

Original Article

Leks in ground-displaying birds: hotspots or safe places?

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We studied the effects of female distribution, topography, and human infrastructures on lek-site selection in a ground-displaying bird, the great bustard *Otis tarda*. Our aim was to investigate the relative importance of maximizing visibility to females (hotspot hypothesis) versus minimizing predation risk (predation avoidance hypothesis). Using a geographic information system, a very high-resolution digital elevation model, and an extensive survey database, we compared the 350 lek centers known in Spain with randomly generated sites. Males preferred lek sites that increase their visibility to surrounding females, reduce the distance to them, enhance the probability of detecting predators, and increase the distance to human disturbance sources. Logistic regression analyses confirmed these patterns. A final model identified five relevant variables indicative of higher short-range visibility, more centered location with respect to females, and farther distance to human disturbance sources in lek centers compared with random points. The viewshed gain of lek centers relative to random points was maximal at the center and disappeared gradually at randomly generated replicas located progressively farther away from the center, but still within a buffer equivalent to the home range of the male flock during the display period. Visibility maximization may be the reason why lek centers are extremely fixed within and between consecutive breeding seasons. Our results are compatible with both hotspot and predation avoidance hypotheses. We suggest that both models are important, at least for species displaying in open habitats. Lek-site selection probably represents a combined response to female attraction and predator avoidance selective pressures. *Key words:* great bustard, hotspot, lek, *Otis tarda*, predation risk, visibility. [*Behav Ecol* 23:491–501 (2012)]

INTRODUCTION

Leks are clusters of males that females attend primarily for the purpose of mating (Höglund and Alatalo 1995). One of the most debated hypotheses to explain lek evolution has been that males clump at places where the probability of encountering many females is highest (hotspot model, Lill 1976; Emlen and Oring 1977; Payne RB and Payne K 1977). Although this model has been one of the most influential for the formation of leks, it has received partial support mainly from bird studies (e.g., Bradbury 1981; Bradbury et al. 1986; Théry 1992; Schroeder and White 1993; Westcott 1994; Gibson 1996; Westcott 1997; but see Wegge and Rolstad 1986; Jiguet and Bretagnolle 2006; Duraes et al. 2007), but not so much from lekking ungulates (reviewed by Balmford et al. 1993; Clutton-Brock et al. 1993; Bro-Jørgensen 2003). Recent studies have claimed again more attention for alternative explanations of lek evolution. One of these explanations, perhaps the most basic and historically the earliest one, is predation risk avoidance. Predation was invoked to explain social courtship displays quite early (Lack 1968; Wiley 1974; Oring 1982; Trail 1987), but later depreciated in favor of sexual selection mechanisms (Emlen and Oring 1977; Bradbury 1981; see Boyko et al. 2004). Reduced predation risk should indeed be a major advantage to males displaying on leks as compared with dispersed territories (Lack 1968; Wiley 1974; Wittenberger 1978; Oring 1982). The main reasons why aggregating males

could enjoy protection from predators are increased corporate vigilance, dilution of risk, and mobbing of predators (Oring 1982; Trail 1987). However, conspicuousness and permanent location of leks in most species may attract predators, limiting and even offsetting antipredator advantages (Wiley 1991; Balmford and Turyaho 1992; Gibson and Bachman 1992). Recent studies have provided further support to the importance of predation in lekking behavior. For example, Gibson et al. (2002) presented indirect evidence that males may join leks to reduce predation by showing that other grouse species actively form mixed-species leks even though this does not increase mating opportunities for males of the joining species. Boyko et al. (2004) showed the importance of predation risk in explaining male and female lek attendance patterns. Finally, Aspbury and Gibson 2004 provided evidence that leks are positioned at locations that reduce long-range visibility to predators.

If predation is an important selective pressure favoring lek formation, lekking species should have developed mechanisms to compensate for the higher predation risk at leks. Besides concentrating display on hours of minimum predator activity (Hjorth 1970; Hartzler 1974), one of these mechanisms may be the selection of display grounds with minimum risk of predation (Wiley 1973). However, few studies have investigated the lek-site selection at detailed scale from the perspective of predator avoidance (a notable exception is Aspbury and Gibson 2004). In nonlekking species, the choice of song posts by territorial birds has been shown to be sensitive to the risk of predation (Krams 2001; Duncan and Bednekoff 2006; Møller et al. 2006; Parker and Tillin 2006). In line with the results of Aspbury and Gibson (2004), we propose that lekking species should also favor locations where the surrounding topography minimizes predation risk, either maximizing predator visibility

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to males at the lek or minimizing visibility of lekking males to predators.

An interesting aspect of predation risk that has recently raised growing concern is the evolutionary consequences of anthropogenic disturbances and human harvesting on wild populations (Stankovich and Blumstein 2005; Blumstein 2006; Allendorf and Hard 2009; Mysterud and Bischof 2010). However, the possible effect of human-induced risk on display site selection has been a relatively neglected and little studied aspect of lekking behavior. Most species usually balance predation risk and foraging or breeding benefits (Lima and Dill 1990; Cowlishaw 1997; Heithaus and Dill 2002). Since man has become a universal predator, adaptive behaviors to minimize human-derived perceived risks are expected in animals after a long coexistence with humans. It has been argued that disturbance stimuli could even be analogous to predation risk from an evolutionary perspective (Frid and Dill 2002). Therefore, anthropogenic disturbances should also be included as an important additional threatening factor when investigating the effects of predation risk on display site selection in lekking species living in humanized environments.

