IBIS The International Journal of Avian Science BOU
Ibis (2012), **154**, 85–95

The importance of traditional farmland areas for steppe birds: a case study of migrant female Great Bustards *Otis tarda* in Spain

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A detailed knowledge of the habitat requirements of steppe birds living in farmland habitats is necessary to identify agricultural practices compatible with their conservation. The globally threatened Great Bustard *Otis tarda* is a partial migrant in central Iberia, but factors affecting its winter habitat use have not been identified. We assessed habitat differences between breeding and wintering areas and winter habitat selection of radiotagged migrant female Great Bustards in central Spain. Of 68 tagged females, 35% moved to wintering areas located 64.3 ± 24.0 km south of their breeding areas, and 80% wintered in a single area of *c.* 236 km^2. A census of the population in this area identified it as one of the most important wintering areas of this species in the world, holding *c.* 1500 individuals. There were significant differences between breeding and wintering habitats of individually marked migrant females. Compared with breeding areas, wintering areas of migrant females were located further from roads and urban nuclei, had lower human population densities and area of urban developments, and a higher diversity of land-use types, with less cover of cereals and more vineyards and olive groves. Within this area, radiotracked migrant females preferred sites with more vineyards and a lower land-use diversity. Our results highlight the importance of traditional Mediterranean dry farmland mosaics, and suggest that different conservation strategies are needed for migrant and resident populations in winter to secure the conservation of suitable wintering habitat for Great Bustards in the Iberian Peninsula.

Keywords: bird migration, habitat mosaic, Mediterranean, radiotracking, wintering grounds.

Low-intensity cereal farmland areas of the Iberian Peninsula hold the most important populations in the European Union of several endangered steppe birds (Santos & Suárez 2005). Many of these species are considered to be conservation priorities due to their declining populations (Tucker & Heath 1994, BirdLife International 2004). Such declines are usually attributed to agriculture intensification and land-use changes (Krebs *et al.* 1999, Donald *et al.* 2001, 2006, Vickery *et al.* 2004, Santos & Suárez 2005). A detailed knowledge of the habitat requirements of steppe birds is necessary to plan appropriate land management practices in areas used by these species through their annual cycle (Sutherland 1998). This is particularly important during the winter period, when some of these species congregate in certain areas where they may be particularly vulnerable (Blanco *et al.* 1998, Tella & Forero 2000, Silva *et al.* 2004, Suárez *et al.* 2004). Using this knowledge to plan future agricultural developments could enable the reversal of the continued biodiversity loss of the last 50 years and avoid further adverse environmental impacts (Royal Society 2009, Wilson *et al.* 2009, 2010). Some research results have already been translated into successful conservation actions for farmland birds (e.g. Aebischer *et al.* 2000).

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One of the steppe birds best adapted to dry cereal farmland in the Iberian Peninsula is the Great Bustard *Otis tarda*, a globally threatened species classified as Vulnerable at world, European and national scales (BirdLife International 2004, Palacín *et al.* 2004, IUCN 2010). Spain holds the largest number of this species, with over 60% of the world population (Palacín & Alonso 2008). However, the future of this population is not secure in many regions of the Iberian Peninsula where agricultural intensification, infrastructure (highways, high-speed rail or power lines) and other urban developments are currently increasing (Palacín *et al.* 2004).

The Great Bustard shows a variety of migratory patterns across its Palaearctic range. Asian populations are obligate winter migrants (Kessler 2010) and Eastern European populations migrate from Russia to wintering areas in South Ukraine (Watzke 2007). Central European populations are facultative winter migrants in response to extreme weather (Streich *et al.* 2006); and Iberian populations are partial and differential migrants by sex, with variable proportions of both sexes migrating according to sex-specific patterns (Alonso *et al.* 2000, 2001, 2009, Morales *et al.* 2000). In central Spain, Great Bustards are partial migrants, with sedentary and migratory birds of both sexes coexisting in the same populations (Palacín *et al.* 2011). They also show differential migration by sex (Palacín *et al.* 2009): the proportion of migrants is higher in males (*c.* 85%) than in females (*c.* 50%). Most males abandon the lek site between early May and late June and migrate to summering areas located up to 180 km northwards, whereas females remain at the breeding areas for another 3–7 months, and migrate in November to wintering areas located up to 110 km southwards. Migrant males use two different post-breeding (summer and autumn) areas, whereas migrant females use one (winter). Males return to the leks earlier (September–March) than females (January–April).

