

Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort

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Abstract We examined how mating success varied in relation to age, weight, body size, and display behavior among great bustard *Otis tarda* males. The estimated mating success was strongly skewed, with 45% of adult males being involved in copulation attempts and only 9.7% actually seen copulating successfully. Unlike most birds, body size continued increasing in great bustards several years after reaching sexual maturity. Age, weight, and display effort were all significant and independent predictors of male mating success. The higher display effort involved performing longer full-display bouts. Older males could detach from the male flock earlier in the season as well as on each day and spend longer seasonal and daily periods displaying as solitary birds, which contributed to increase their mating success. In contrast, males weighing more did not invest more in display, which suggests that they could be recognized as dominants by other males and selected by females through assessment of their plumage sexual traits. In contrast to most other bird species, the system described for great bustards resembles that found in some lek-mating ungulates, where social rank is a complex trait determined by both age and mass, and as in these

mammals, it suggests that sexual selection continues to favor a high male weight in this extremely sexually dimorphic species.

Keywords Age · Great bustard · Lek · Mating success · Sexual selection

Introduction

Sexual selection is particularly strong among males in polygynous mating systems, where males compete intensely for mates and mate with more than one female during a single reproductive season (Andersson 1994). These systems include *female defense* or *harem* polygyny, in which some males control access to several females simultaneously, and *resource defense* polygyny, in which the male's territory includes environmental resources of potential use to the females with whom he breeds. A high variance in male mating success is a typical feature of these systems, as reproductive success of males is only constrained by their ability to sire offspring (Trivers 1972; Emlen and Oring 1977). But perhaps the strongest sexual selection and skew in male mating success is found in the *male dominance* or *lek* polygyny, where males perform displays at a communal display site, provide no material resources but genes, and are visited by females only for copulation (Bradbury and Gibson 1983; Wiley 1991).

In lek-mating species, several traits have been found to be positively correlated with male mating success, such as morphologic attributes, spatial features of male territories, and behavioral traits such as display activity and lek attendance (Höglund and Alatalo 1995; Fiske et al. 1998). For example, body size or body mass are often essential, because of the advantage they imply during male–male

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combats and endurance rivalry and also sometimes due to a female preference for larger males (Andersson 1994; Dunn et al. 2001). Body size has indeed been found to be a major contributing factor to male reproductive success in some insects, some frogs, several lekking ungulates (Clutton-Brock et al. 1982; 1988, McElligott et al. 2001; Pelletier and Festa-Bianchet 2006; Bowyer et al. 2007; Natoli et al. 2007), and other mammals of various orders where male–male competition is important (Fisher and Lara 1999; Clinchy et al. 2004; Zedrosser et al. 2007). In birds, however, plumage traits, display intensity, and territory characteristics are usually stronger predictors of male mating success than weight (reviewed in Andersson 1994; Johnsgard 1994; Höglund and Alatalo 1995; see also e.g., Rintamäki et al. 2001; Shorey 2002; Westneat 2006; Nooker and Sandercock 2008).

In numerous species, mating success is also correlated with male age. This has been interpreted as a female preference for older males because old age is proof of higher survivorship and older males are of higher genetic quality (Trivers 1972; Halliday 1978, 1983; Manning 1985, 1989; Kirkpatrick 1987; Andersson 1994). These ideas, known as age indicator mechanism hypothesis, were later supported by models including life history effects (Kokko and Lindstrom 1996; Kokko 1998; but see Hansen and Price 1995; Beck and Powell 2000; Brooks and Kemp 2001; Beck and Promislow 2007). However, identifying the effect of age may be difficult because age is usually correlated with other morphologic, territorial, and behavioral traits. In some long-lived lekking species, older individuals have higher mating success due to their higher social rank (McDonald 1989; Hass and Jenni 1991, Pelletier and Festa-Bianchet 2006). An alternative argument is that older males are more honest signallers, revealing more information in their sexual displays (Proulx et al. 2002). Whatever the mechanisms involved, it is widely held that age itself is positively correlated with mating success, at least in some harem-holding or lekking species with marked dominance rank hierarchies (Andersson 1994; Johnsgard 1994; Höglund and Alatalo 1995). Finally, male mating success is also influenced by other factors like display intensity, territory quality or centrality, or lek attendance (Andersson 1994).