In the present study, we consider the effects of female distribution, topography, and major human infrastructures (roads and urban nuclei) on lek-site selection in a ground-displaying bird, the great bustard *Otis tarda*. Our aim was to investigate whether males select lek locations on the basis of female distribution, topographic features that change their visibility to potential mates, or predators including humans, or both. Male great bustards of a given lek gather each winter at the same site, where all individuals of the flock perform their characteristic balloon display through several weeks preceding the mating period (Hidalgo and Carranza 1991; Magaña et al. 2011). Display involves inflation of the gular pouch and a remarkable body contortion to show the white wing and tail under coverts. It has a dual function of communicating status to other males of the flock and sexual advertisement for females (Alonso et al. 2010a, 2010b; Magaña et al. 2011). The large size of the males and the extensive white plumage exposure makes displaying birds visible over several kilometers in the open grassland habitat where they live. This essentially visual display evidently serves to attract females and has probably evolved to maximize long-distance sexual advertisement (Andersson 1994; Johnsgard 1994; Bradbury and Vehrencamp 1998). Thus, according to currently accepted models, female distribution should be one of the determinant factors for lek-site selection. However, the remarkably fixed use of the same site year after year by the male flock performing this communal premating display strongly suggests that lek sites are significantly associated to specific topographical features that could help minimize predation risk, enhance their visibility to potential mates, or both. Specifically, we tested whether locations selected for display are 1) where females are most likely to be encountered (hotspot hypothesis), 2) at sites that maximize their long-range visibility to surrounding females (sexual advertisement), 3) at sites from which males have a better view of or are less visible to approaching predators (predator avoidance hypothesis), and 4) at sites where human-derived disturbances may be minimized (predator avoidance hypothesis). To investigate these questions, we carried out a detailed topographic analysis of the site selected by lekking males to perform their premating group display. Our sample was large (350 lek locations), and wide-ranging (distributed over all Spain), enabling a reliable characterization of lek-site selection in our study species. The long-term series of surveys at 2 intensive study regions (respectively, 7 and 13 years) provided an accurate delimitation of the distribution of females. Finally, our topographic analysis was based on a high-resolution digital elevation model (DEM), which made it possible to obtain very accurate viewsheds of the lek-site surroundings. The 5 m DEM

has been available only very recently, and a topographic mosaic at a geographic scale used here has never been achieved before in similar studies.

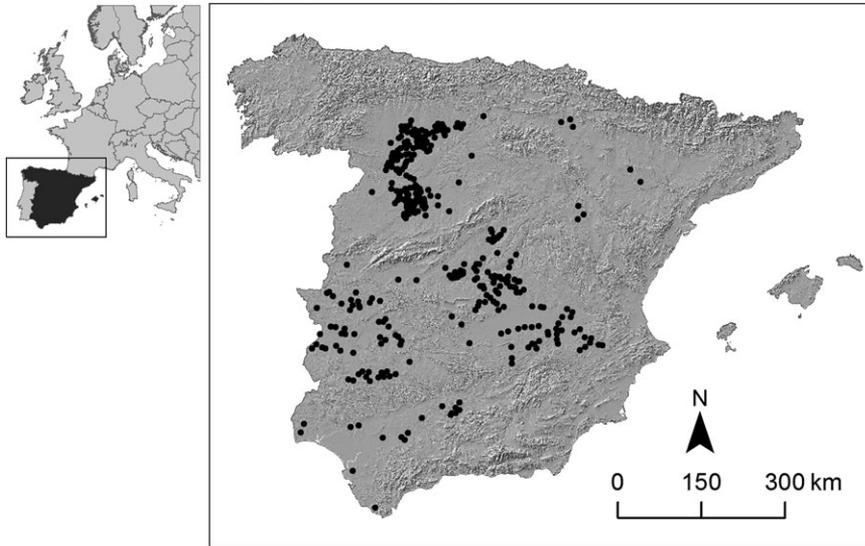
MATERIALS AND METHODS

Study species and lek census database

We used published and unpublished results of great bustard spring censuses carried out in Spanish regions during the last 2 decades (1988–2010; 1–14 years per region, mean = 5.5; Figure 1). Our most complete census reached 26 532 birds (between 77% and 90% of the, respectively, maximum and minimum population estimated for the whole country, Alonso and Palacín 2010), and covers all Spanish regions with great bustards. However, all available locations from multiple years were used to determine lek centers (see below). Spring censuses were normally conducted in late March by one or, in larger areas, more teams working simultaneously and in contact to avoid double counts of flocks. Each team consisted of 2 observers with extensive experience in great bustard surveys, operating from a 4-wheel drive vehicle, using binoculars and telescopes $\times 20$ –60, GPS and maps 1:10 000 to 1:50 000. Surveys started at dawn and ended at dusk, with a pause during midday (10:00–15:30 h GMT), when bustards lie down and become difficult to see. During one observation period, morning or evening, each team surveyed an area of approximately 50 km². The census itinerary was covered at low speed, with frequent stops at vantage points to carefully look for birds.

Adult males and females live in separate flocks throughout the whole year, and as a rule show marked lek-site fidelity (Alonso et al. 1995, 2000; Magaña 2007). Males arriving from the postbreeding or wintering areas start gathering at the lek area by December–January (Palacín et al. 2009). All males of a lek usually form a single flock in a specific site of the lek area that is repeatedly used year after year (Magaña 2007). Between January and late March (pre-mating period), males tend to keep remarkably close to this site, remaining as a flock within a small area (28–111 ha, mean = 69 ha, data from a 5 year study at 4 leks, Magaña 2007). Between late March and early April, males later disperse more or less radially from the site used by the flock to display as single individuals over a larger area and mate in April (exploded lek phase, Alonso et al. 2010a, 2010b; Magaña et al. 2011). We defined as “lek center” the location of the male flock during the late winter–spring censuses up to late March. In the present study, we were interested in this site selected by the male flock where they perform the communal display, not in the sites selected by each individual male after lek explosion. When late winter–spring censuses were available for more than 1 year, we calculated the centroid of all locations of the male flock in different years, and defined as lek center the flock location closest to that centroid. The sample for all Spain reached 350 lek centers (Figure 1). To assign great bustard flocks located during March surveys to mapped lek centers, we used a minimum distance criterion, refined with the presence of flock distribution discontinuities and significant physical barriers (roads, rivers, and high elevations), as well as with our experience from intensive study areas at 5 regions where we carried out long-term radio-tracking studies of several hundreds of marked birds during the last 2 decades.

For each lek center, we randomly generated alternative locations, which we defined as “random lek center,” within the minimum convex polygon of all flocks assigned to that lek center. To prevent random centers to be too close to lek centers, that is, within the small areas used by the male flock through the premating and mating periods, we constrained them to fall at > 1 km of lek centers (Figure 2).

