

Original Article

Male display areas in exploded leks: the importance of food resources for male mating success

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The distinction between true lekking and resource-defense mating systems is difficult in exploded-lekking species, where resources in male territories may influence female choice. Here, we propose the use of path analysis as a way to establish the relative importance of phenotypic characteristics versus food resources on mating success and hence decide whether a population is closer to one or the other extreme of an exploded lek-resource-defense continuum. Using great bustards *Otis tarda* as model species, we first performed logistic regression analyses of potential predictors of display sites in three leks. Males selected sites with high visibility, close to resources, and exposed to females. Second, we examined through path analysis how the mating success of radiotagged males was affected by resources, females and competitors, compared with age and weight, the major phenotypic correlates of mating success. The direct effects of age and weight were much higher than their indirect effects via resources or females. This suggests that female choice based on male characters is the most important sexual selection mechanism during mating and supports defining the great bustard mating system as a true exploded lek. However, half of the males showed a variable degree of resource defense toward intruders, indicating that both mating tactics, exploded lekking and resource defense, occur together in the same population. We suggest that individual variability in the use of resource defense might exist in many other exploded-lekking species, increasing the difficulties found in fitting their mating behavior to accepted definitions of alternative mating tactics. *Key words*: exploded lek, great bustard, mating tactic, *Otis tarda*, path analysis, resource defense. [*Behav Ecol*]

INTRODUCTION

In exploded leks, where males are less clumped than in classical leks (Emlen and Oring 1977), it is relatively frequent that male display areas may contain food or nesting resources useful for females. This raises the question whether in such cases females base mate choice just on phenotypic male characters, a fundamental assumption of lek systems, and casts doubts on whether some exploded leks should be considered true leks. Therefore, in studies of exploded-lekking species, it has often been difficult to define clear limits between a *true exploded lek* system, where male territories may contain resources but these are not critical for females and do not influence mate choice, and two systems where resources play a role, namely the *resource-based lek*, where males display close to resources useful for females (frequent in insects, Alexander 1975; Thornhill and Alcock 1983; but rare in birds, Stiles and Wolf 1979) and the *resource defense (or territorial) polygyny*, a nonlekking system in which females feed and breed within male territories, and male attractiveness is related to within-territory resources (Höglund and Alatalo 1995; Ligon 1999). For example, Jiguet et al. (2000, 2002) observed little bustard *Tetrax tetrax* males

defending resources used by females but concluded that male attractiveness was related to phenotypic characteristics and not to resources. They interpreted the system as a true exploded lek but admitted serious difficulties in defining the limits between resource-defense polygyny and extreme exploded or resource-based leks. In a different study area, Delgado et al. (2010) found that little bustards might not employ a lek system, even though certain features of exploded leks were met. Houbara bustards *Chlamydotis undulata* also show a somewhat undefined mating system, which Hingrat et al. (2007, 2008) found fitting an exploded lek because males were apparently unable to monopolize the uniformly distributed food resources in their display territories. In a recent study with the cichlid fish *Simochromis pleurospilus*, Kotrschal and Taborsky (2010) found that in spite of homogeneously distributed resources and male and female dispersion patterns fitting the definition of an exploded lek, males were able to create high-quality feeding patches for females through defense, a key feature of resource-defense mating systems. The authors concluded that this system could not be unambiguously assigned to one mating system category. The presence of males exhibiting similar resource-defense mechanisms has been described in other typically exploded-lekking species from various animal taxa (e.g., Uganda kob *Adenota kob*, Leuthold 1966; topi antelopes *Damaliscus lunatus*, Gosling and Petrie 1990; Bro-Jorgensen 2008; see review for ungulates in Isvaran 2005; red-headed manakin *Pipra rubrocapilla*, Castro-Astor et al. 2004; purple-throated carib *Eulampis jugularis*, Wolf 1975; wool carder bees *Anthidium spp.*, Sugiura 1991; Würtz 1992).

This wide spectrum of taxonomic groups where it has been difficult to distinguish true lekking from resource defense suggests that a continuum between both mating systems

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might be a universal phenomenon, both between populations of a given species and between individuals within the same population. One way to examine whether a population is closer to one or the other extreme of an exploded-lek resource-defense continuum is to establish the relative importance of phenotypic characteristics versus food resources on the mating success of individual males. Here, we propose the use of path analysis, also known as causal modeling (Wright 1934; Li 1975), as an appropriate analytical tool to establish these relative importances. As for within-population variability in mating behavior, it is common in diverse animal taxa (Davies 1991; Lott 1991; Gross 1996; Brockmann 2001), but indeed has been shown to be particularly marked in lekking species, both in birds and ungulates (Johnsgard 1994; Jiguet et al. 2000; Isvaran 2005). Moreover, at least in birds exploded-lekking species are more likely to show intraspecific variation in their mating system than classical-lekking species (Jiguet et al. 2000). In the present study, we explore individual variability in mating tactics through individual marking.

We combined high-resolution topographic analyses, detailed food resource estimates, and intensive radio-tracking of marked birds to investigate the role of food resources and male and female distribution in the lek on male mating success in the exploded-lekking great bustard *Otis tarda*. Bustards are good model species to study the phenomenon of a continuum between exploded lekking and resource defense because on the one hand, exploded leks are the most widespread mating system in this family, and on the other hand, many bustard species show a variety of mating systems (Johnsgard 1991; Jiguet et al. 2000; Morales et al. 2001). First, we analyzed the patterns of display-site selection in males using a set of predictors including topography, visibility, and distribution of food resources and females. Our objectives were 1) to determine whether display-site selection by males was mainly related to the distribution of resources or females and 2) to examine whether changes in male and female distribution during lek explosion supported a true lekking structure in great bustards, as opposed to resource-defense polygyny. Briefly, the process

leading to the exploded lek in this species is as follows. In winter, all males of a given lek are usually aggregated in a single flock at a traditional lek centre, where they perform communal display to establish a hierarchy (Alonso, Magaña, Martín et al. 2010; Magaña et al. 2011). During winter, and up to the mating time, female flocks are dispersed over fields with food resources. From late March, males start splitting up to display as singles close to females (exploded lek) and flock together again at the end of the mating season (early May, Magaña 2007; Alonso, Magaña, Palacín et al. 2010; see Figure 1). Thus, in agreement with a male dominance polygyny typical of lek systems (see Höglund and Alatalo 1995), we hypothesized that the time sequence of events was as follows: resources attract females (winter), females attract males (lek explosion), males display close to females (exploded lek phase), and finally single females approach selected males for copulation (mating period). An alternative hypothesis compatible with resource-defense polygyny would be that solitary males dispersed first to occupy resources and used them to attract females.