In this study, we (1) quantified the mating skew among great bustard (*Otis tarda*) males and (2) examined how male mating success correlates with age, body mass, and several behavioral parameters describing display effort and intensity in this species. A previous study based on a very small sample of only eight marked birds suggested a positive correlation between body condition and mating success, but the effect of age could not be established (Morales et al. 2003). Here we present the results of the first study based on a large sample of individually marked

birds of this lekking species. Several morphologic and behavioral traits make it an ideal species to study the influence of age, weight, and behavior on mating success. First, great bustards show the highest sexual size dimorphism among birds, and males are the heaviest flying birds (Alonso et al. 2009). Such extreme sexual size dimorphism has probably been favored by strong sexual selection, which has likely pushed male weight close to the limit imposed by powered flight. Second, male–male competition is intense in great bustard leks, where combatants grip each other with their bills and shove and jostle breast to breast sometimes for more than 1 h, until eventually the loser abandons (personal observation). Third, sexual selection may have also favored a rapid growth of young males, by increasing their competitive ability during the immature period and probably also their fitness as breeding adults (Alonso et al. 1998). Young males that fed at higher rates or received more feedings from their mothers became independent at a younger age, integrated earlier into adult male flocks, and settled earlier at their definitive leks. Thus, we should expect a significant influence of body size or weight on mating success of great bustard males. Finally, great bustards could be expected to show a positive influence of age on mating success, given their high longevity (up to 14–15 years; own unpublished data) and fidelity to their leks (95%–100% lifetime lek fidelity), which are remarkably stable in size and location from year to year (Morales 2000; Magaña 2007). Age has indeed been found to contribute to increase reproductive success in some long-lived, lek-mating species where aggregation of the same individuals at leks year after year may lead to age-dependent social dominance structuring (reviewed in Andersson 1994; Johnsgard 1994; Höglund and Alatalo 1995). Our study represents one of the few examples where age, weight, and display behavior have been examined simultaneously in a highly sexually dimorphic, long-lived, lekking bird species.

Methods

This study is based on behavioral observations of 41 great bustard males captured at nine lek sites in Madrid province, central Spain (36 captured as adults in 1998–2001, 5 as chicks 1995–1997), and radiotracked during one to three mating seasons each. The province holds a population of ca. 1,400 great bustards (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).

Trapping and morphometrics

Adult males were captured with rocket nets in February, 2 months before the peak mating season. Young birds were captured in July, when they were 3–10 weeks old and still dependent on their mothers, by chasing them down. Adults were immediately immobilized using specially designed jackets and their heads, as those of chicks, covered to minimize capture stress. All birds were released once processed, within 20 min after capture. Each captured bird was fitted with a backpack radio-transmitter (TW3 model, Biotrack Ltd., UK) using elastic band as harness material. In addition, birds were provided with PVC wing-tags (juveniles) or dorsal tags glued to the transmitters (adults) for visual identification in the field. Battery life was 4–5 years in the 2×AA transmitters (60 g) used for juveniles and up to 7–8 years in the 3× AA model (95 g) used for adults). The total weight of transmitter plus harness did not exceed the recommended limit of 3%–5% of the bird's weight (Kenward 2001). We did not observe any harm in the plumage or behavioral alteration of the birds as a result of marking. After marking, we located all radio-tagged individuals by triangulation using TR2–TS1 scanner-receivers from Telonics, USA, several days before starting behavioral observations, to check that birds behaved normally. When a marked bird was not found from the ground, we used small aeroplanes (E-24 Bonanza, Beechcraft).