**Figure 1**

Map of Spain showing the location of the 350 great bustard lek centers identified during censuses carried out in 1988–2010. Data sources by region (number of birds, census years, and authors): Andalucía (370; 1999–2010; Alonso et al. 2005; Junta de Andalucía, unpublished data); Aragón (111; 2003, 2004, and 2009; SODEMASA-Departamento de Medio Ambiente del Gobierno de Aragón, unpublished data; Torrijo A, unpublished data; own unpublished data); Castilla-La Mancha (7292; partial surveys 1994, 2001–2010; Estudios Territoriales Integrados SL, unpublished data; Palacín et al. 1996; Gosálvez et al. 2002; Campos B, Miñano R and Picazo J, unpublished data; Estudios Territoriales Integrados SL, unpublished data; own unpublished data); Castilla y León (14 101; partial surveys 1988–2010, complete surveys 1998, 2008; Alonso and Alonso 1990; Estudios Territoriales Integrados SL, unpublished data; Palacín and Alonso 2010; own unpublished data); Extremadura (3261; 2010; Dirección General del Medio Natural, Junta de Extremadura, unpublished data); Madrid (1372; 1997–2010; Alonso et al. 2005; own unpublished data); and Navarra (25; 2002, 2008; Onrubia A, unpublished data).

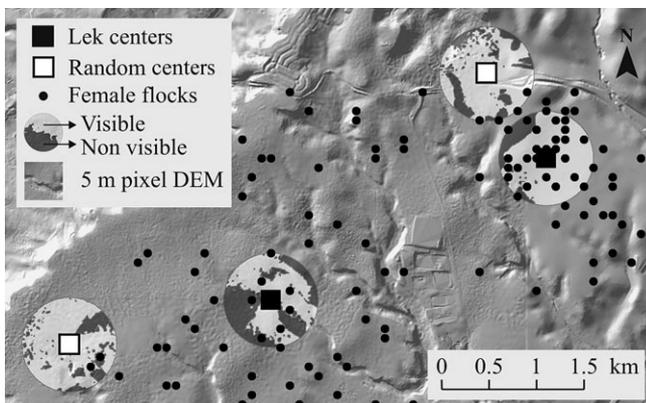
We mapped all lek and random centers onto a continuous DEM of 5-m spatial resolution (CNIG 2011) and made all calculations below, using ArcInfo desktop GIS version 10 (ESRI 2010).

Variables used

To characterize lek and random centers in relation to viewshed, topography, female distribution, and human infrastructures, we calculated the following variables (see Tables 1 and 2 and Figure 2):

(i) Viewshed

Visibility. We calculated the area visible from a lek center or random lek center as the number of 5×5 m pixels in the DEM that could be seen from it, that is, with no other pixel exceeding the elevation of a straight line between the lek center and the focal pixel. We performed short-range and long-range viewshed area calculations, to account, respectively, for an average escape distance from terrestrial predators and for maximum visibility of displaying males for searching females. In the first case, we set the maximum viewshed radius at 500 m. This is the average flight distance at which great bustards tend to escape approaching predators, including humans, or other sources of risk like cars in most areas (Sastre et al. 2009; personal observation). A similar distance (560–750 m) was the security band kept from roads in one of our study areas

**Figure 2**

Map of a sector of the study area in central Spain showing 2 great bustard lek centers (black squares) and their corresponding random points (open squares) in 2010, superimposed on the DEM. The circles around centers are the 500 m buffer zones, and within these, the visible area from lek and random centers is indicated in light gray and the non-visible area by a dark gray. Black dots are female flocks located during winter-spring censuses 1997–2010.

Table 1

Differences between lek centers and random centers in visibility, topographic features, and location with respect to human infrastructures

Variable (units)	Radius (m)	Lek centers mean \pm SD	Random centers mean \pm SD	Z	P
Short-range visibility (ha)	500	37.3 \pm 15.2	34.9 \pm 14.7	2.325	0.020
Long-range visibility (ha)	3000	351.8 \pm 252.7	337.1 \pm 260.8	1.016	0.310
Distance to nonvisible areas					
Minimum distance to a terrain unevenness (m)	500	81.6 \pm 69.6	58.7 \pm 60.2	4.828	<0.001
Mean distance (m)	500	363.7 \pm 26.2	356.3 \pm 22.6	3.375	0.001
SD	500	99.8 \pm 17.7	105.4 \pm 15.9	4.038	<0.001
Topographic variables					
Altitude (meters above sea level)	500	662.4 \pm 202.9	662.5 \pm 203.9	0.208	0.835
Curvature (dimensionless, from -1 to 1)	500	-0.0003 \pm 0.005	$6 \times 10^{-7} \pm 0.006$	4.796	<0.001
Slope (degrees)	500	2.082 \pm 1.256	2.249 \pm 1.439	6.771	<0.001
Roughness (degrees, SD of slope)	500	1.282 \pm 0.750	1.551 \pm 1.148	4.943	<0.001
Eastness (dimensionless, from -1 to 1)	500	0.630 \pm 0.091	0.623 \pm 0.096	0.084	0.933
Southness (dimensionless, from -1 to 1)	500	-0.009 \pm 0.300	-0.010 \pm 0.303	0.297	0.766
Location relative to human infrastructures					
Distance to roads (m)		1643.4 \pm 1075.5	1453.4 \pm 1082.7	3.186	0.001
Distance to urban nuclei (m)		3539.9 \pm 2002.5	3409.8 \pm 2033.6	2.172	0.030

Sample size = 350 lek/random centers of all leks identified during great bustard surveys in Spain 1988–2010. Radius: radius of the buffer around the lek center, where variables were measured; Z: Wilcoxon test statistic.

(Torres et al. 2011). In the case of long-range viewshed areas, that is, maximum visibility of displaying males for searching females, we set the limit at 3000 m radius from the lek center. We based our estimate on the published visual acuity values of birds, among which that of wedge-tailed eagles *Aquila audax* is the highest, being 2.5 times that of human eyes (Hodos 1993). Under ideal visibility conditions, a human eye can see a 1 m wide white object (ca. the maximum width of a full-displaying great bustard male) at 3437 m (Martin G, personal communication). Considering a range of potential acuities of 0.5–2 times that of the human eye, the visibility of a displaying male great bustard for a female would range between 0.5 and 2 times that distance, that is, 1718–6874 m. Adding the fact that at >3000 m, atmospheric conditions are likely to degrade the light between target and observer, a reasonable guess for the maximum distance at which a great bustard could see another one displaying would be 3000 m (Martin G, personal communication). Practical field trials showed that a flock of displaying male great bustards can be seen by the human eye at approximately 2–4 km depending on flock size light conditions (per-

sonal observation). Our estimated visual acuity might even be considered conservative considering the fact that great bustard males of a flock frequently display simultaneously and very close to each other, thus being visible at longer distances than single displaying males. To account for the height of males at the lek and females observing them, we added offset heights of 0.5 m to lek centers and 0.3 m to all other pixels. The 2 buffer zones (500 m radius and 3000 m radius) created around the lek and random centers were also used to calculate other topographic and female presence variables (see below).