Second, to corroborate the patterns found in the display site-selection analysis and investigate whether patterns varied among individual males, we studied the behavior of marked males. Specifically, we aimed to ascertain 1) whether display areas were of exclusive use by individual males and 2) whether food resources found within male display areas and used by females affected male mating success, compared with male age and weight, the two phenotypic characteristics which we already know are important mating success correlates (Alonso, Magaña, Palacín et al. 2010). In a true exploded lek system, we should expect male distribution to fit resource distribution but no influence of resources on male mating success. Thus, older and heavier males would have high mating success, independently of resources in their display areas. If mating success is more influenced by the amount of resources, the system could not be defined as a true lek: in that case it would be either a resource-defense polygyny (if access of females to resources was controlled by males) or a resource-based lek (if access was not controlled by males).

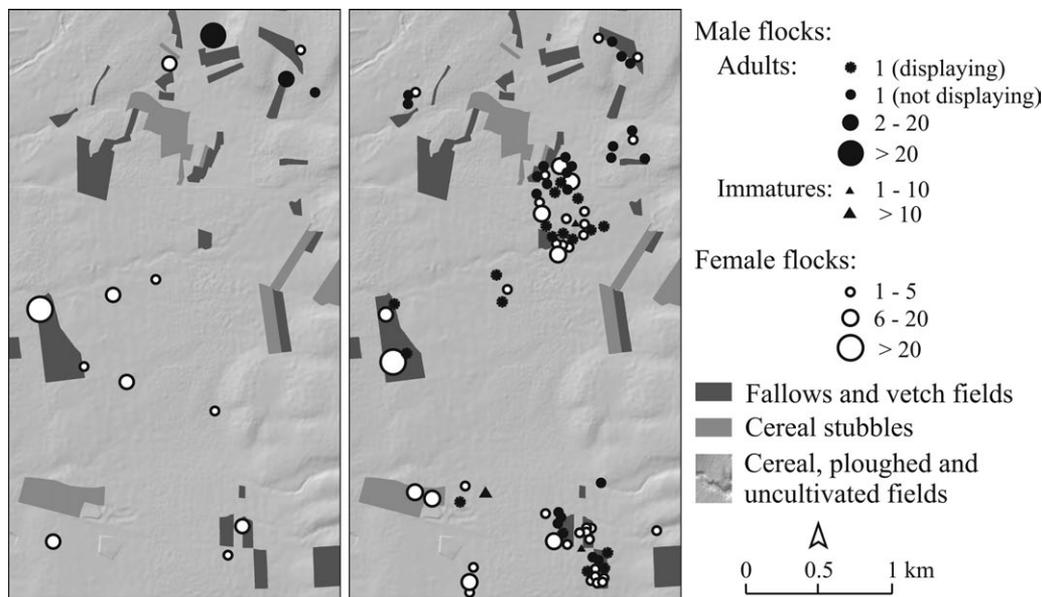


Figure 1

Maps of the central sector of lek "Campo Albilló," before male dispersion from the winter flock (left map, 27 March 2000) and once all adult males were established in their display areas in the exploded lek (right map, 12 April 2000) as an example of the process of lek explosion. Females were generally foraging on fields with food resources prior to the start of the exploded lek phase, when males dispersed from the centrally located winter male flock to approach foraging females. Males performing display just when we carried out the survey are indicated by asterisks, but any of the nondisplaying males could perform display shortly before or after our survey was done.

We used path analysis (Wright 1934; Li 1975) to examine this web of relationships and obtain a model providing an appropriate interpretation of the mating system of great bustards. Based on our knowledge of the mating biology of the study species, we proposed an initial path model, examined whether it adequately described the relationships among variables, and improved the model fit by deleting nonsignificant variables or paths. The final model helped understanding the relative importance of each variable in our system (Pedhazur 1982). Finally, path analysis enabled us to 1) evaluate the relative importance of two sexual selection mechanisms (male–male competition versus female choice) during the mating phase. Very few studies have used path analysis to quantify alternative sexual selection mechanisms important in mating systems (e.g., Sheldon and Ellegren 1999; Sih et al. 2002), in spite of the potential of this technique as a means of comparing the relative importance of different causal pathways of selection (Kingsolver and Schemske 1991; Mitchell 1992; Irschick et al. 2008). In our system, older males detach earlier from the male flock in spring and display longer time as singles to attract females, which results in a higher mating success (Alonso, Magaña, Palacín et al. 2010). However, it is not known whether this positive effect of age, as well as that of a higher weight, is attained through direct female preference based on assessment of plumage sexual traits of males or through male–male competition which would enable older and heavier males to move freely through the lek and spend longer time displaying as singles because they are recognized as dominants by other males (Alonso, Magaña, Palacín et al. 2010; Alonso, Magaña, Martín et al. 2010; Magaña et al. 2011). Path analysis helps evaluating the relative importance of these two behavioral mechanisms via comparison of the magnitudes of direct versus indirect effects of the path diagram (e.g., Sih et al. 2002). If female choice is more important, we should expect a higher magnitude of age and weight direct effects on mating success. If male–male competition is more important, age and weight should show higher indirect effects through intermediate variables such as more food resources, more females using these resources, or fewer competitor solitary males within display areas.

MATERIALS AND METHODS

Study area

The study was carried out in the Special Protection Area for Birds no. 139 (40°45' N, 3°30' E; 33 110 ha), central Spain, where a population of ca. 1000 great bustards is distributed among 8 leks (for details, see Alonso et al. 2003). Great bustards live in open, flat to gently undulated areas with an average altitude of 650 m a.s.l. The land is mostly cultivated with cereal (mainly wheat and barley). Some minor crops are legumes, olive trees, and vineyards. The Mediterranean climate of the area is characterized by dry, hot summers, and cold winters with moderate rainfall (ca. 500 mm per year).

Distribution of resources, females and males in the lek area

To study display-site selection, we compared display sites with random points using a set of predictors and later built multivariate models of display sites. During the mating periods (late March to early May) of 1998–2003, we carried out weekly surveys of all great bustards found at 3 leks in Madrid province, central Spain (Campo Albillo, Muela, and Camarma). The sum of individuals at these 3 leks during the study period was relatively stable at 104–119 males and 340–385 females. We defined lek area as the minimum

convex polygon containing all great bustard locations during the mating period through the 6 study years. Leks were usually surrounded by areas not used by great bustards. In case of 2 neighbor leks to delimit the borders between both lek areas, we used our extensive database of marked bird locations gathered during our long-term radio-tracking study in the last 2 decades. In each survey, one observer mapped all birds at 1 lek, using maps 1:10 000 and ×20–60 telescopes from one or more vantage points, from which he could see the whole lek area (respectively, 1304, 899, and 1004 ha for the 3 leks). A lek survey covered the period of highest sexual activity (Magaña 2007; Alonso, Magaña, Palacín et al. 2010), starting at dawn and ending 60–120 min later, depending on number of birds and their dispersion. For each bird or flock, we recorded the age composition (for display-site selection analyses, we used only adult males (≥4 years old, Alonso et al. 2006), substrate (cereal field, ploughed field, stubble, fallow, vetch, uncultivated with trees or bushes), and activity (feeding, resting, standing vigilant, displaying). Before starting the surveys, the substrate type of each field was registered on the map and updated weekly through the study period.