The following morphometric measurements were taken during handling: body mass (± 50 g); wing arch: maximum distance between the carpal joint and the tip of the longest primary (± 1 mm), measured with a tape along the dorsal side of the wing; tarsus length: distance between the notch on the back of the intertarsal joint and the lower edge of the last complete scale before the toes diverge (± 1 mm); central toe length: distance between lower end of tarsus and central toe tip excluding the claw, with the toe stretched (± 0.1 mm); and head length: maximum distance between the occipital end of the head and the tip of the bill (± 0.1 mm). When extraction from the net took more time than expected, we released some birds without measuring their tarsus, central toe, and head, to reduce handling time. Wing length was the variable with highest loading (0.95) in the first principal component of a principal component analysis (PCA) of 10 morphometric measurements performed on a larger sample of adult great bustards (Alonso et al. 2009) and was therefore used as index of body size in the present study. The age of birds captured as adults was estimated using our own results from a previous study based on 31 males captured as chicks and radio-tracked over 10 years between 1987 and 1999 (Alonso et al. 2006). In that study, we improved the aging techniques proposed by Gewalt (1959) and established several head and neck shape and plumage details, which allow distinguishing five

age classes between ages 1 and ≥ 8 years in April, when age differences acquire their maximum expression. Although weight is potentially subjected to interannual variability, we did not try to recapture and weigh our marked birds every year, to avoid excessive disturbances. Thus, we repeated most analyses using first, only data of the capture year when we had weighed the bird, and next, data from all years, assuming that weight values measured on the first year were reasonably representative for the 1- to 3-year tracking period of each male. This assumption is supported by the following facts. First, the only available data on weight variation are in this species, which are from eight birds kept in captivity through 18 months (Carranza and Hidalgo 1993). The two birds showing highest weights during the peak mating season also weighed more than the other males 3 months earlier, and these two males kept their status and weight in the following breeding season. Second, in our marked males, the development of whiskers in spring, a sexual trait identified as best indicator of weight, varied little between-years. Moreover, in the relative expression of this trait among males of the same lek did not usually change between years, suggesting that rank order in weights remained more or less stable from 1 year to the next (Magaña 2007).

Behavioral observations

Marked males were tracked 2–3 days per week over one to three mating seasons following capture (from the last week of March to the second week of May). Observations were carried out from dawn to 1300 h, since activity in general, and particularly sexual activity, is much reduced during midday when birds usually lay down and rest (Martínez 2000; Morales et al. 2003). Observations were made from ground vehicles at 1–3 km from the focal bird using 20–40× and 60–90× telescopes. The number of observers varied between four and five; each observer tracked one male per day, and observation effort was distributed uniformly among individuals and throughout each season. However, local observation conditions determined differences among birds in the total annual observation time that could be defined as useful for analysis (48–1,373 min per bird and season and 60–2,650 min per bird summing all seasons). Our total sample was 177 useful days and 509 useful observation hours, i.e., after discounting periods of bad weather or when birds were disturbed, or not visible from our observation points. Data collection consisted of ad libitum recording (Martin and Bateson 1993) of all significant behaviors and the duration (to the nearest second) of each behavioral bout of the focal bird. We considered the following behaviors: *feeding*: bird actively looking for food, including the brief vigilance bouts in-between; *vigilance/resting*: bird with neck stretched, head