Distance to nonvisible areas. We measured the minimum, mean, and standard deviation (SD) of the sample of distances between the lek or random center and all pixels of the 500 m buffer zone, which were not seen from the center. The minimum distance identifies the closest terrain unevenness or topographic obstacle that could create a nonvisible spot or small area where an ambush predator could hide, within a range close enough to the male flock to be potentially dangerous. Because a single elevated pixel could be close to the lek center just by chance, but isolated from other nonvisible spots and therefore, not easily accessible

Table 2

Differences between real lek centers and random centers in distance and visibility to females in the lek

Variable (units)	Radius (m)	Lek centers mean \pm SD	Random centers mean \pm SD	Z	P
(a) Overall female-lek distance (m)		2045.6 \pm 1399.6	2363.7 \pm 1319.6	18.482	<0.001
(b) Within lek female-center distance (m)		1851.8 \pm 648.3	2353.0 \pm 894.4	4.227	<0.001
(c) Number of females within buffer	500	137.5 \pm 135.4	62.4 \pm 71.9	2.746	0.006
	3000	1538.7 \pm 1125.3	1497.2 \pm 1223.7	0.638	0.524
(d) Number of females visible from center	500	92.0 \pm 100.6	38.3 \pm 58.1	2.543	0.011
	3000	327.1 \pm 431.2	188.3 \pm 335.4	3.363	0.001
(e) Number of females visible from lek or random core area	500	123.8 \pm 125.3	55.2 \pm 67.8	2.584	0.010
	3000	624.0 \pm 599.3	461.1 \pm 549.9	1.687	0.090

Sample sizes = (a) 5076 flocks; (b)–(e) 30 leks. Based on winter–early spring surveys carried out 1988–2010 at 2 intensive study areas in Villafáfila, northeastern Spain (19 surveys) and Madrid, central Spain (39 surveys). Radius: radius of the buffer around the lek center, where variables were measured; Z: Wilcoxon test statistic; lek and random core area: minimum convex polygon comprising the lek center plus 5 randomly generated replicas (see MATERIALS AND METHODS). (a) Mean distance of all female flocks to nearest lek or random center ($n = 5076$ flocks); (b) mean distance of each lek's female flocks to lek or random center (flocks assigned to lek centers using Thiessen polygons generated from a set of sample points, in this case, lek and random centers; each polygon defines an area of influence around its sample point, so that any location inside the polygon is closer to that point than any of the other sample points; Thiessen 1911; ESRI 2010); (c) numbers of females located within a 500/3000 m buffer around lek centers and random centers; (d) numbers of females located within the viewshed of lek/random centers at the 500/3000 m buffer; (e) same as (d), but using the accumulated viewshed of lek/random male flock core areas (centers plus their 5 replicas).

for an approaching predator, we also calculated the mean distance to all hidden pixels. This informs about the average location of all invisible areas within the 500 m buffer, and not only isolated pixels, with respect to the lek center.

To improve our visibility analyses, we also considered a more realistic scenario, where the male flock was mobile, rather than permanently fixed at the lek center throughout the display period. Our field observations indeed show that the male flock moves within an area of some tens of hectares around the lek center, displaying at variable intervals from different points around that center throughout the whole premating period (January–March; Magaña 2007). To simulate these flock movements, for each of the 350 lek centers, we generated 5 replicas within a radius of 500 m (one replica within every 100-m-wide-circular ring from the center). We then recalculated, within the 500 m lek center buffers, the accumulated viewshed from the minimum convex polygon comprising the lek center plus its replicas, which we defined as “lek center core area.” An equivalent “random center core area” was calculated for random centers, and the differences in the accumulated visibilities between lek and random core areas were tested. Assuming males moved in a circular area around our recorded lek center, a 500 m radius means 78.5 ha, very close to the mean surface obtained in a 5-year field study at 4 leks (69 ha; Magaña 2007).

(ii) Topography

Mean values and SDs of the following variables were obtained for all the pixels of the 5×5 m DEM in the 500 m buffers:

Altitude. Altitude above sea level, in meters.

Curvature. Curvature is calculated as the second derivative of the surface, which indicates whether a given part of a surface is convex or concave. Values vary from -1 (identifying valleys or concave surfaces) to 1 (convex parts like ridges, generally more exposed than other areas).

Aspect. Aspect defines the downslope direction of the maximum rate of change from each cell to its neighbors. It can be interpreted as the slope direction. Aspect has been calculated as a continuous variable with values from 1 to -1 (i.e., eastness and southness) to account, respectively, for east–west and south–north downslope directions.

Slope. Slope represents the maximum rate of change from each pixel to its neighbors, in degrees.

Roughness. SD of the slope, in degrees.

(iii) Female distribution

In addition to variables describing visibility and topography, we also wanted to examine where lek centers and random centers were located in relation to the distribution of females in the lek. Specifically, we aimed to test whether lek centers were located at closer distances to females than random centers and if from lek centers males could see more females than from random sites. Because a large data set was required to establish a reliable distribution of females within leks, for these analyses, we could not use the whole sample of 350 lek centers identified in Spain. We selected the 2 Spanish regions (Villafáfila and Madrid; 30 leks in total), where we had carried out in previous years long-term behavioral studies, including multiple surveys and also extensive radio-tracking of a large number of individuals through several years (respectively, >100 and >800 marked birds). We mapped all females counted during the months preceding the mating season (November–March, 19 surveys between 1988 and 2007 in Villafáfila, 39 surveys between 1988 and 2010 in Madrid; 5076 flocks and 54 858 individuals in total). We included the winter months because winter female distribution could also be relevant for the males' decision where to establish their lek site. This assumption is reasonable considering that males start aggregating at the lek site well in advance of the mating season, sometimes as early

as in December (Palacín et al. 2009; Magaña et al. 2011). We compared distances and visibilities between lek or random centers and female flocks using 5 variables (see Table 2).