From lek surveys, we extracted the sample of adult males displaying as solitary individuals in each year (yearly samples varied between 25 and 40 males for 1998–2003, see Table 1; within each year, display sites of the 3 leks were added into a single sample, after checking that there were no between-lek differences). For each year separately, display sites were compared with an equal sample of points generated randomly within the 3 lek areas, taking care that numbers of random points were equal to numbers of display points in each of the 3 leks. To avoid within-year pseudo-replication of display locations, of the 5 weekly great bustard surveys performed per year, only that one showing the highest dispersion of displaying males in each year (usually coinciding with the peak mating frequency between the 2nd and 3rd weeks of April, Magaña 2007) was used for display-site-selection analysis. All other weekly surveys (25 in total in the 6 study years) were discarded for analyses and were only used to 1) examine whether females or males used food resources first (see below) and 2) ensure that random points did not fall at <100 m of any male display site recorded in any of the selected or discarded surveys.

We mapped all display and random sites and made all calculations below using ArcInfo desktop GIS version 10 (ESRI, 2010). Display and random sites were characterized through the following variables defining important selection aspects related to topography, viewshed, and distribution of resources, females and competing males (see Table 1):

(i) Topographic variables: We characterized the relief of the terrain through the variable *Roughness*: standard deviation of the slope (i.e., of the maximum rate of change from each pixel to its neighbors, in a 500-m buffer around the display or random point), in degrees (obtained from a 5-m spatial resolution digital elevation model [DEM], CNIG, 2011).

(ii) Viewshed variables: We calculated the area visible from a display site or random point as the number of 5×5 m pixels in the DEM which could be seen from it, that is, with no other pixel exceeding the elevation of a straight line between the display/random point and the focal pixel, within a circular buffer zone set by a predefined maximum distance. First, we calculated a *Short range visibility* to account for the visibility of the displaying male to females located within an area equivalent to the male's home range during the mating period. Assuming this home-range circular, with a surface equal to the mean extent of the display area of our sample of 16 radio-tracked adult males (31.4 ha, see below), the radius of this *Short range visibility* buffer would be 316 m. During random-point generation, we took care that none of these 316 m

Table 1

Differences between display sites of males and random points in topographic features, visibility, and presence of conspecifics and food resources within a buffer of 316 m radius around the display/random point

Variable name (units) ACRONYM	Differences between display sites and random points: <i>P</i> -values and significance after Holm–Bonferroni correction*						Means ± SD of yearly values 1998–2003	
	1998 <i>n</i> = 35	1999 <i>n</i> = 27	2000 <i>n</i> = 29	2001 <i>n</i> = 40	2002 <i>n</i> = 32	2003 <i>n</i> = 25	Display sites	Random points
<i>Topography</i>								
Roughness (degrees, SD of slope) ROUGH	0.000*	0.021	0.004*	0.361	0.778	0.154	1.36±0.2	1.78±0.24
<i>Visibility</i>								
Long range visibility (ha) (up to 2000 m) VISIBLONG ^a	0.012*	0.924	0.001*	0.194	0.020	0.491	238.55±29.47	191.03±20.81
Short range visibility (ha) (up to 316 m) VISIBSHORT ^b	0.058	0.144	0.078	0.459	0.361	0.097	17.13±1.38	15.15±1.11
<i>Individuals visible in the 316 m buffer^c</i>								
Number of males visible VISIBMALES	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	10.03±5.5	0.42±0.1
Number of females visible VISIBFEMALES	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*	9.09±2.24	1.16±1.01
Estimated food resources in the 316 m buffer ^d RESOURCES	0.000*	0.000*	0.216	0.000*	0.762	0.001*	3.09±1.03	1.88±0.33

Display sites and random points were recorded at 3 leks in central Spain through 6 consecutive years (1998–2003). Data are *P*-values between display sites and random points, and asterisks denote the significance of the differences after Holm–Bonferroni correction (Mann–Whitney test). For each variable, the signs of the differences between display sites and random points were identical among years and coincided with those shown in the last two columns, which give the means and SD of the 6 yearly values 1998–2003.

^a 2000 m is a conservative guess for the distance at which a great bustard could see another one displaying (G. Martin, in litt., see MATERIALS AND METHODS).

^b 316 m is the radius of the average display area extent of a sample of 16 radiotracked males; so this buffer represents an average display area (see MATERIALS AND METHODS).

^c Number of males and females in the buffer of 316 m radius around the display or random point, which were visible from the display/random point.

^d Based on arthropod abundance and weed cover (see MATERIALS AND METHODS for details).

buffers intersected the lek area perimeter. Second, we calculated a *Long range visibility* buffer of 2000 m radius to simulate the maximum distance from which a displaying male would be seen by other bustards in the lek (visual acuity estimated by Graham Martin, in litt.).

(iii) Visibility to other males and females: The *Number of females and males visible* within the 316-m buffer around the display site was intended to show whether displaying males could be seen by a larger number of females (possible mates) and males (possible competitors that could provoke a copulation disruption). A higher number of females within sight of the displaying male would increase its mating opportunities by enhancing the attraction potential of its display. On the other hand, a higher number of males within sight of the displaying male would increase the probabilities of an aggressive encounter (attack, displacement, or copulation disruption, see Magaña et al. 2011).

(iv) Distribution of resources: Through the variable *Estimated food resources in the buffer*, we aimed to quantify the value of food resources within the 316-m buffer around the display site. Based on substrate selection by females during spring (Magaña 2007), diet composition based on fecal analyses, and arthropod density and weed cover values obtained through transects (Alonso JC, Magaña M, Álvarez-Martínez JM, unpublished data), we quantified the value of each substrate type as a food resource for a female, obtaining resource values of 62 for fallow fields, 55 for vetch fields, 45 for stubbles, 5 for cereal fields, 4 for ploughed fields, and 0 for uncultivated fields.

Finally, we measured the distance from each solitary male and female flock on the date of maximum dispersion in April (exploded lek) to the nearest location of, respectively, male

and female flocks just before lek explosion (late March). To determine which of the two hypothesized processes was correct (i.e., resources first attract females, then females attract males—compatible with lekking system—versus exploded males occupy territories with resources prior to female arrival—compatible with defense polygyny), we compared the distributions of males and females and the distances moved by both sexes between late March and late April (maximum dispersion of males during the peak exploded lek phase).