up; *lying*: bird lying on the ground, resting; *aggression*: any form of aggression from/to other males; *display*: we distinguished the following phases of display (see Gewalt 1959; Glutz et al. 1973; Hidalgo and Carranza 1991; for a full description of display behavior in the great bustard): *D0*: male standing or walking with tail spread out, showing the conspicuous white under tail coverts; *D1*: neck vertical, gular poach, and oesophagus (neck) slightly inflated, whiskers partly standing on end, wings slightly hanging down, and tail spread over back; *D2*: neck tilted over the back, breast lowered down and abdomen raised over horizontal body line, neck notably inflated, whiskers partly standing on end, wings turned upside down, and tail spread over back, both showing the white under coverts; *D3*: like *D2* but neck completely inflated and reclined over back, whiskers vertical, and bird moving sideward or shivering, usually when females are present; we defined as a *full display* or *D30* bout the total time spent on continuous *D3* plus interspersed short *D0* bouts just to change position, usually when females are close. The time devoted to each activity by each male was divided by the total net time of observation during the corresponding 1-h period to obtain an hourly rate. A mean value of hourly rate for the behaviors defined above was calculated for each focal male. Simultaneously, changes in flock size and composition were also recorded ad libitum for each focal male, as well as any variation in its location and that of surrounding male and female birds or flocks within a radius of 1 km from the marked male. We also recorded the first and last date through the mating season when each marked male was seen displaying as a solitary bird and defined *first date of solitary display* and *period of solitary display* (days from first to last date). All males of a given lek are usually aggregated in a single flock (sometimes two to three flocks if the lek is large) in winter. From late March on, males start splitting up from the flock to display as singles, at 100–300 m (mean, 265 m) from each other (*exploded lek*), and flock together again at the end of the mating season (Magaña 2007). Through each day, males may also spend midday hours, when they do not display, in a flock. We recorded these times and defined a *daily time of solitary display*.

Mating success

Given the practical difficulties of assessing the number of offspring sired by each male, mating success in lekking species is usually measured through copulation rate (see Höglund and Alatalo 1995). However, in contrast to many other classical lekking birds, for which copulation rate is relatively easily monitored at display arenas, in great bustards, it was difficult to record copulation rates of more than a single male simultaneously, as they disperse over a wide area (*exploded lek*). Moreover, the number of

effective copulations seems to be quite low in this species (Gewalt 1959; Hidalgo and Carranza 1990; Hellmich 1991; Morales 2000; Morales et al. 2003). In the present study, we only saw eight copulations, a number clearly insufficient for statistical analyses. Therefore, as a statistically more practical parameter we calculated for each male an *estimated mating success* per 10 h, by adding observed effective copulations plus copulation attempts, 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, i.e., by approaching him and turning around him to inspect his plumage, ending up pecking his cloacal region (see detailed description of copulation behavior in Hellmich 1991). To support the reliability of our estimated mating success, we had previously tested that the rates of effective copulations and copulation attempts were positively correlated ($r=0.33$, $P=0.020$, $n=48$ marked males combining samples of the present and a previous study; Morales et al. 2003).

Statistical analyses

For each marked male, we first calculated a mean annual value of all behavioral variables defined above. To increase the significance of mean values for each individual, particularly the copulation attempt rates, we later obtained overall mean values for each male, after testing that there were no significant differences between years. However, since the males were weighed only in the year of capture (first tracking year), the analyses involving weight were carried out using both, the behavioral means for the first year only and those for the overall tracking period (1–3 years). We discarded males with an observation sample of <200 min (10 birds), and for analyses relating phenotypic features with display rate and estimated mating success, we excluded another five birds of two leks where the hilly terrain forced us to carry out the observations from a too close distance, which might have affected the behavior of the birds. Final sample sizes varied among analyses because it was not possible to measure every attribute for all males.

We calculated two indices of mating skew: λ and B . The first varies from 0 (random mating) to 1 (one male obtains all matings). This index allows the intensity of sexual selection to be compared across leks regardless of lek size (Kokko and Lindström 1997). It has been widely used to measure mating skew in lek-mating species, but inference is hampered because variance cannot be calculated. The binomial index (B) improves upon λ because confidence intervals can be calculated and therefore allows statistical comparisons (Nonacs 2000). We calculated both λ and B values (including 95% confidence intervals and P values for B values) for male mating skew with Skew Calculator 2003 PC (Nonacs 2003).