Habitat preferences of Great Bustards have been studied at the breeding areas (e.g. Lane *et al.* 2001, Moreira *et al.* 2004), but no study has focused on seasonal habitat differences and winter habitat selection of the migrant subpopulation of females. Here we describe the winter habitat use of migrant female Great Bustards using a sample of birds marked at their leks in central Spain and radio-tracked through consecutive years. This allowed us to assess the specific environmental conditions selected by each marked individual in spring and winter, in contrast to previous studies based on unmarked birds, where the precise breeding locations of the wintering populations studied cannot be ascertained. Our objectives were to (1) identify habitat differences between breeding and wintering areas of marked migrant females, (2) examine seasonal changes in habitat preferences of marked migrant females and (3) assess habitat selection of migrant females in winter. In addition, a census of a main Great Bustard wintering area in central Spain and data on wintering site fidelity are presented.

METHODS

Study area

The study was carried out in the provinces of Madrid and Toledo (central Spain), which are located within the Meso-Mediterranean climatic region of the Iberian Peninsula (Fig. 1). The weather is characterized by dry, hot summers, wet autumns and cold winters. At the breeding areas, the mean annual temperature was 14.1 °C, with a maximum monthly mean of 24.5 °C in July and a minimum of 5.4 °C in January; 378 mm mean annual rainfall (maximum in May, mean 47 mm; minimum in August, 12 mm); and an average of 2 days of snow per year (Bustamante 2003, Instituto Nacional de Meteorología 2005). Mean altitude varies between 785 m asl (Campo Real, Madrid, Spain) and 530 m asl (Camarenilla, Toledo, Spain). The habitat used by Great Bustards is mainly flat to slightly undulating low-intensity, dry cereal farmland with interspersed vineyards *Vitis vinifera*, olive groves *Olea europaea* and fields planted with legumes *Vicia* sp. in some areas. The Madrid region holds *c.* 1600 Great Bustards distributed in 14 leks. Approximately 1100 are found in the Special Protection Area (SPA) 139 'Estepas Cerealistas de los Ríos Jarama y Henares' (40°45′N, 3°30′E, 331 km^2) and other smaller areas located in the south and southeast of Madrid province (Alonso *et al.* 2003a).

Capturing and tracking birds

During 1999–2004, we captured 43 female Great Bustards using rocket nets. In 1995–2004 a further 25 female chicks were captured in July, when they were 3–10 weeks old and still dependent on their

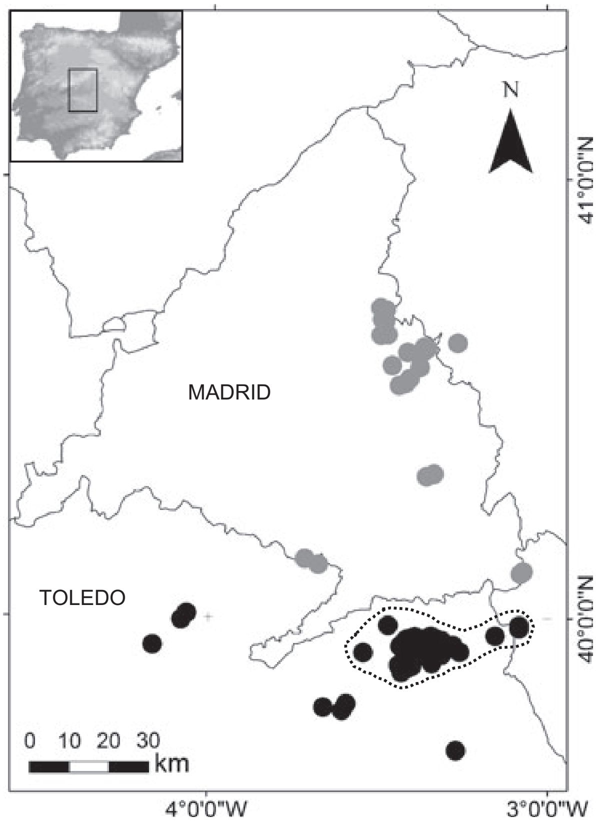

Figure 1. Location of the study area in the Iberian Peninsula showing the breeding sites of migrant females (grey dots), the wintering sites of migrant females (black dots) and the winter census area (dotted line).