(iv) Human infrastructures

Finally, to explore the possible effects of human infrastructures on lek center locations as compared with random points, we used 2 variables:

Distance to nearest road. Distance to nearest road is the straight linear distance from lek or random center to the nearest road (highway, main or secondary road);

Distance to nearest urban nucleus. Distance to nearest urban nucleus is the straight linear distance from lek or random center to the nearest city, village, or urbanized area.

The GIS database about human infrastructures (BCN200) at a 1:200 000 scale was obtained from CNIG (2011).

Statistical analyses

In a first step, we made bivariate comparisons of all predictor variables (see i–iv above) between lek centers and their matched alternatives, the random centers. Because data were in general not normally distributed (Kolmogorov–Smirnov and Shapiro–Wilk, $P < 0.01$), we used Wilcoxon matched-pairs signed-ranks tests. As a second step, to identify the most important among all predictors, we built Generalized Linear Models (GLZ) with binomial errors and logit function (McCullagh and Nelder 1989) using all independent variables and lek/random center as the response variable. We carried out this multivariate analysis initially with the whole sample of 350 leks for all Spain, including visibility, topographic, and human-related predictors. To reduce colinearity, we previously obtained a correlation matrix among all predictors and excluded the one with the least biological meaning from all pairs of correlated variables ($r_s > 0.7$, Spearman correlation) (Randin et al. 2006). All possible subsets of predictor variables were analyzed and Akaike's Information Criterion (AIC) was used to select the best subset, that is, that with the smallest AIC value, which indicates the most parsimonious candidate model. Models with $\Delta AIC < 2$ are considered as being substantially supported by the data and similar in their empirical support to the best model (Burnham and Anderson 2002). With all possible candidate models, we performed an average model estimation, in which the parameter estimates of all models were combined (Burnham and Anderson 2002). Finally, in a third step, we built the final GLZ using the procedure described in the second step, and the sample of 30 leks from the intensive study areas (Villafáfila and Madrid), and including the visibility, topographic and human-related predictors identified as significant in the model averaging in the previous step, plus the 2 predictors characterizing female distribution (Within lek female–center distance, and Number of females visible from the core area in a 500 m buffer), after discarding those that were correlated ($r_s > 0.7$) with other more meaningful variables. To further reduce the number of predictors to be included in the model with 30 cases, from the 5 predictors identified as significant after model averaging in step 2, we discarded Curvature which was the last of topographic variables. The 6 predictors finally included in these GLZ analyses are listed in Table 5. To assess the model fit, we used the *R*-square of Nagelkerke (R_N^2 , Nagelkerke 1991), which gives a measure of the approximate variance that is explained by each independent variable. The aim of this third step was to identify which predictors were statistically most important from the whole set of variables showing some degree of influence on lek location in great bustards in previous univariate and multivariate analyses. This should enable us to infer which of the main alternative hypotheses, hotspot, or predation

risk, seem more important from an evolutionary point of view in the selection of lek-site in this species or whether both of them are relevant. All statistical analyses were performed with IBM SPSS Statistics 19 (IBM Company 2010) and R 2.14.2 statistical software (R Development Core Team 2011).

RESULTS

The visibility of lek centers was higher than that of random sites, although differences were only significant within the 500-m buffer area (Table 1). From lek centers, great bustard males could see on average 47.5% of the 500 m buffer around them, a 7% more than from random sites. Considering a 3 km buffer, males could not see a significantly larger surface from lek centers than from random sites (Table 1). All 5 randomly generated replicas of the lek center had larger viewsheds than their paired random center replicas (respectively, 36.5, 36.2, 34.7, 31.6, and 28.8 ha for lek center replicas 1–5; and 34.8, 34.3, 33.5, 30.5, and 28.1 ha for random center replicas 1–5). However, the paired differences between lek and random replicas decreased progressively as the distance from replica to center increased (Figure 3). In other words, as simulated locations fell farther away from the actual center selected by displaying males, the benefit of a higher visibility from lek center compared with a random center vanished. The accumulated viewshed was slightly, but not significantly ($P = 0.312$) larger from the lek center core area (which simulated the male flock home range during the premating display period) than from the random center core area (respectively, 63.0 and 62.6 ha).

Compared with random sites, lek centers were a 39% farther away from the closest terrain unevenness or topographic obstacle creating a nonvisible area (Table 1). The average distance to all nonvisible pixels of the 500 m buffer was also greater in lek centers than random sites. This, together with the smaller SD of distance values indicates that nonvisible spots were distributed on a narrower more peripheral band of the buffer zone in the case of lek centers.

The 500 m buffer zones surrounding lek centers were more concave, horizontal, and flat than those surrounding random sites (Table 1). No differences were found in altitude and

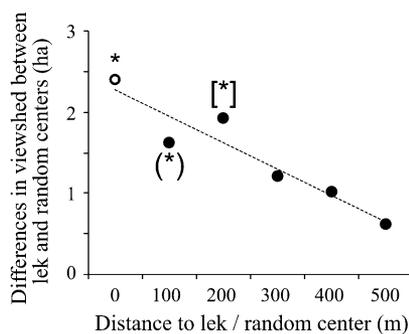


Figure 3

Decrease in viewshed gain of lek centers relative to random centers as the male flock location is simulated farther away from the actual center. Data points in the graph represent viewshed differences between lek center and random center (open dot), and their 5 replicas (black dots). The 5 replicas of lek/random centers were randomly generated within the 500 m buffers around the centers, each in one of the five 100-m-wide-concentric circular rings. The aim was to simulate possible alternative locations of the male flock during the premating display period. The graph shows a clear decreasing trend of the lek minus random difference for increasing distances to the center. The asterisks indicate statistical significance values: $*P = 0.020$, $(*)P = 0.074$, $[*]P = 0.058$, other differences not significant (Wilcoxon matched-pairs signed-ranks test).

mean aspect between areas around lek centers and random centers. Lek centers were located at farther distances from roads and human settlements than random centers, the differences being highly significant (Table 1).