Study of marked males

We studied the use of space in 16 adult males at the 3 leks through radiotracking. Limited capture permits of this endangered species did not allow increasing of this sample size. The birds were captured with rocket nets in February, 2 months before the peak mating season, and fitted with a backpack radio transmitter (TW3 model, Biotrack Ltd., UK) using elastic band as harness material. In addition, birds were provided with polyvinyl chloride (PVC) wing tags or dorsal tags glued to the transmitters for visual identification in the field. The birds were weighed, and their age estimated using our own results from a previous study based on 31 males captured as chicks and radiotracked over 10 years between 1987 and 1999 (Alonso et al. 2006). In that study, we proposed a method to estimate the age of great bustard males based on the following criteria: 1) a gradual increase in the extent and brightness of the white color of the upper neck, 2) the contrast between this and a progressively more intense chestnut brown at the neck base, 3) the front shape of the chestnut collar which in birds aged 7–8 is open, with the white of the upper neck reaching the lower breast, 4) a bare skin streak

that is visible below the chin along both sides of the neck in birds aged 7–8 years, and 5) the length of breast feathers. A combination of rank values for the above criteria allowed us to estimate ages ≥ 8 years, covering the average longevity of great bustard males (estimated at ca. 8–9 years according to a large sample of marked birds; Alonso JC et al, unpublished data). We repeated these age estimations for each male several times through the mating season to check for possible changes in rank values assigned due to variable light conditions or bird postures. Of course, this age estimation may be subject to some uncertainty, which we could guess at ± 1 year (see details in Alonso et al. 2006, Fig. 1b). To maximize the reliability of our age-assignment technique, we continued ageing our males during 2–6 years after ending the present study. Because any possible errors in age estimation were small and age had been shown to correlate with mating success in previous studies with larger samples of birds including some marked as young (Alonso, Magaña, Palacín et al. 2010; Alonso, Magaña, Martín et al. 2010), we do not think that these small errors would have significantly affected the results of the current study. Marked males were tracked 2–3 days per week more than 2–3 mating seasons following capture (from the last week of March to the second week of May). Observations were carried out from ground vehicles at 1–3 km from the focal bird using $\times 20$ –40 and $\times 60$ –90 telescopes, covering the period of highest sexual activity between dawn and 1300 h. Each observer tracked one male per day, recording continuously its behavior (feeding, vigilance/resting, lying, aggression, display; details in Alonso, Magaña, Palacín et al. 2010), whether the male was in a flock or as single, and its itinerary on a 1:10 000 map containing all details necessary for a precise location.

We calculated each male's *Display area* as the minimum convex polygon containing all locations where the male was observed single during the mating season. In exploded leks, these display areas may be considered the equivalent to male territories in classical leks. We also recorded ad libitum the position of any male or female in the surroundings (up to ca. 1 km) of our focal male and any possible interactions among them. For each male, we calculated an estimated *Mating success* as the number of observed effective copulations plus copulation attempts per 10 h, defining these as only those instances when a male was seen full displaying in very close proximity to one or more females (< 3 m), and these females showed obvious precopulatory behavior, that is, by approaching him and turning around him to inspect his plumage, ending up pecking his cloacal region. Copulation attempts were added to increase the typically low number of observed copulations in this species and obtain a statistically more practical parameter. In a larger sample of 48 males from previous studies, frequency of affective copulations and attempts were indeed correlated (more details in Alonso, Magaña, Palacín et al. 2010; Alonso, Magaña, Martín et al. 2010). We also calculated the following variables defining the amount of resources and the presence of females and males within the male's display area. *Food resources*: we calculated the percent represented by the three main food resources in the male's display area (resources used by female great bustards were fallow, vetch, and stubble fields, see above, (iv) Distribution of resources) with respect to total food resources in the lek area; *Percent females*: mean percentage of all females of the lek observed within the display area through the mating season; *Density of solitary males*: average number of solitary displaying males per hectare within the display area through the mating season; *Quota of females*: average number of females divided by number of males within 500 m from the focal male through the mating season; this variable helped identifying those males who displayed close to a high number of females and at the same time a low number of

solitary males which could be possible competitors disrupting their displays or copulation attempts; this situation could be either because the focal male inspired respect and was avoided by other males or because the focal male actively defended and excluded other males from his display area; *Distance to nearest solitary male*: mean of all hourly distances in meters to the closest solitary male through the mating season. Finally, we also calculated a *Display site defense rate* as the number of aggressions to other males of the lek per 100 min, which could be interpreted as some kind of territorial defense actions (e.g., displacements, direct attacks, threats that stopped approaching males) and where the focal male starting the aggression was the winner. Because there were no significant differences between years in any of the behavioral parameters (Alonso, Magaña, Palacín et al. 2010; Alonso, Magaña, Martín et al. 2010), we used the mean values obtained through the 2–3 tracking years. As for weight, we only had the value of the first tracking year, when the birds were captured. However, as shown in Alonso, Magaña, Palacín et al. (2010), correlation analyses using only the first year gave identical results to those using the means of all years (in both cases, significant partial correlations of estimated mating success with age and weight: respectively, $r = 0.49$, $P = 0.026$ and $r = 0.42$, $P = 0.033$, $F = 4.63$, $P = 0.013$ for first year data; $r = 0.47$, $P = 0.025$ and $r = 0.41$, $P = 0.043$, $F = 4.54$, $P = 0.015$ for means of all years).

Statistical analyses

Display-site selection in males

In a first step, we made bivariate comparisons between display sites and random points for all predictor variables selected to characterize display sites (see *i*, *ii*, *iii*, and *iv* above). Because data, in general, were not normally distributed (Kolmogorov-Smirnov and Shapiro-Wilk, $P < 0.01$), we used Mann-Whitney *U*-tests. To avoid pseudo-replication, we analyzed the differences between display and random sites separately for each year, and to estimate significances of these differences, we applied Holm-Bonferroni correction, a powerful method to counteract the problem of multiple comparisons (Holm 1979). Performing display-site-selection analyses over 6 years rather than in a single year was useful to 1) guarantee a more accurate delimitation of the lek areas and a more precise differentiation of areas not used by males to display, that is, where random points (pseudo-absences) should be generated, and 2) provide a more reliable, multiple-year mean estimate for each variable characterizing display-site selection, and some kind of sensitivity analysis of the trend and magnitude of the difference between display and random points (see also Fang et al. 2007; Álvarez-Martínez et al. 2011).

In a second step, to identify the most important among all possible predictors, we built for each year separate Generalized Linear Models with binomial errors and logit function (McCullagh and Nelder 1989) using noncorrelated predictor variables and display/random point as the response variable. To reduce colinearity, we previously obtained for each year a correlation matrix among all predictors and excluded the one with the least biological meaning from all pairs of correlated variables ($r_s > 0.5$, Spearman correlation in at least 3 of the 6 years) plus *Long range visibility* (significantly correlated with *Roughness* and *Short range visibility*, and less important than the latter for the purposes of this study; 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. Models with $\Delta AIC < 2$ are considered being substantially supported by the data and similar in their empirical support to the best model (Burnham and Anderson 2002). With all candidate models for each year, we performed an average model estimation, in which the parameter estimates of all models

were combined (Burnham and Anderson 2002). Finally, to estimate the relative importance of each variable in the combined 6 yearly analyses, for each predictor we calculated the mean and standard deviations of the relative importance (Σ , sum of Akaike weights of the models in which the predictor was present), mean and standard deviations of regression coefficient (b), and mean values of 95% confidence interval (CI) for b . To assess the model fit, we used the R-square of Nagelkerke (R^2_N , Nagelkerke 1991), which gives a measure of the approximate explained variance compared with the total variance of the data. The aim of this analytical second step was to identify which predictors were statistically most important from the whole set of variables showing some degree of influence on display-site location by great bustard males in univariate analyses. All statistical analyses were performed using IBM SPSS Statistics 19 (IBM Company 2010) and R 2.14.1 statistical software (R Development Core Team 2011).