mothers, by chasing them down. We tracked these birds for at least two consecutive winters after they reached maturity. Each captured bird was fitted with a backpack radio-transmitter (Biotrack model TW3, powered by two AA batteries) using an elastic band as harness material. The total weight of transmitter plus harness did not exceed 3–5% of the bird's weight. In addition, birds were provided with PVC wing tags for visual identification in the field. Wing tags also enabled location of marked birds after transmitter batteries were exhausted (battery life was 4–5 years). We did not observe any plumage damage or behavioural alteration of the birds as a result of marking. We located all radiotagged individuals by triangulation using TR2 receivers-TS1 scanners (Telonics, Mesa, AZ, USA) and subsequent visual observation with ×20–60 telescopes at least once, and more frequently several times per month. The location of a bird was determined with a GPS (Garmin, Olathe, KS, USA) with a maximum error of 100 m. When a marked bird was not found from the ground we used small aeroplanes (E-24 Bonanza; Beechcraft, Wichita, KS, USA). Aerial tracking enabled us to obtain breeding and wintering locations of all marked birds, thus avoiding the bias derived from emigration outside the study area. We recorded location data for 68 females from 10 different leks in Madrid province. Each female was tracked for between 1 and 11 years (average 4.7 ± 2.3 years). Twenty-four of the 68 females died during the study period and were radiotracked for 3.5 ± 1.9 years. All other females were radiotracked for an average of 5.3 ± 2.2 years. In total, we obtained 2704 locations from our marked birds. Females were considered migrants when they performed a regular seasonal movement between separate breeding and wintering areas (*sensu* Newton 2008). We estimated the interannual fidelity to wintering areas as the percentage of birds using the same area in consecutive years. For this analysis we defined the wintering area as the minimum convex polygon (Mohr 1947) encompassing all locations during one wintering season (December–February) using ARCGIS 9.2 (ESRI, Redlands, CA, USA) and the software extension HAWTH'S TOOLS (Beyer 2004). We considered annual wintering areas to be the same across years if the annual minimum convex polygons overlapped (*c.* 50%).

Wintering population census

We carried out two censuses (December 2000 and January 2004) of the Great Bustard population wintering at Mesa de Ocaña, North Toledo (236 km^2, *c.* 39°52′N, 3°23′W), the area where 80% of the marked migrant females wintered (Fig. 1). A major part of this dry cereal farmland area has been declared a Special Protection Area (SPA 170 'Area Esteparia de la Mancha Norte'). Each survey was made over two consecutive days. The censuses were conducted by two teams working simultaneously and in contact through radio to avoid double counts of flocks located close to borderlines between their respective census areas. Each team consisted of two observers with extensive previous experience in Great Bustard surveys, operating from a four-wheel drive vehicle, using binoculars and ×20–60 telescopes, GPS and 1 : 50 000 maps. Surveys started at dawn and ended at dusk, with a pause during midday (12:00–14:00 h GMT), when Bustards usually lie down and become difficult to see. During one observation period, morning or evening, each team surveyed an area of *c.* 50 km^2. The census itinerary was covered at low speed, with frequent stops at vantage points to look carefully for birds.

Habitat variables

The environmental variables used as predictors of migrant female habitat requirements were based on previous work (Lane *et al.* 2001, Suárez-Seoane *et al.* 2002, Moreira *et al.* 2004), processed using GIS, and rasterized in IDRISI (Eastman 2000) to either 1-km^2 resolution (topographic and climatic variables) or 1-ha resolution (land cover variables; see Table 1). Three variables described the topographic structure of areas of 2000 m radius: altitude (m asl), slope (degrees) and surface undulation (% variation in slope estimated as the mean of all standard deviations of altitudes in each pixel, calculated from digital terrain model). To describe the climatic conditions we used the mean monthly temperatures (in °C) in April and January, mean annual temperature, mean annual rainfall (in mm) and mean annual sunshine (in kJ/cm^2). These variables were obtained from the models with 1-km^2 resolution produced for the whole Spanish territory using interpolation techniques: trend surfaces, multiple regression with predictors derived from a digital elevation model (DEM) and kriging (Bustamante 2003). A third set of variables describing the habitat used by the birds was obtained from the Geographic Database on Land Use of the European Union Corine Land Cover 2000, from satellite imagery scale 1 : 100 000 with

Table 1. Mean and standard deviation (sd) of environmental variables measured at random points (circle of 2000 m radius) in breeding and wintering areas of Great Bustard migrant females in central Spain, and univariate differences measured by Mann–Whitney *U*-test.