As for the relationships with female distribution during the winter-early spring months, we found that lek centers were closer than random centers to female flocks, both considering the population as a whole and lek by lek (Table 2). The numbers of females around lek centers were higher than around random points, though differences were only significant in the case of 500 m buffers. Moreover, males selected lek centers from which they could see many more females compared with random points (140% and 74% more females, respectively, in the 500 m and 3000 m buffers; Table 2). Finally, the numbers of females seen from the simulated male flock core ranges were higher than from equivalent random core ranges (Table 2). The differences were highly significant with females in 500-m buffer zones. In the case of 3000 m buffer zones, differences were marginally significant with the nonparametric test, but significant using a paired t -test ($P = 0.039$).

Logistic regression analyses for lek-site selection with the sample of 350 leks known in Spain using all independent topographic and human-related predictors showed 2 plausible candidate models (Table 3). After model averaging, 5 variables retained by these models were identified as significant (Table 4). Incorporating a selection of the most important variables from these analyses (see details in MATERIALS AND METHODS) together with unrelated female distribution variables into a logistic regression resulted in 5 plausible candidate models (Table 5). The best of these models retained 2 topographic variables related to visibility (Roughness and Short-range visibility), 2 variables defining female distribution (within lek female-center distance and Number of females visible from core area in a 500 m buffer), and 1 variable indicative of human disturbance risk (Distance to roads). The other human-related variable (Distance to urban nuclei) was retained in the second, third, and fourth candidate models. The approximate variance explained by the model including these 6 predictors was 43.3% (Nagelkerke R^2). After model averaging, 3 of the variables retained by the 5 candidate models were identified as significant: Roughness, Short-range visibility, and Number of females visible from core area in a 500 m buffer (Table 6).

DISCUSSION

The results from our univariate analyses show that great bustard males lek at sites that increase their visibility to surrounding females, reduce the distance to them, enhance the probability of detecting approaching predators, and increase the distance to human disturbance sources. Logistic regression analyses confirmed these patterns and corroborated the importance of several variables defining visibility, female distribution, and human-induced risk in shaping lek-site selection in this species. A final model identified at least 5 relevant variables indicative of higher short-range visibility, more centered location with respect to females, and farther distance to sources of human disturbances of lek centers compared with random points. The 2 variables reflecting human-derived risk were excluded as significant predictors after model averaging, yet they were retained in most of the best candidate models for lek-site selection.

Increasing conspicuousness through selecting a lek-site with higher visibility has conflicting implications. On the one hand, it enhances the sexual advertisement efficiency of displaying males and thus may contribute to the female attraction effect attributed to leks. On the other hand, it increases exposure to predators, yet at the same time makes it also easier for males to detect approaching predators (Andersson 1994; Johnsgard

Table 3**Logistic regression models for lek-site selection using 10 variables characterizing visibility, topography, and distance to human infrastructures**

Model	AICc	Δ AIC	ω AICc
CURV + ROUGH + VISIBSHORT + DISTSHADOW + DISTROAD	945.45	0.00	0.41
CURV + ROUGH + VISIBSHORT + DISTSHADOW + DISTURBAN + DISTROAD	947.33	1.88	0.16
CURV + ROUGH + VISIBSHORT + DISTSHADOW	947.82	2.36	0.12
ROUGH + VISIBSHORT + DISTSHADOW + DISTROAD	948.10	2.65	0.11
CURV + ROUGH + LONGVISIB + VISIBSHORT + DISTSHADOW + DISTURBAN + DISTROAD	949.21	3.76	0.06
ROUGH + VISIBSHORT + DISTSHADOW	950.48	5.02	0.03
CURV + ROUGH + DISTSHADOW + DISTROAD	950.80	5.35	0.03
CURV + ROUGH + EAST + LONGVISIB + VISIBSHORT + DISTSHADOW + DISTURBAN + DISTROAD	951.17	5.72	0.02
ROUGH + DISTSHADOW	952.54	7.08	0.01
CURV + ROUGH + DISTSHADOW	953.02	7.57	0.01

Sample of 350 pairs of lek centers–random centers identified for great bustards in Spain. We show the best ten models ranked from best to worst according to Δ AIC, indicating AICc, Δ AICc, and Akaike weight (ω AICc) values. Models with Δ AIC < 2 are in bold. The following 10 predictors were included in these GLZs: Altitude (ALT), Curvature (CURV), Roughness (ROUGH), Southness (SOUTH), Eastness (EAST), Long-range visibility (VISIBLONG), Short-range visibility (VISIBSHORT), Minimum distance to a terrain unevenness (DISTSHADOW), Distance to urban nuclei (DISTURBAN), Distance to roads (DISTROAD).

1994; Höglund and Alatalo 1995; Bradbury and Vehrencamp 1998). To cope with different scenarios resulting from these trade-offs, we analyzed visibility at 2 different scales, short range (immediate surroundings of the lek center) and long range (area limited by the maximum estimated visual acuity of the species). The dissimilar results obtained for lek-random visibility differences at both scales suggest different explanations. Within a short-range scale, lek centers had significantly higher visibility than random points. This higher viewshed from lek centers was confirmed by the significantly higher values of parameters denoting horizontal visibility (minimum and mean distances to terrain unevenness places where ambush predators could hide, flatness, and degree of concavity). Great bustard leks are thus typically located in wide valleys or dips surrounded at a distance by low hills, coinciding with the usual situation described for sage grouse leks (Aspbury and Gibson 2004). For various reasons, we interpret that lek centers have been selected mainly to enhance short-range predator detection, rather than visibility to nearby females, although the latter may have also played a role. First, because when males start displaying in winter most females are not yet arrived at the lek center, and though within the lek area limits, they are often even far away and out of sight of the male flock (Palacín et al.

2009; Magaña et al. 2011). Second, because when females approach at 500 m to the males they surely need no additional increase in visibility to locate them. Third, risk perception by great bustards increases markedly at distances under 500–700 m (Sastre et al. 2009; Torres et al. 2011).