Path analysis of male mating success

Although causality cannot be easily modeled with standard regression techniques, path analysis allows evaluating the relative importance of each link in the path diagram. This technique has been successfully used to investigate causal relationships in various other sexual and natural selection processes (e.g., Pedhazur 1982; Arnold and Wade 1984; Arnqvist 1992; Mitchell 1992; Scheiner and Callaghan 1999; Sih et al. 2002; Lehmann et al. 2007; Oufiero and Garland 2007; Fanson et al. 2011).

The age, weight, and various estimators of resources, abundances of females and males within the display areas of the 16 radiotracked males were entered into a path analysis to assess the relative contributions of each variable and each pathway in determining mating success. Following our hypothesis (see INTRODUCTION), we wanted to test whether a possible effect of food resources controlled by older (and/or heavier) males was significant in increasing their mating success, and in that case, how large this effect was compared with the effect of age and weight known from previous studies. Thus, in the path diagram, we included food resources as an endogenous variable linked to age as the main exogenous variable. A similar link with weight was initially tested but later discarded in the final version after model pruning (see Figure 2). A previous study showed that the age of male great bustards is positively correlated with display effort, calculated as the first principal component of a PCA including 12 variables measuring display duration and frequency ($r = 0.41, P = 0.05$, Alonso,

Magaña, Palacín et al. 2010). In addition, inclusion of display effort decreased the model fit, showing a nonsignificant standardized partial regression coefficient of only 0.244 between display effort and mating success. Therefore, because of that age-display effort correlation, and to avoid model overfitting, display effort was excluded in the final model. We assessed the relative weights of each causal relationship linking age and weight with mating success by calculating the standardized partial regression coefficients (β s), which measure the relative strength of the link, and enabling to identify the more influential variables in the path diagram. Standardized regression coefficients allow comparing direct effects of the exogenous variables (age, weight) on mating success with their indirect effects (obtained by multiplying the coefficients of the successive links; see Alvin and Hauser 1975; Sih et al. 2002). This should also enable us to infer which of the main alternative behavioral mechanisms, male-male competition or female choice, seems more important in generating sexual selection in this species, or whether both of them are relevant (Bart and Earnst 1999; Sih et al. 2002).

We examined the effects of minor changes in the diagram (adding or deleting a variable or link), and observed that they did not alter the qualitative results. Starting from an initial model including all biologically meaningful variables and possible relationships, we slightly modified some to check whether the model fit improved. As our final model, we selected that showing the highest fit values with the lowest number of variables and effects, provided no conceptually important effect was suppressed. Model fit was examined using the most frequently used model fit indexes: Pearson χ^2 generalized likelihood ratio, minimum discrepancy CMIN/DF, comparative fit index (CFI), root-mean-square error of approximation (RMSEA), AIC, and its Bozdogan’s consistent version CAIC, Browne-Cudeck criterion (BCC), and Bayes information criterion [BIC; see contents of IBM SPSS AMOS 19 (IBM Company 2010) and Marcoulides and Hershberger (1997)]. Path analyses were performed with IBM SPSS AMOS 19 (IBM Company 2010).

RESULTS

Display-site selection

During the peak mating period in mid April (exploded lek phase), the mean distance from a displaying male to the

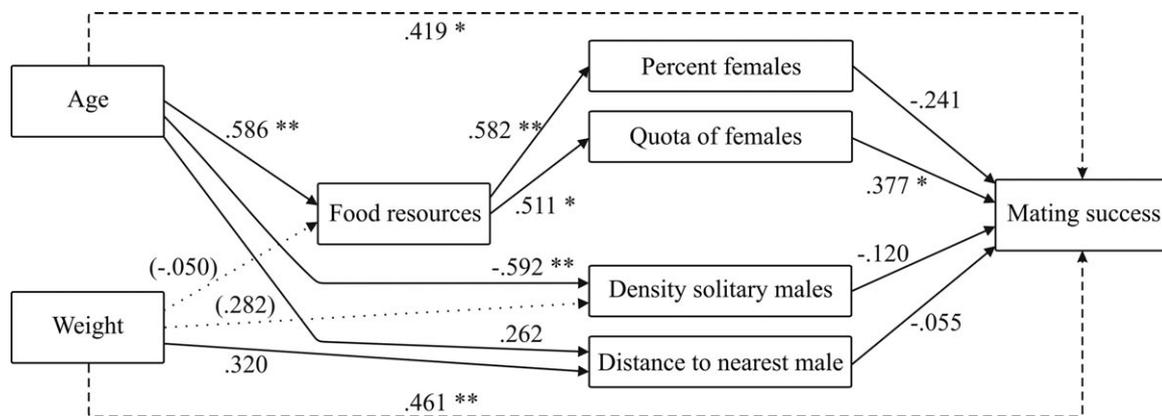


Figure 2 Path diagram showing the hypothesized causal relationships of age and weight on mating success in male great bustards. Standardized partial regression coefficients showing the relative importance of each link in the path diagram are indicated. Pathways corresponding to male-male competition are indicated by solid lines and those corresponding to female choice by dashed lines. See text for justification of the relationships represented and sexual selection mechanisms suggested.

nearest solitary male was 159.6 m (average of the 6 annual mean distances 1998–2003: respectively, 154.9 m, standard deviation [SD] = 118.8, $n = 45$; 128.0 m, SD = 117.0, $n = 40$; 136.9 m, SD = 189.4, $n = 62$; 201.5 m, SD = 223.9, $n = 63$; 165.2 m, SD = 296.2, $n = 43$; 171.0 m, SD = 201.1, $n = 50$; range = 10–1642 m). This distance did not significantly differ among leks or years (respectively, $F = 0.46$, $P = 0.63$, degrees of freedom [df] = 2, 295; and $F = 0.91$, $P = 0.47$, df = 5, 295; ANOVA of all solitary males sampled during 1998–2003).

Solitary males tended to display on sites with lower roughness and higher long-range visibility than random points (both variables showed the same trend in all 6 years, though differences were significant only in 1998 and 2000 and marginally significant in 1999 for roughness and 2002 for visibility; Table 1). Within a buffer equivalent to an average display area (316 m around displaying males), higher numbers of females and males were visible from display sites than from random points (significant differences in all years; Table 1). Finally, buffers around display sites contained more food resources than buffers around random points (same trend in all years, differences significant in four of six years; Table 1).