Several of the behavioral variables were correlated. Thus, we used PCA to obtain principal components of behavior that were orthogonal. The first two principal components were easily interpretable and thus later used as behavior factors in correlations with age, weight, and wing length or in multivariate analyses. We used Spearman rank correlation, Mann–Whitney *U*-test, and Kruskal–Wallis test (Siegel and Castellan 1988) to explore increase in morphometric and behavioral traits with age and simple and multiple (partial) regression analysis to examine the effects of male traits (biometry, weight, age) on estimated mating success, after appropriate transformation of all variables (e.g. Höglund and Lundberg 1987; Shorey 2002). Finally, we also performed a logistic regression including male traits and the two principal components of behavior to compare unsuccessful (estimated mating success =0) and successful males (estimated mating success >0; see, e.g., Gibson and Bradbury 1985; Höglund et al. 1997). To further explore the relative importance of each explanatory variable, we used the Akaike's information criterion ($\Delta\text{AIC} < 2$) to select the best models from a set of candidate models with different combinations of predictor variables. All statistical analyses were performed with STATISTICA 6.0 (Statsoft, Inc. 2001, Tulsa, OK), assuming two-tailed tests.

Results

Increase in body size and weight with age

Wing length increased with age through at least 3–4 years after reaching adulthood (Fig. 1; male great bustards are sexually mature at an age of ca. 4 years; Glutz et al. 1973; Magaña 2007). Head length and width showed also positive correlations with age, although statistical significance was

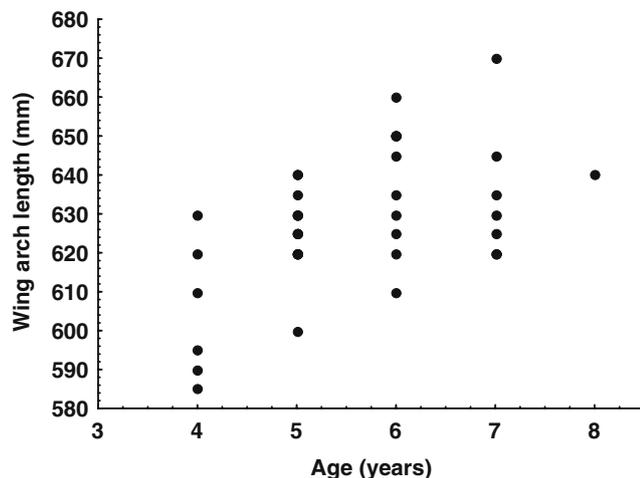


Fig. 1 Increase in wing arch length with age in adult male great bustards. The correlation is significant ($r_s=0.50$, $P=0.001$, $n=39$)

not reached due probably to small sample sizes ($r_s=0.39$, $P=0.194$, $n=13$; $r_s=0.48$, $P=0.156$, $n=10$, respectively). Tarsus and central toe lengths did not correlate with age ($r_s=-0.09$, $P=0.716$, $n=19$; $r_s=-0.05$, $P=0.882$, $n=11$, respectively). Weight also increased with age, though apparently only between four years and older ages (Fig. 2). Controlling the effect of wing length through partial correlation, weight still increased between 4- and 5-year-old males ($r=0.49$, $P=0.032$, $n=21$), but not at older ages ($r=0.04$, $P=0.841$, $n=35$). This suggests that weight was independent of body size among adults older than four years.

Male mating success

Over 4 years and 509 useful observation hours of 31 marked males, we only observed eight successful copulations (four in only three of the marked males—or 9.7% of the sample—plus four in nonmarked males). Therefore, successful copulations were quite infrequent events, occurring at an average rate of 0.76 copulations per male in 10 h. We also recorded 84 copulation attempts (38 of marked males plus 46 of nonmarked males) that did not result in successful matings. In total, only 14 of the 31 marked males (45%) made a copulation attempt. The estimated mating success was strongly skewed overall ($\lambda=0.83$, $\text{SD}=0.22$; B value=0.39, $\text{SD}=0.45$, $P<0.001$) and at most leks (Fig. 3). λ values for male mating skew ranged from 0.35 to 1.00, and B values ranged from -0.21 to 1.09. B values indicated that mating was significantly skewed on 7 of 17 lek-years: 1 of 3 years in Campo Albillo (year 2000: $B=0.94$, $P=$