In contrast to the short-range visibility, long-range visibility was not significantly higher from the lek center than from a random site. This suggests that displaying males probably gain no benefit by increasing their long-range viewshed. It might even represent a disadvantage from the point of view of predation risk. For example, Aspbury and Gibson (2004) found that lek sites of sage grouse had lower long-range visibilities than random sites, and interpreted this as a way to reduce their vulnerability to golden eagles. In our study, when we combined long-range viewshed with female distribution, we found that the number of females visible from the lek center was significantly higher than the number of females visible from a random point. Curiously, these differences in visible females were highly significant in spite of similar absolute numbers of females within the 3 km buffers around lek and random centers. These results suggest that what is probably more important for displaying males at a long-range scale is to increase their visibility to possible mates looking at them from distant areas. Males apparently selected lek centers that maximized the number of visible females without further increasing their own conspicuousness to possible predators. Considering also the shorter average distance between all female flocks of the lek and the lek center compared with a random center, we can conclude that males selected lek sites that increased the probability of encounters with potential mates.

An interesting result of our study was the clear decreasing trend in the viewshed gain of lek center replicas versus random center replicas as the distance from replica to center increased. The interpretation of such decrease strongly supports the idea that lek centers are indeed selected to maximize visibility. This may be the reason why the home range of the male flock during the premating display period is so small and why this home range and specifically the lek center are remarkably fixed throughout consecutive years. Indeed, any movement away from that center would result in a decrease in the viewshed for the males.

Supporting the effect of predation risk on lek-site selection, we also found that lek centers were farther from roads and towns than random points. This means that males selected

Table 4

Model-averaged estimates of lek-site predictor variables selected in the 2 significant models of Table 3, listing relative importance (Σ , sum of Akaike weights of the models in which the predictor was present), regression coefficient (b), unconditional standard error (SE), and 95% coefficient interval (CI) for b

Predictor	Σ	b	SE ^b	Lower CI	Upper CI
ROUGH	1	-0.704	0.200	-1.10	-0.31
VISIBSHORT	1	-0.523	0.195	-0.91	-0.14
CURV	1	-0.365	0.173	-0.70	-0.02
DISTROAD	1	0.333	0.162	0.02	0.65
DISTSHADOW	1	0.606	0.168	0.28	0.94
DISTURBAN	0.28	-0.058	0.169	-0.39	0.27

Statistically significant predictors are in bold. Roughness (ROUGH), Short-range visibility (VISIBSHORT), Curvature (CURV), Distance to roads (DISTROAD), Minimum distance to a terrain unevenness (DISTSHADOW), Distance to urban nuclei (DISTURBAN).

Table 5

Logistic regression models for lek-site selection using predictors, indicating female distribution at the 30 pairs of lek centers–random centers in the 2 intensive study areas (Madrid and Villafáfila)

Model	AICc	Δ AICc	ω AICc
DISTFEMALES + DISTROAD + VISIBFEMALESSHORT + ROUGH + VISIBSHORT	73.19	0	0.16
DISTFEMALES + DISTROAD + DISTURBAN + VISIBFEMALESSHORT + ROUGH + VISIBSHORT	73.23	0.04	0.16
DISTFEMALES + DISTURBAN + VISIBFEMALESSHORT + ROUGH + VISIBSHORT	73.24	0.05	0.16
DISTROAD + DISTURBAN + VISIBFEMALESSHORT + ROUGH + VISIBSHORT	73.77	0.58	0.12
DISTFEMALES + ROUGH + VISIBSHORT	74.57	1.38	0.08
VISIBFEMALESSHORT + ROUGH + VISIBSHORT	75.86	2.67	0.04
DISTFEMALES + DISTROAD + DISTURBAN + ROUGH + VISIBSHORT	75.97	2.78	0.04
DISTFEMALES + ROUGH	76.91	3.72	0.03
DISTFEMALES + VISIBFEMALESSHORT + ROUGH	77.33	4.13	0.02
DISTFEMALES + DISTURBAN + ROUGH	78.06	4.86	0.01

We show the best 10 models ranked from best to worst according to Δ AICc, indicating AICc, Δ AICc, and Akaike weight (ω AICc) values. Models with Δ AICc < 2 are in bold. The following 6 predictors were included in these GLZs: Within lek female–center distance (DISTFEMALES), Distance to urban nuclei (DISTURBAN), Distance to roads (DISTROAD), Number of females visible from core area in a 500 m buffer (VISIBFEMALESSHORT), Roughness (ROUGH), Short-range visibility (VISIBSHORT).

to display those sites of the lek where the risk of encounters with humans—one of its main current predators—was low. Today great bustards, as many other lekking species, use humanized agro-steppes as surrogates of the primeval natural steppes, which constituted their original habitat. During the last tens of thousands of years, great bustards have coexisted with humans, first most likely as their prey as suggested by evidences dating from the 350 000–118 000 years old fossils (Sánchez 1995) or the Neolithic paintings in various Iberian sites (Brodick 1965; Acosta 1968; cited in Hidalgo and Carranza 1990) to Medieval times (Hernández 1993), and later persecuted as a game species especially during the display period at the lek (Chapman and Buck 1910; Trigo de Yarto 1993). Hunting has been identified as a major cause of population declines during the twentieth century worldwide in this species (Palacín and Alonso 2008). Today, great bustards surely still perceive humans as one of their main predators and have incorporated human-induced risks to their lek-site selection patterns. Although this is the most plausible interpretation of our results, we cannot discard that great bustards may form leks away from human develop-

ments in part to minimize noise disturbance (e.g., Francis et al. 2009; Barber et al. 2010).

Minimizing predation risk is indeed particularly important for species displaying in open areas. During both display and mating, males and females pay less attention to predators and are thus especially vulnerable. Great bustard males in particular experience a significant reduction in visual capacity during their characteristic balloon display, when they spend long bouts with a lowered head, contorted plumage, and up-raised whiskers at both sides of the head, obstructing their visual field. Whatever the mechanisms lekking species use to reduce predation risk, the fact is that low predation rates have been found in most lekking species (greater prairie-chickens *Tympanuchus cupido*, Berger et al. 1963; white-bearded manakins *Manacus manacus*, Lill 1974; golden-headed manakins *Pipra erythrocephala*, Lill 1976; sharp-tailed grouse *Tympanuchus phasianellus*, Oring 1982; black grouse *Tetrao tetrix*, Alatalo et al. 1991; greater sage grouse *Centrocercus urophasianus*, Gibson and Bachman 1992; Aspbury and Gibson 2004; lesser prairie chickens *Tympanuchus pallidicinctus*, Behney et al. 2011). Predation rate seems to be very low also in great bustard leks. During 640 whole-day observation periods through 8 years, at more than 10 leks, we did not observe any successful attack from raptors or mammalian predators. Due to their large size, great bustards seem to be less vulnerable to aerial than terrestrial predators. Indeed, very few predators other than humans (e.g., the wolf *Canis lupus*) live currently in great bustard areas in the Iberian Peninsula. Finally, we tested whether great bustards preferred surfaces that would maximize the efficiency of sexual communication by benefiting from the sunlight during early morning or late afternoon (i.e., lek-site facing, respectively, to east or west). Several species take advantage of particular lighting conditions to maximize visual contrasts of their displays (Théry and Vehrencamp 1995; Endler and Théry 1996; Heindl and Winkler 2003; Uy and Endler 2004; Dakin and Montgomerie 2009; Olea et al. 2010). Our results, as well as those of the study by Aspbury and Gibson (2004), did not support a significant effect of an increase in conspicuousness affecting the lek-site selection of a particular orientation to east (sunrise) or west (sunset).

