patch-type diversity, females might be further minimizing predation risk. Various studies have shown that habitat heterogeneity contributes to increasing the edge effect and vulnerability to predators, whereas in homogeneous habitats, nest predation risk decreases as the distance to the field edge increases (Koivula *et al.* 1993, Chalfoun *et al.* 2002).

An interesting result suggesting additional adaptation against predation pressure was the larger visual field of nest-sites as compared with both sets of control sites (Tables 4 and 5). Good visibility from the nest allows female Great Bustards to detect predators or disturbances in good time to escape discreetly if necessary. Both in foraging and in incubating birds, maximization of concealment may not be the best strategy, as cover provides a hiding place against possible attacks but also obstructs the view of approaching predators (Lazarus & Symonds 1992, Götmark *et al.* 1995). Particularly in many ground-nesting species in which incubating adults may benefit from the protection provided by their cryptic plumage, extreme concealment of the nest might not be necessary, or could even be detrimental. Götmark *et al.* (1995) suggested that a trade-off between nest concealment and the need to maintain some view of the surroundings while incubating would be a wide-

spread strategy in many species when predation is a major selection pressure. Our results support this view for Great Bustards. Cereal fields probably offer an ideal combination of cover and visibility to incubating females, due to the alternation of rows with plant stems and rows without vegetation in these fields. Moreover, the relatively long neck of females may allow them to scan for predators while incubating in dense vegetation. On the other hand, as Great Bustard nests are frequently found aggregated in favourable areas (Demeter 1995, pers. obs.), a female detecting an approaching predator could alert others nearby. However, high vegetation density may reduce visibility. In Saratov, the main Great Bustard breeding region in Russia where plots of natural steppe of Feather Grass *Stipa* spp. and mixed sagebrush associations still exist, no nests were found on either steppe patches or old set-asides. Here, excessive vegetation density was thought to restrict the female's visibility while incubating, and the ability of the chicks to move around (Trofimova 2007, Watzke 2007). Yang *et al.* (2003) observed that Houbara Bustards *Chlamydotis undulata* also preferred to locate their nests on flat ground with high visibility. In Canada Geese *Branta canadensis*, sites allowing an early detection of predators were important characteristics of nest-site quality (Miller *et al.* 2007).

A second benefit of nesting in fields with dense vegetation cover may be the improved thermoregulation conditions of these fields with respect to

more open patch types (Farago 1986). A significant preference for nesting on grounds with a slope orientated towards the southeast also suggests that females actively seek sites protected from the cold and wet northwesterly winds which are prevalent in our study area. In another ground-nesting species, the Lesser Rhea *Rhea pennata pennata*, protection from strong westerly winds was also interpreted to be one of the main factors in nest-site selection (Barri *et al.* 2009). In the northern hemisphere, slopes orientated towards the south are also those benefiting from the highest exposure to the sun in spring, which may help keep the eggs warm when the female leaves the nest for feeding. Orientation and other microclimatic conditions protecting nests from extreme temperatures have been shown to increase nesting success in ground-nesting species (Gloutney & Clark 1997, Hoekman *et al.* 2002, Kim & Monaghan 2005, Burton 2007, Fast *et al.* 2007).

Another advantage of nesting on fallows and cereal fields is probably related to food availability. An optimal nest location should be close to appropriate feeding grounds to ensure that hatchlings can find enough food during their first weeks of life, when they have high energy demands and are unable to fly or walk long distances (Watters *et al.* 2002, Amar *et al.* 2004). Among all patch types in dry cereal farmland, fallows and harvested cereal fields offer in early summer the highest numbers and diversity of arthropods (own unpubl. data), the main component of the diet of young birds (Palacios *et al.* 1975, Sterbetz 1980, Ena *et al.* 1985, Farago 1988, Lane *et al.* 1999). These fields are indeed selected as the main feeding grounds by females with chicks during summer (Hidalgo de Trucios & Carranza 1990, Martín 1997, Martínez 2000, Farago *et al.* 2001).

The preference of sown fields for nesting is probably the main cause of the distances moved by females between consecutive years. As a rule, this breeding dispersal distance was only a few hundred metres, confirming the strong nest-site fidelity found in previous studies of marked females of this species (Alonso *et al.* 2000). Because the farming system in our study area is a 2-year rotation system where cereal fields of one spring will be ploughed fields the next spring, females nesting on a cereal field on a given year will have to move a certain distance between consecutive years in order to nest again on a sown field. Indeed, the distance between nest locations of the same female on consecutive

years was closely correlated with the distance from the first-year nesting location to the closest sown field on the second year ($r = 0.80$, $P < 0.001$, $n = 20$ females). The three females performing long-distance movements of 4.27, 19.21 and 24.53 km between years were excluded from this analysis as they were either immature birds moving to the area where they established permanently as breeding adults or, in one case, a female of unknown age moving to a completely different nesting area after an unsuccessful breeding attempt. This correlation strongly suggests that the 2-year rotation farming cycle was a major factor determining the distance between nests of consecutive years found in our study area.

The only significant social variable was the distance to lek centroids. Nest-sites were closer to the centroids of the three closest nests than control sites, but not significantly closer to the nearest lek centre than C1 sites. As control sites were uniformly distributed in the study area, this result indicates that nests were not particularly aggregated around the centre of the closest lek. Rather, many females nested at moderate distances from lek centres (up to 17.95 km from the closest lek centre, see Table 1), in areas between two neighbour leks or even outside any lek site (e.g. nesting aggregation in the northeast extreme of our study area where no lek exists, see Fig. 1). A tendency to nest outside the central areas of leks has also been described for the Houbara Bustard (Hingrat *et al.* 2008; 22% of nests within leks, 78% aggregated in the periphery). Nest-sites of Houbara Bustards were also not closer to lek centres than random sites. The dispersal of nesting females to nesting sites far from their lek centres is a common feature of many lek breeding species (Johnsgard 1994, Höglund & Alatalo 1995).

Finally, the sample circles containing nest-sites included a significantly smaller surface area of human infrastructures than control sites. Previous studies had shown that human infrastructures are generally avoided by Great Bustards and contribute to the fragmented distribution of this species in central Spain (Lane *et al.* 2001, Osborne *et al.* 2001). One of the reasons may be that Great Bustards are particularly sensitive to human disturbances such as car traffic or pedestrians (Sastre *et al.* 2009). However, the effects of human infrastructures on nest-site selection had not yet been studied in this species. The evidence presented

here suggests that females also prefer to nest far from these human features.

Based on the results of the present study, the following management recommendations could be suggested. First, farming operations on cereal fields, the preferred patch type for nesting, should be adapted to the phenology of nesting Great Bustards. In particular, the timing of harvest should be delayed as much as possible, at least until the chicks are able to escape from harvesters. Also, certain practices should be avoided, including nocturnal harvesting or inward concentric harvesting and stubble burning after harvesting. Routine agricultural works seem to be the main cause of nest destruction and desertion in other Great Bustard areas in central and eastern Europe (Flint & Mischchenko 1991, Farago *et al.* 2001, Watzke 2007, Dawes *et al.* 2008), and in the Little Bustard *Tetrax tetrax* in France (Bretagnolle & Inchausti 2005). Secondly, because some nesting areas seem to be relatively far from lek centres, habitat conservation measures should not be restricted to lek sites, but should also include areas of appropriate nesting habitat in-between. Finally, in line with the suggestions to reduce the negative effects of recent agricultural intensification to farmland bird populations (Donald *et al.* 2001, Whittingham & Evans 2004), small plots of fallow land should be left within large areas of continuous cereal fields to allow families to use them as refuges once the main cereal areas are harvested in summer.

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