	Breeding		Wintering			
Variable	Mean	sd	Mean	sd	*U*	*P*
Topographic structure						
Altitude (m)	681.9	68.1	741.5	22.1	3.903	0.000
Terrain slope (°)	1.0	0.4	0.4	0.2	6.003	0.000
Terrain undulation (% variation in slope)	19.1	9.4	7.2	5.2	5.426	0.000
Climatic						
Mean annual sunshine (kJ/cm^2)	2017.6	11.2	2018.4	4.2	0.015	0.988
Mean annual rainfall (mm)	4437.8	275.3	4584.0	93.9	2.203	0.028
Mean annual temperature (°C)	13.3	4.0	13.5	1.4	3.305	0.001
Mean January temperature (°C)	4.8	3.9	5.1	1.4	3.859	0.000
Mean April temperature (°C)	10.9	4.2	11.0	1.5	1.893	0.058
Land cover (ha)						
Dry cereal farmland	893.7	226.8	316.8	313.8	5.574	0.000
Irrigated farmland	67.0	134.2	11.2	48.9	2.239	0.025
Vineyards	6.9	27.1	165.6	235.6	4.904	0.000
Olive groves	18.4	48.8	3.3	11.8	2.344	0.019
Pastureland	40.3	67.3	3.0	10.3	3.691	0.000
Dry farmland mosaic	0.0	0.0	358.7	319.7	6.926	0.000
Agricultural land with natural vegetation	24.4	49.5	6.5	18.4	2.180	0.029
Open-wooded oak-tree *dehesas*	2.8	12.5	26.2	72.7	1.880	0.060
Woodland	18.9	37.6	0.0	0.0	3.615	0.000
Sclerophyllous vegetation	34.7	67.2	10.7	25.0	1.701	0.089
Transition scrubland-woodland	10.2	32.0	2.0	7.7	1.220	0.223
Substrate diversity (SDI)	0.8	0.3	1.0	0.3	1.390	0.165
Human influence						
Minimum distance to nearest road (m)	829.3	790.3	1812.2	1440.4	2.913	0.004
Road length (m)	5915.1	3815.3	3630.9	4282.6	2.488	0.013
Mean distance to urban areas (m)	3171.8	1401.5	5137.6	2014.0	3.807	0.000
Surface of urban areas (ha)	42.3	41.3	6.9	18.1	5.226	0.000
Surface of quarry (ha)	9.5	20.2	0.0	0.0	2.785	0.005
Human population density (no. human/km^2)	208.1	586.8	19.5	10.7	5.043	0.000

1-ha resolution (European Environment Agency http://www.eea.europa.eu/data-and-maps). We considered the following land-use types: dry cereal farmland, irrigated farmland, vineyards, fruit tree plantations, olive groves, pastureland, dry farmland mosaic (formed by small vineyards and olive groves with interspersed small cereal fields), non-arboreal natural vegetation, arboreal vegetation (mostly open-wooded oak-tree *dehesas* and uncultivated areas with natural arboreal or scrub vegetation), and areas with sclerophyllous vegetation. The diversity of substrate types was quantified through Shannon's diversity index (SDI). The SDI is influenced by the number of land-use types in the landscape and by their specific share of total area. The index increases as the number of different land-use types increases and/or the proportional distribution of area among patch types becomes more equitable. The SDI was computed using the Patch Analyst extension of ARCGIS (Rempel & Carr 2003). A fourth group of variables was used to describe the degree of human influence: minimum distance to nearest road, road length, mean distance to urban areas and area of urban cover (obtained from cartography BCN 200, Centro Nacional de Información Cartográfica, http://www.cnig.es); and human population density (number of inhabitants of the village closest to the central coordinate of the circle divided by the surface of the municipality in km^2; data for 2003 from the Instituto Nacional de Estadística, http://www.ine.es and the Dirección General del Catastro, http://www.catastro.minhac.es).

For each marked migrant female, we calculated her activity centres (based on visual locations of the marked birds) for the breeding (March–May) and wintering (December–February) seasons for which we had the highest number of locations (20.5 ± 10.6 locations per bird and year). We used only data after each bird had established as a breeding adult at a lek site, which in Great Bustard females occurs at the age of 2–3 years (Alonso *et al.* 1998, Martín *et al.* 2008). Around these spring and winter activity centres, we established circles of 2000 m radius within which we calculated the values of all environmental variables used to characterize these sites. Our radiotracking data showed that these circles encompass the core home-ranges (60% Kernel contours; Worton 1989) of Bustards both in spring and winter and thus represent adequately the environmental requirements of birds (e.g. Alonso *et al.* 2009). Means and standard deviations of all variables were extracted using ARCGIS 9.2 (ESRI). To compare habitat differences between breeding and wintering areas of radiotracked migratory females we generated a sample of random points (30 at the breeding areas, 30 at the wintering areas). The random points were obtained from a map of potential habitat for the species, based on spring and winter censuses of the breeding and wintering areas, respectively (years 2000 and 2004). The potential habitat was defined by the 100% Kernel contour of the census locations, following the cross-validated fixed Kernel method (Seaman & Powell 1997), using HAWTH'S TOOLS extension (Beyer 2004) in ARCGIS 9.2 (ESRI). To determine habitat selection in the wintering area, we generated 30 pseudo-absence points in the wintering area, ensuring that none of these points overlapped with bird observations by applying a 2000-m exclusion buffer around each presence data point.