Logistic regression analyses for display-site selection using independent predictors for topography, resources, and visibility to conspecifics showed three to seven plausible candidate models per year (Table 2). The best candidate model from all annual model sets retained VISIBFEMALES (the number of females visible from the display site) and in 4 of the 6 years also retained RESOURCES (Table 2). After model averaging, the number of females visible from display sites and resources contained in the display-site buffer showed the highest weights in the models (Table 3). The variance explained by

the full models including all 4 predictors varied between 20% in 2002 and 81% in 1999 (mean for the 6 years is 56%; Nagelkerke R^2).

The distance moved by males between their locations in late March and their display sites in April was roughly double than the distance moved by females during the same period (Table 4). This, and the sequence of events observed in all 6 years (see example in Figure 1), confirms that males approached females when these were already foraging on resources, and not the opposite way.

Male display areas

In late March to early April, marked males dispersed to specific locations of the exploded lek area, where they performed display during the whole mating season (around 1 month). The mean distance from a marked male to the nearest solitary male was ca. 200 m (Table 5). However, display areas of individual males were highly variable in size (mean 31.4 ha or a 3% of the lek area, SD = 26.2; Table 5). We explored this variability by means of simple correlation analysis. The extent of a display area was correlated with male age ($r = 0.69$, $P = 0.003$, $n = 16$), but not with weight ($r = 0.32$, $P = 0.22$, $n = 16$). Extent of display area and proportion of the lek's food resources contained in it were strongly correlated ($r = 0.87$, $P < 0.001$, $n = 16$).

Each male tended to use approximately the same display areas on consecutive years (mean between-year overlap = 30.3%). On the other hand, there was a relatively high overlap between display areas of different males. Among marked males only such overlap averaged 30.1%, but marked

Table 2

Logistic regression models for display-site selection (0,1, respectively, for random and display sites) in each of the 6 study years, using four noncorrelated variables characterizing topography, visibility, resource availability, and number of females visible within the 316-m buffer around these sites

Year	Variables included in the models				AICc	Δ AICc	ω AICc	Explained deviance (%)
	ROUGH	VISIBSHORT	VISIBFEMALES	RESOURCES				
1998			●	●	52.842	0.000	0.476	48.99
	●		●	●	54.012	1.170	0.265	49.18
		●	●	●	54.068	1.226	0.258	49.11
1999			●	●	27.966	0.000	0.474	67.25
	●		●	●	28.999	1.032	0.275	67.79
		●	●	●	29.295	1.328	0.237	67.41
2000			●	●	34.545	0.000	0.208	61.27
	●		●	●	34.777	0.233	0.182	62.67
			●	●	34.841	0.297	0.176	59.41
		●	●	●	35.515	0.970	0.126	61.83
	●	●	●	●	35.917	1.373	0.103	63.06
	●		●	●	36.018	1.473	0.098	59.58
2001			●	●	36.077	1.532	0.095	59.46
			●	●	92.801	0.000	0.256	18.21
	●		●	●	93.344	0.543	0.198	18.80
			●	●	93.605	0.804	0.174	18.58
		●	●	●	93.913	1.112	0.149	18.30
	●	●	●	●	94.350	1.549	0.120	19.07
2002	●	●	●	●	94.433	1.632	0.115	19.00
			●	●	80.998	0.000	0.375	11.10
	●		●	●	82.131	1.133	0.211	11.23
			●	●	82.137	1.140	0.211	11.23
		●	●	●	82.248	1.250	0.199	11.10
2003			●	●	42.692	0.000	0.499	43.43
		●	●	●	44.043	1.352	0.245	43.60
	●		●	●	44.095	1.404	0.239	43.53

Each line in Table 2 shows the variables retained by 1 model (black dots), its AICc, Δ AICc, Akaike weight (ω AICc), and deviance explained; best models were selected according to Δ AICc, other models with Δ AICc > 2 not shown. See definition of variables in Table 1.

Table 3

Model-averaged estimates of display-site predictor variables retained in the significant models of Table 2

Predictor	Mean Σ	SD Σ	Mean b	SD b	Mean lower CI	Mean upper CI
VISIBFEMALES	1.000	0.000	10.800	11.829	2.107	19.503
RESOURCES	0.645	0.402	0.820	2.198	-1.405	3.043
ROUGH	0.230	0.055	-0.081	0.645	-1.984	1.822
VISIBSHORT	0.197	0.023	-0.137	0.302	-1.795	1.522

For each predictor variable, the following parameters are given: mean Σ = the six-year average relative importance (Σ is the sum of Akaike weights of the models in which the predictor was retained); SD Σ = standard deviation of the sample of 6 mean Σ values; mean b = 6-year average of the regression coefficients; SD b = standard deviation of the sample of 6 b values; mean lower and upper CI = 6-year averages of 95% confidence intervals (CI) for b . See definitions of variables in Table 1.

males represented only a small fraction of all males in the lek, which suggests that true overlap figures among all males were much higher. For example, we recorded an average 18% of all males of the lek at least once within the boundaries of the display area of a given marked male. This represents a density of 0.10 solitary males per hectare within another male's display area, that is, 8.9 times more than the mean density of solitary males in the whole lek area. These results indicate that males in general tolerated other solitary males within their display area. This was also corroborated by the very low mean display-site defense rate (Table 5).

During the mating season, females showed a strong preference for fallow fields, stubble fields, and vetch fields as foraging substrates (Table 6). Similar selection values were observed in males, although males spent only a 13% time feeding ($n = 16$ marked birds), devoting most of their time budget to display-related activities. The average amount of resources in the display area of a male represented 5.32% of the total resources estimated for the lek. However, this varied greatly between individuals (0.73–15.18%; Table 5), depending mostly on how large the display area was (see correlation between extent of display area and food resources above). Display areas also contained many females (16.19% of all females in the lek; Table 5), also with large variation among males (1.13–81.13; Table 5), as percentages of females and resources within a display area were highly correlated ($r = 0.66$, $P = 0.005$, $n = 16$). The mean density of females in a display area was 0.32 females per hectare, 7.6 times greater than the overall density for the whole lek area.

Table 4

Distances (mean \pm SD (sample size)) between great bustard locations during the exploded lek phase (date of maximum dispersion in April) and nearest flock locations just before lek explosion (late March)

Year	Solitary males	Female flocks	Significance of difference
1998	1024.9 \pm 711.2 (52)	690.6 \pm 660.6 (31)	**
1999	1358.4 \pm 1175.0 (54)	613.5 \pm 441.0 (55)	***
2000	728.0 \pm 502.6 (66)	444.9 \pm 423.2 (63)	**
2001	901.4 \pm 693.4 (65)	753.6 \pm 554.5 (89)	Ns
2002	1740.1 \pm 869.1 (54)	606.0 \pm 320.1 (43)	***
2003	1044.5 \pm 549.8 (53)	592.2 \pm 298.3 (53)	***
All years	1112.2 \pm 836.0 (344)	621.8 \pm 472.7 (334)	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 5

Mean, SD, maximum and minimum values of variables characterizing the display areas used by the 16 radiotracked great bustard males, their aggression rates to other males, and mating success

Variable names (units)	Mean	SD	Minimum	Maximum
Extent of display area (ha)	31.44	26.20	4.55	94.19
Food resources (% of total lek resources)	5.32	4.82	0.73	15.18
Percent females (% of total females in the lek)	16.19	20.67	1.13	81.13
Density of solitary males (per ha)	0.10	0.06	0.02	0.27
Quota of females (females/males within 500 m)	1.87	1.77	0.38	7.02
Distance to nearest solitary male (m)	191.87	108.17	22.50	358.24
Display site defense rate (per 100 min) ^a	0.19	0.25	0.00	0.79
Mating success (per 10h)	1.14	1.04	0.00	3.56

^aIncludes all aggressions to other males, which could be interpreted as some kind of territorial defense actions (e.g., displacements, direct attacks, threats that stopped approaching males).