Our results are compatible with both, the hotspot and the predation risk hypotheses of lek evolution. Discarding some

Table 6

Model-averaged estimates of lek-site predictor variables selected in the 2 significant models of Table 5, listing relative importance (Σ , sum of Akaike weights of the models in which the predictor was present), regression coefficient (b), unconditional standard error (SE), and 95% coefficient interval (CI) for b

Predictor	Σ	b	SE ^b	Lower CI	Upper CI
ROUGH	1	-2.76	1.090	-4.95	-0.57
VISIBSHORT	1	-2.16	0.891	-3.94	-0.38
VISIBFEMALESSHORT	0.88	1.92	0.956	0.0065	3.84
DISTFEMALES	0.82	-1.57	0.822	-3.22	0.07
DISTROAD	0.65	1.12	0.774	-0.42	2.67
DISTURBAN	0.64	-0.96	0.711	-2.39	0.46

Statistically significant predictors are in bold. Roughness (ROUGH), Short-range visibility (VISIBSHORT), Number of females visible from core area in a 500 m buffer (VISIBFEMALESSHORT), Within lek female–center distance (DISTFEMALES), Distance to urban nuclei (DISTURBAN), Distance to roads (DISTROAD).

lek evolution models as quite unlikely (e.g., information sharing or passive attraction), others as improbable for most birds (black hole model), or for species lekking year after year at the same place (hotshot model, see Höglund and Alatalo 1995), we centered our study on the 2 most probable candidate models explaining leks in great bustards and other bustard and galliform species displaying in open places, the hotspot and the predation avoidance models. Some decades ago, the predation risk hypothesis was already proposed to explain why most grouse of open habitats lek, while most forest grouse display solitarily (Wiley 1974; Wittenberger 1978, 1979). The argument was that forest environments are unfavorable for the evolution of leks because predator detection is difficult in thick vegetation (Trail 1987; and references therein). Compared with the hotspot hypothesis, only some studies have recently investigated the lek-site selection from the perspective of predation risk (e.g., Gibson and Bachman 1992; Gibson et al. 2002; Boyko et al. 2004) and only some have formally analyzed how signaling animals exploit topography to decrease predation risk (e.g., Aspbury and Gibson 2004). Our main interest in the present study was to find answers to where a lek should form, rather than to why leks form. Therefore, instead of trying to provide direct tests for all of the usually debated model predictions, we put the emphasis on analyzing the physical properties that might differentiate lek locations from random locations from the perspective of the 2 models considered as most probable.

With respect to previous studies, our study incorporates various methodological highlights that enable a detailed insight into this question and well-founded support for our conclusions. First, the wide geographic scale of our study area. Second, our sample of 350 lek sites covered a broad variety of topographic situations, a fact that strengthens the patterns drawn from the analyses by removing flaws typical of small sample sizes or restricted study areas. Third, lek locations and female distribution were based on, respectively, multiple annual or long-term series of surveys, which provided enhanced accuracy. Fourth, we included analyses dealing with the simulated movements of the males within their usual displaying range, a much more realistic scenario than just analyzing the differences between single fixed lek and random centers. Fifth, the selection of random points only within the area where flocks were located during surveys ensured that the patterns found refer specifically to lek-site selection and not simply to broad habitat selection by the species. Finally, to our knowledge, this is the first time a very high-resolution DEM (5 m) has been used to assemble a remarkably detailed landscape mosaic, significantly reducing the uncertainty typical of these models.

An aspect of lek location that has consistently evoked a relationship with predation is the marked fidelity to the lek site year after year. Lek stability is a puzzling and not yet completely resolved question about lekking, because even if it may contribute to attract predators (Wiley 1991; Balmford and Turyaho 1992), it seems an almost universal feature of leks in vertebrates (Bradbury et al. 1989; Wiley 1991; McDonald and Potts 1994; Höglund and Alatalo 1995; Widemo 1997; Castro et al. 2004; Hingrat et al. 2008). Remarkable lek-site fidelity is also the rule in great bustards (Alonso et al. 1995, 2000; Magaña et al. 2011). The idea that leks are generally in the same locations year after year possibly because they have proven to be safe in the past was already proposed by Lack (1968). Various studies supported later this hypothesis by showing an association between lek stability and certain topographical or habitat properties that may help individuals reduce predation risk (Trail 1985; Gosling and Petrie 1990; Deutsch and Weeks 1992; Westcott 1994; Aspbury and Gibson 2004). Indeed, the selection of a lek-site that offers these particular topographic features favoring either a higher concealment of displaying

males from predators, or a higher detectability of predators, might certainly be one of the factors conditioning the marked lek stability in many ground-displaying species.

In sum, we have provided evidence that simple physical factors enhancing visibility of the lek surroundings, together with female distribution and proximity of human infrastructures, affect the choice of lek location in the great bustard. We conclude that lek-site selection represents a combined response to selective pressures that have to do with female attraction (sexual selection) and defense against predators (natural selection). Within a range of possible sites fulfilling one of the main requirements of leks, that is, a maximum probability of encountering females (hotspot hypothesis), males may refine the selection by choosing sites that minimize predation risk, another important requirement (predation hypothesis). Both models are compatible and probably very important for all species, particularly for those displaying in open habitats and therefore most vulnerable to predators, like most lekking bustard and galliform species.

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