Statistical analyses

To assess habitat differences between breeding and wintering areas of migrant females, we used exploratory univariate Mann–Whitney *U*-tests comparing all variables in circles of 2000 m around both samples of random points. To assess seasonal changes in habitat preferences of marked migrant females, exploratory univariate analyses of the differences between spring and winter values of each variable in the circles of 2000 m radius around the presence data points of migrant females were carried out using Wilcoxon's matched pairs tests. Next, a Hotelling's T^2 test (MANOVA one-sample test) with Wilks' lambda estimation was used to assess whether, considering all variables together, the difference between spring and winter in the environmental characteristics of locations used by females in both seasons could be considered significantly different from zero (Winer *et al.* 1962, Waldorp *et al.* 2006, Wallace *et al.* 2006). The H_0 predicts no differences between spring and winter in the set of variables describing the characteristics of the 2000-m circles used by the migratory females. Prior to the multivariate analysis, all variables were transformed to attain equal variance and normality. After testing the significance of the multivariate model, univariate *post-hoc* analyses were performed to obtain the *F*-values for each variable, and variables that were highly correlated ($r > 0.70$) with other predictors were excluded.

These *post-hoc* univariate analyses of variance are protected against the probability of a type I error (Winer *et al.* 1962).

To assess habitat selection in the wintering area, we first performed exploratory univariate Mann–Whitney *U*-tests comparing all variables in circles of 2000 m around the presence data points of marked females and pseudo-absence points. Variables showing no significant differences ($P > 0.05$) were excluded from further analysis (Hosmer & Lemeshow 2000). As a second step, we used presence data points of marked migrant females vs. pseudo-absence locations of the wintering sites to build models with logistic regression (generalized linear model with binomial errors and logit function: Quinn & Keough 2002). To select variables, we analysed the correlation matrix among predictors. Where bivariate correlation exceeded $r_s > 0.7$ (Spearman rank correlation), the variable with the least biological meaning was excluded (Randin *et al.* 2006). The best models were selected by the Akaike's information criterion for small samples (AICc) with smaller values indicating a more parsimonious model. Models with ΔAICc < 2 are considered to be substantially supported by the data and similar in their empirical support to the best model (Burnham & Anderson 2002). We performed an average model estimation, in which the parameter estimates of all models are combined (Burnham & Anderson 2002). Models were constructed with the data of the year for which we had a highest number of locations for each marked bird. STATISTICA 6.0 (StatSoft) and SPSS 18 (SPSS Inc., Chicago, IL, USA) software were used for analyses. The average model was performed using library *MuMIn* (Barton 2009) in R (R Development Core Team 2009).

RESULTS

Fidelity to wintering areas of migrant females and winter census

Twenty-four of the 68 females radiotracked moved to wintering areas located 30–110 km from their breeding sites (mean ± sd = 64.3 ± 24.0 km). Only 16% of all females changed their migratory pattern (migratory to sedentary or vice versa) across two consecutive winters. For 19 marked birds with data from two or more winter seasons we calculated a site fidelity of 77% among years. Most of the migrant females (80%) wintered in one area of 236 km^2 located at Mesa de Ocaña, North Toledo (Fig. 1). Sedentary females ($n = 44$) remained at the breeding areas in winter, performing local movements (mean = 6.8 ± 7.1 km).

At the main wintering area of migrant females, 1162 Great Bustards (851 females and 311 males) were counted in December 2000, and 1499 (1092 females, 336 males and 24 birds of unknown sex) in January 2004 (Fig. 1).