Male phenotype, display area characteristics, and mating success

Age was positively correlated with the extent of the display area ($r = 0.69$, $P = 0.003$, $n = 16$ in this and all following correlations), food resources ($r = 0.62$, $P = 0.011$), quota of females ($r = 0.49$, $P = 0.054$), distance to nearest solitary male ($r = 0.52$, $P = 0.041$) and mating success ($r = 0.69$, $P = 0.003$), and negatively correlated with density of solitary males ($r = 0.66$, $P = 0.005$). Weight was positively correlated with distance to nearest solitary male ($r = 0.57$, $P = 0.020$) and mating success ($r = 0.56$, $P = 0.023$).

Path coefficients relating male age and weight with mating success are shown in Figure 2. Age showed significant positive effects on the amount of food resources and negative effects on the density of solitary males found in the display area. The causal links between food resources and both variables reflecting abundance of females in the display area (percent and quota of females) were also moderate and significant, and a smaller but significant link joined quota of females with mating success. Finally, age also had a significant direct effect on mating success (Figure 2). Whereas these effects of age were similar in different versions of the model, inclusion of indirect effects of weight through food resources and density of solitary males resulted in significant reductions of most model fit indexes, so these links were suppressed in the final model (Figure 2). In the final model, weight had a significant

Table 6

Substrate type selection (Ivlev's index) by females and males during the mating season

	Females	Males
Fallow fields	0.58	0.41
Stubble fields	0.35	0.02
Vetch fields	0.22	0.28
Ploughed fields	-0.17	0.10
Cereal fields	-0.47	-0.30
Uncultivated	-0.67	-0.72

Sample sizes: 1578 female flocks, 1437 male flocks (data for 1998–2003 pooled).

Table 7
Decomposition of total effects of the model of mating success in male great bustards into their constituent direct and indirect effects

Dependent variable	Predetermined variable	Total effect	Indirect effects via					Direct effects
			Food resources	Distance to nearest solitary male	Density of solitary males	Quota of females	Percent females	
Food resources	Age	.586						.586
Distance to nearest solitary male	Age	.262						.262
	Weight	.320						.320
Density of solitary males	Age	-.592						-.592
Quota of females	Age	.299	.299					
	Food resources	.511						.511
Percent females	Age	.341	.341					
	Food resources	.582						.582
Mating success	Weight	.443		-.018 ^a				.461
	Age	.506		-.014 ^b	.071 ^b	.113 ^b	-.082 ^b	.419
	Food resources	.053				.193	-.140	
	Distance to nearest solitary male	-.055						-.055
	Density of solitary males	-.120						-.120
	Quota of females	.377						.377
	Percent females	-.241						-.241

^a-.018 represents 3.8% of the total effect ($=-.018/[-.018 + .461]$, see Alvin and Hauser 1975).

^bThe sum of these indirect effects equals a total indirect effect of age on mating success of .087.

direct effect on mating success, and some yet nonsignificant effect on distance to nearest solitary males (Figure 2).

Table 7 summarizes the decomposition of total effects quantified by our model into their constituent direct and indirect effects. Age and weight of a male could influence its mating success either directly, that is, through selection of phenotypic characteristics of the male by females (female choice selection mechanism) or indirectly through displaying closer to more resources and/or females without increased presence of competitors and thus having access to more copulation opportunities (male-male competition mechanism). Effect decomposition showed that age had an effect of 0.506 on mating success, of which 0.087 (17.2%) was transmitted via a higher density of females and a lower density of solitary males and 0.419 (82.8%) was unmediated by variables in the model (Table 7). As for the effect of weight, only 0.018 (3.8%) was transmitted via a higher distance to competitor males, the major effect (96.2%) being direct, that is, explained by male attributes which are independent of females, males, and resources nearby.

Display-site defense rate and variability in mating tactics among males

The rate of display-site defense aggressions to nearby solitary males varied between 0 and 0.79 per 100 min (Table 5). Nonzero rates were recorded for 8 of 16 marked males and only when females were in close proximity. Display-site defense rate was not correlated with age, weight, or mating success of the male. It was only positively correlated with the average distance to the nearest solitary male ($r = 0.58$, $P = 0.023$, $n = 16$ marked males).

DISCUSSION

Our results suggest that great bustard males do not primarily use resources in their display areas to attract females. First, visibility to females had a much stronger effect than amount of resources on display-site selection (respectively, 7.8 and 1.6 times higher at display than at random points; Table 1).

Second, the much longer movements performed by males compared with females just before the exploded lek phase, and the comparison of male and female distributions before and after male dispersion, support our interpretation that males dispersed to approach females foraging on resources and contradict the alternative possibility that solitary males occupied resources prior to female arrival. Third and most important, the effect decomposition from path analysis suggested a much higher direct effect of the phenotypic quality indicators of a male on its mating success (82.8% for age and 96.2% for weight) compared with the indirect effect via females, males, or resources in its display area.

These results confirm that the mating system of great bustards fits the definition of a male dominance polygyny and enable qualifying it as a true lekking system, as opposed to a territorial or resource-defense polygyny. As for the factors influencing mating success of individual males, we know from previous studies that older males are more successful because they spend longer seasonal and daily periods on solitary display and probably also due to a female preference for older males, as in numerous other polygynous bird and mammal species and some insects (Alonso, Magaña, Palacín et al. 2010 and references therein; see also Kokko 1998; Brooks and Kemp 2001). The present study shows that older males had also larger display areas, which held higher proportions of food resources. Although this could suggest that old, more successful males could use resources as an important additional factor to attract females, we interpret that resources are more an indirect consequence of an old male's higher status than a relevant cause of its mating success. We base this on our previous studies, where we showed that the higher status of older males is respected by other individuals, enabling older males to roam freely through a larger extent of the lek, display to attract females, and thus have more chances to copulate without being displaced or disrupted by neighbors (Alonso, Magaña, Palacín et al. 2010; Alonso, Magaña, Martín et al. 2010; Magaña et al. 2011). Even assuming that some older males might have controlled resources in their display areas—which did not generally happen in most birds—path analysis effect decomposition indicated that resources

themselves would represent only a small additional factor contributing to enhance mating success compared with male phenotype. This result, together with the typically low aggression rates observed during the mating period (Magaña et al. 2011), suggests that during the exploded lek phase, female choice is a more important sexual selection mechanism than male–male competition, in contrast to the premating period, when male–male competition is the strongest and lead to the establishment of a male hierarchy in the lek (Magaña et al. 2011).