Habitat characteristics of wintering areas of migrant females

The wintering areas used by migrant females comprised 33% dry-land arable crops, 30% agricultural mosaic complex (consisting of small plots of less than 25 ha of dry-land cereal crops, vineyards and olive groves, with Holm Oak *Quercus ilex* or Almond *Prunus dulcis* trees on the edge of plots), 20% traditional vineyards (where vines reach a maximum height of *c.* 1 m and have no wire-supported elements), 5% sclerophyllous vegetation and 2% pastures. All other crop types occupied less than 2% of the area. Univariate exploratory analyses revealed significant differences ($P < 0.05$) between breeding and wintering areas of migrant females for 20 habitat variables (Table 1). Wintering sites had lower terrain slope and undulation values and higher altitudes than breeding areas. They also had higher mean annual and January temperatures, were located at greater distances from urban areas, smaller areas of human infrastructures and dry cereal farmland, and higher areas of vineyards and vineyard–olive grove–cereal mosaic farmland than breeding areas. Finally, wintering areas held lower human population densities than breeding areas.

Considering all variables together, there were significant differences between breeding and wintering areas of individually marked migrant females (Hotelling's $T^2 = 51.92$, $F_{19,5} = 13.66$, $P = 0.004$). The model explained 98.1% of the variance in environmental structure (Wilks' lambda = 0.018). The variables showing significant effects (Table 2) confirmed the patterns found in univariate analysis. Wintering sites had higher areas of vineyards and vineyard–olive grove–cereal mosaic farmland, were located in areas with lower human population density and higher distance to urban areas, and were characterized by lower terrain undulation values, higher January temperatures, and less sclerophyllous and non-arboreal natural vegetation and substrate diversity.

Table 2. Environmental variables showing significant differences (one-way ANOVAs) between breeding and wintering sites used by 24 migrant females after testing the significance of a multivariate model including all variables.

Variable	$F_{1,23}$	P
Area of dry farmland mosaic	60.20	< 0.001
Area of vineyards	56.68	< 0.001
Human population density	51.70	< 0.001
Terrain undulation	49.21	< 0.001
Land-use diversity (SDI)	34.63	< 0.001
Area of urban areas	20.37	< 0.001
Mean distance to urban areas	18.33	< 0.001
Mean January temperature	12.55	0.001
Area of sclerophyllous vegetation	10.87	0.003
Area of non-arboreal natural vegetation	6.88	0.015

Winter habitat selection of migrant females

Univariate exploratory analysis showed significant differences ($P < 0.05$) in winter habitat selection by migrant females for nine variables (Table 3): wintering locations had lower terrain undulation values than pseudo-absence points, were located at greater distances from roads, intersected less with them, had smaller surfaces of irrigated farmland, *dehesas*, and transition of scrubland-woodland, and were characterized by a lower land-use diversity.

The best models selected through logistic regression analysis using AICc criteria are shown in Table 4. According to the average model estimation (Table 5), the area of vineyards and substrate diversity were the most important predictors of habitat selection of migrant females at the wintering areas.

DISCUSSION

In this study, we identified one of the most important Great Bustard wintering areas in the Iberian Peninsula (Mesa de Ocaña, Toledo, Spain) and, consequently, worldwide. The species here reaches densities of 6.3 birds/km^2 (1499 individuals in 236 km^2) and maximum flock sizes of over 200 birds. These are among the highest aggregation values for this species worldwide, and they equal or exceed maximum densities cited previously for the SPA Lagunas de Villafáfila in northwestern Spain (Alonso *et al.* 2003b). The wintering habitat described in the present study might thus be considered optimal for the winter requirements of migrant Great Bustard females in central Spain. These wintering areas of migrant females were mainly characterized by their greater distances to roads and urban areas, lower human population densities, and a reduction of the cereal area in favour of a dry farmland mosaic of vineyards and olive groves, compared with breeding areas of migrant females. This suggests that one of the main requirements of migratory Great Bustards is reduced disturbance in winter. A recent study has shown that whereas farming and sheep herding cause minor disturbance to Great Bustards, hunting and other human activities associated with the proximity to towns such as vehicle traffic or pedestrians may increase the level of restlessness (Sastre *et al.* 2009). The large increase (118%) in

Table 3. Mean and standard deviation (sd) of environmental variables showing significant differences between locations of 24 marked migrant females (2000-m radius around female locations) and 30 pseudo-absence points (2000-m radius around random points) at wintering areas of Great Bustard migrant females in central Spain, and univariate differences measured through Mann–Whitney *U*-tests.