As a rule, each male established its display area year after year in the same sector of the lek, which indicates some degree of territorial faithfulness similar to that typical of classical leks. Such fidelity to a preferred territory has been also observed in other exploded-lekking species (Castro-Astor et al. 2004; Hingrat et al. 2007). However, areas of different males typically overlapped, indicating that they were not of exclusive use. Most males indeed allowed other individuals to enter, and even temporarily display within the boundaries of their own areas. Aggression rates were either absent or very low in a majority of males, confirming our suggestion from previous studies that a lek hierarchy is well established before the mating period and generally respected by all males (Alonso, Magaña, Martín et al. 2010; Magaña et al. 2011).

Most marked males behaved in the way described above, that is, according to a true exploded lek system where males tolerate each other and individual mating success depends on male quality rather than resource monopolization. However, half of the males showed a variable degree of display-site defense, and a few frequently displaced intruders when these approached, suggesting some kind of territorial behavior. Aggressive rate was not correlated with male age, weight, or any relevant feature of the display area including amount of resources. A higher aggressive rate did not result in a significantly higher mating success (the two males with highest defense rates, respectively, 0.79 and 0.52, had mating success values rating 0.91 and 2.06, which did not differ much from those of the two males with lowest, nonzero defense rates, respectively, 1.83 and 2.41). However, males showing higher defense rates were able to keep higher minimum distances to neighbors, which possibly facilitated an undisrupted access to females and eventually might contribute to increase mating success in some individuals. Resource defense might thus represent an additional component of the mating tactic of these males.

We conclude that, in spite of the much higher relevance of phenotypic characteristics on mating success, at least some males probably complemented their attractiveness with a certain degree of control over resources in their display areas. This resource-defense component was variable among individuals, which suggests that the two mating tactics, exploded lekking and resource defense, occur together in the same population. Coexistence of alternative mating tactics is a widespread phenomenon in many species (Davies 1991; Lott 1991; Gross 1996) and seems particularly frequent in ungulates (Isvaran 2005), a group of mammals with which great bustards share many behavioral adaptations conditioned by their sexual size dimorphism and strong sexual selection. Both in ungulates and birds, lekking species show higher mating tactic variability than other species (Jiguet et al. 2000; Isvaran 2005). Alternative mating tactics may be maintained through coexistence of 1) irreversible phenotypes, where individuals adopt a single tactic over all of their lifetime, and 2) reversible phenotypes, where individuals either adopt different tactics sequentially or switch between tactics (Isvaran 2005). In lekking birds, phenotype-limited alternative mating tactics have been suggested in some species (see Höglund and Alatalo 1995) and have evolved to an extreme in the ruff,

where certain tactics are fixed for life and associated with differences in plumage color and size of the individuals (van Rhijn 1991; Lank et al. 1995).

Individuals may adopt different tactics based on their condition, status, or external factors, but alternative phenotypes may also be maintained in a population by frequency-dependent selection influencing a genetic polymorphism (Rubenstein 1980; Maynard-Smith 1982). There is increasing evidence that these and other mechanisms maintaining alternative tactics within a population are not exclusive and may act together (Gross 1996; Brockmann 2001; Isvaran 2005). Variation among males of a population in the optimal switch point between the two mating tactics can create a continuum of responses within the population. We believe this might be the case in our great bustard population, where rather than two opposing alternatives, a whole continuum of tactics may exist between the most common exploded lekking tactic based on exhibition of male attributes and the less-frequent resource-defense polygyny. Radiotracking data from multiple years (Magaña 2007) and observations on some of the males of this study in later years (Alonso JC, Magaña M, unpublished data) confirmed that each male tended to follow the same mating tactic in consecutive years, which suggests a case of irreversible phenotypes. We do not discard, however, that significant changes in individual condition and/or external factors might modulate the optimal tactic of each male.

According to the environmental potential for polygyny (Emlen and Oring 1977; Oring 1982), leks are the male dominance polygyny default tactic that evolves when neither resources nor females can be monopolized by males. This occurs when female home ranges are large and their densities are relatively high (Oring 1982). In accordance with this, the two great bustard males following a mating tactic closer to a resource defense occupied relatively marginal display areas within their leks, where male and female densities were lower than in the lek centre (details in Magaña 2007).

Finally, in a previous study, we observed a remarkable coincidence between the mean date of maximum dispersion of displaying males and highest copulation frequency (both on 18 April, with only 4 days between-year variation), as well as a correlation between both dates in a 3-year comparison (Magaña 2007). This notable concurrence strongly suggests that the main cause leading to the evolution of exploded leks in this species was to facilitate mating, by enabling a sufficient distance between males to minimize copulation disruption, a frequent event in great bustards (Magaña 2007; Magaña et al. 2011). The average between-male distances recorded in our study (160 m in lek surveys, 192 m using marked birds) were within the range of values recorded for other exploded lek-breeding birds (Johnsgard 1994; Höglund and Alatalo 1995; Morales et al. 2001; Castro-Astor et al. 2004; Hingrat et al. 2008). Like most of these authors, we interpret these results as providing support to suggestion of Foster (1983) that exploded leks may have evolved from the more clumped classical leks to balance the benefits to females of a rapid and easy comparison of all males of the lek with the benefits to males of a low disruption rate.

To sum up, we suggest that the use of analytical tools such as path analysis should enable establishing the relative importance of phenotypic characteristics versus food resources on mating success and hence deciding whether a population is closer to one or the other extreme of an exploded-lek resource-defense continuum. In most exploded-lekking species, males probably display close to resources primarily as a way to increase the probability of encountering females and not to monopolize resources (see also Höglund et al. 1998; Jiguet et al. 2002; Hingrat

et al. 2008). Thus, *display-site* selection would have evolved in exploded-lekking species following similar patterns to those proposed by the hotspot hypothesis for *lek-site* evolution in classical lekking species (Bradbury and Gibson 1983). However, in great bustards and possibly in many other species, the breeding strategy of some males may show a variable component of a resource-defense mating tactic. This variability among males may in part explain the difficulties found in fitting observed mating behaviors in exploded-lekking species to accepted definitions of alternative mating tactics (Höglund and Alatalo 1995; Ligon 1999; Jiguet et al. 2000, 2002; Hingrat et al. 2007; Delgado et al. 2010; Kotschal and Taborsky 2010). In line with the idea posed by Kotschal and Taborsky (2010), we believe that in species mating in exploded leks, variability between males in the use of resource defense can create an intraspecific continuum between true lek and resource defense, and we suggest that such variability may occur in more species than earlier realized.

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