	Random locations		Wintering locations			
Variable	Mean	sd	Mean	sd	U	P
Terrain undulation	9.6	6.1	0.0	0.0	6.267	0.000
Minimum distance to nearest road	1084.7	1127.8	1697.2	1549.9	2.263	0.024
Road length	5669.7	3790.5	3749.9	2934.7	2.104	0.035
Area of urban areas	15.4	34.2	2.3	7.9	1.954	0.051
Area of irrigated farmland	57.3	95.2	7.0	23.9	2.469	0.014
Area of vineyards	96.3	183.7	251.0	306.9	2.200	0.028
Area of open-wooded oak-tree *dehesas*	131.7	264.7	3.4	16.5	3.219	0.001
Area transition scrubland-woodland	14.2	44.2	0.0	0.0	2.297	0.022
Land-use diversity (SDI)	1.1	0.3	0.8	0.2	2.803	0.005

Table 4. Logistic regression modelling the probability of use (presence data points vs. pseudo-absence locations) of the wintering sites selected by the 24 marked migrant Great Bustard females. AICc, K (the number of parameters in the model including the intercept and the residual error estimates), ΔAICc and Akaike weight (ωAICc) are given. Models are ranked from best to worst according to ΔAIC. Only models with ΔAICc < 3 are shown. IRRIG, area of irrigated farmland; VINEY, area of vineyards; OAK, area of open-wooded oak-tree; SDI, Shannon diversity index of land-use types; ROADLEN, road length; ROADDIS, minimum distance to nearest road; TERRUND, terrain undulation.

Model	AICc	K	ΔAICc	ωAICc
IRRIG + VINEY + SDI + ROADLEN	50.56	7	0.00	0.24
IRRIG + VINEY + OAK + SDI	51.25	6	0.69	0.17
IRRIG + VINEY + SDI	52.28	5	1.72	0.10
IRRIG + VINEY + SDI + OAK + ROADDIS	52.30	7	1.74	0.10
IRRIG + VINEY + SDI + TERRUND	52.35	6	1.79	0.10
IRRIG + VINEY + SDI + ROADDIS	52.56	8	2.00	0.09
IRRIG + VINEY + OAK + SDI + ROADLEN + TERRUND	53.04	6	2.48	0.07
IRRIG + VINEY + SDI + OAK + ROADDIS + ROADLEN	53.21	8	2.65	0.06
IRRIG + VINEY + SDI + OAK + TERRUND	53.29	7	2.74	0.06

Table 5. Model-averaged parameter estimates of winter habitat selection by migrant females, listing relative importance (Σ, sum of Akaike weights of the models in which the predictor was present), regression coefficient (*b*), unconditional se and 95% confidence interval (CI) for *b*. Estimates where confidence intervals do not overlap zero are in bold.

Predictor	$\sum$	*b*	se	Lower CI	Upper CI
Area of vineyards	1.00	0.007	0.003	**0.0002**	**0.0133**
Area diversity (SDI)	1.00	−5.460	2.16	**−9.7**	**−1.23**
Area of irrigated farmland	1.00	−0.027	0.014	−0.054	0.0005
Road length	0.57	−0.0002	0.0001	−0.001	0.00005
Area of open-wooded oak-tree	0.56	−0.005	0.006	−0.016	0.006
Terrain undulation	0.25	−0.166	0.157	−0.474	0.141
Minimum distance to nearest road	0.24	0.001	0.001	−0.001	0.002

minimum distance to roads and in mean distance to urban areas (62%) in winter with respect to spring, together with a 91% lower human population density, may imply a significant reduction in potential human-induced disturbance factors at the wintering areas of migrant females. Similar avoidance behaviour of human-made structures has been reported for other open-land birds; for example, Little Bustards *Tetrax tetrax* avoid areas near roads and buildings (Silva *et al.* 2004) and Lesser Prairie-Chickens *Tympanuchus pallidicinctus* avoid highways (Pruett *et al.* 2009).

A second major group of variables differentiating wintering from breeding sites of migrant females is related to land use. Wintering areas showed much larger areas of dry farmland mosaic, a land-use type almost absent in the breeding area consisting of small cereal fields interspersed with vineyards, olive groves and other minor crops such as legumes. These areas offer a higher variety of food elements, particularly olives, which are consumed by Great Bustards in autumn and winter (Redondo & Tortosa 1994, Rocha *et al.* 2005). A more uniform habitat in spring, where cereal clearly outweighs other crops, may also be more suitable for activities such as displaying or nesting, for which Bustards tend to select larger, unobstructed fields (Magaña *et al.* 2009).

The difference found between breeding and wintering areas in January temperature was highly significant and, together with the preference for a southward direction, suggests that climatic factors could underlie the evolutionary origin of these migratory movements. Females of central and northeastern Palaearctic Great Bustard populations migrate southwards in winter and this behaviour has been interpreted by most authors as genetically controlled, although the tendency to migrate varies from obligate in most Asian and Russian populations where snow usually covers the ground in winter (Watzke 2007, Kessler 2010), to facultative and weather-dependent in German or Hungarian populations (Streich *et al.* 2006).

Breeding areas of migrant females concur with breeding and wintering areas of sedentary females. Thus, habitat differences between breeding and wintering areas of migrant females can be considered the same as between wintering areas of migrant females and sedentary females. These different wintering strategies denote the partial migration pattern of our study population, with sedentary and migratory genotypes modulated by social transmission coexisting in the same breeding areas (Palacín *et al.* 2009, 2011).

Within the wintering areas, the comparison of female locations with pseudo-absence points indicated a remarkable selection of traditional vineyards (56% higher vineyard surface as compared with random points). In winter, Great Bustards use vineyards as feeding and resting substrates (C. Palacín, pers. obs.). Migrant Great Bustard females also selected wintering locations with lower habitat diversity than random points. This result contrasts with the higher overall habitat diversity of wintering areas considered as a whole, compared with breeding areas, and suggests that once at the wintering areas, females avoided sites with too heterogeneous and patchy a habitat, which were usually characterized by the presence of trees. Site fidelity of Great Bustards (e.g. Alonso *et al.* 2000, 2001, 2009, Lane *et al.* 2001) can dilute habitat selective pressures. Consequently, traditional wintering sites may be used regardless of the availability of suitable habitat elsewhere, and consistent use of these sites may persist in spite of incipient habitat changes. However, a recent study showed that winter locations are less fixed than breeding sites when affected by human-induced disturbances (Torres *et al.* 2011), so habitat changes on wintering areas may imply that birds may disappear from wintering areas where traditional farmland is transformed.

Implications for management and conservation

The results of our study highlight the importance of traditional farmland areas as a wintering habitat for migratory Great Bustard females. Three major habitat management problems severely threaten the conservation of these areas in central Spain: (1) development of human-made structures, e.g. a highway and a high-speed rail line have been built in the main wintering area (respectively, 7.1 km and 17.1 km); (2) crop monocultures, which eliminate the agricultural mosaic typical of most Iberian low-intensive dry cereal farmland and lead to larger fields of a single crop over wide expanses of land; and (3) replacement of traditional vineyards, where vines reach a height of less than 1 m and are dispersed enough to allow steppe birds to use them for feeding or resting, with wire-supported vineyards, which may cause the death of birds through collision (C. Palacín, pers. obs.), and higher human presence to control the irrigation systems. A total of 43 785 ha of traditional vineyards have been transformed in a single year in Castilla-La Mancha, and the transformation of another 100 000 ha is planned in this region. If these plans are carried out, they will significantly reduce the habitat not only for Great Bustards, but also for other endangered steppe bird species in central Spain such as Little Bustard, Black-bellied Sandgrouse *Pterocles orientalis* and Pin-tailed Sandgrouse *Pterocles alchata*. In fact, this farmland mosaic of central Iberia is one of the most important habitats for breeding Little Bustards (Martínez 1994).

Finally, the Special Protection Areas (SPAs) for birds are not satisfactorily fulfilling the main goal for which they were created by the European Union. SPAs are strictly protected sites classified in accordance with EC Birds Directive (79/409/EEC, and 2009/147/EC). They have been created to conserve rare and vulnerable birds and regularly occurring migratory species. Regional authorities are actually supporting the agricultural transformation and permitting the construction of new infrastructures in these protected areas. Great Bustards, like most other steppe birds, are at present dependent on agricultural systems and therefore might suffer sudden declines in the near future if changes in agricultural policies lead to further land-use transformations. The design of appropriate habitat conservation measures is urgently needed not only at sites used all year-round, but also at all areas identified as important wintering areas for migrant Great Bustards.

We are grateful to two anonymous referees for their valuable comments. We especially thank M. Magaña and B. Martín for their collaboration during fieldwork. Additional help was provided by L. M. Bautista, C. Ponce, S. J. Lane, R. Manzanedo, E. Martín and M. B. Morales. We also thank J. M. Álvarez and P. Sastre for their assistance in obtaining GIS variables, and A. Torres for statistical advice. We are especially grateful to the 42 Group of the Spanish Air Forces for their collaboration in locating radiotagged birds. The fieldwork was financed by the Dirección General de Investigación (projects PB91-0081, PB94-0068, PB97-1252, BOS2002-01543 and CGL2008-02567) and the Dirección General de Conservación de la Biodiversidad.

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Received 23 Febuary 2010;
revision accepted 2 October 2011.
Associate Editor: Farah Ishtiaq.