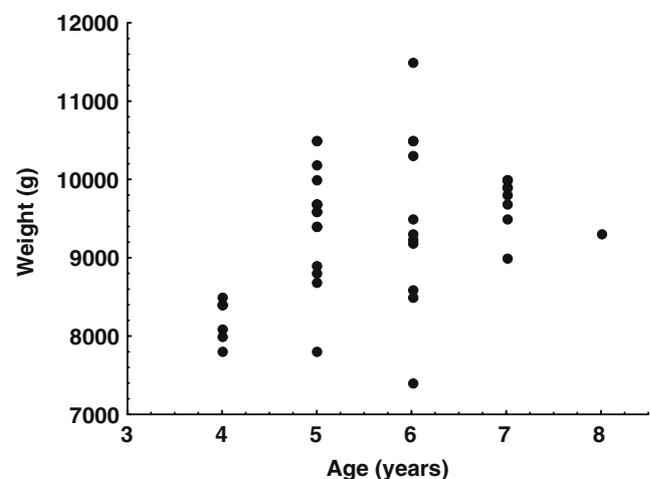


Fig. 2 Weight variation with age in adult male great bustards. The correlation is significant ($r_s=0.40$, $P=0.010$, $n=41$), but not when birds of 4 years are excluded ($r_s=0.07$, $P=0.683$, $n=35$). Differences between age classes are only significant between 4 years and older ages (Mann–Whitney *U*-test, 4–5 years: $Z=-3.01$, $P<0.001$; 4–6 years: $Z=-2.66$, $P=0.005$; 4–7 years: $Z=-3.10$, $P<0.001$; 5–6 years: $Z=-0.33$, $P=0.77$; 5–7 years: $Z=0.89$, $P=0.40$; 6–7 years: $Z=-0.62$, $P=0.54$)

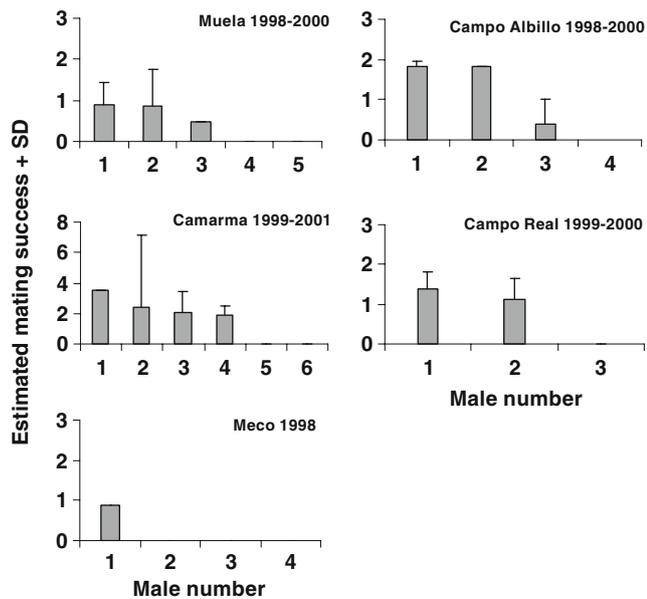


Fig. 3 Estimated mating success (frequency of effective copulations plus copulation attempts per 10 h; see “Methods” for details) of 22 great bustard males at five leks with ≥ 3 marked males. The sample of 31 marked males is completed with 9 males (1 with success, 8 without) tracked at four additional leks which are not represented. Only males ranked 1 at Muela, Camarma, and Campo Real were actually seen copulating (1, 1, and 2 copulations, respectively). Bars and whiskers represent means and SD. Bars without whiskers correspond to males tracked only 1 year

0.014) and Camarma (year 2001: $B=0.63$, $P=0.001$), both study years in Pinto (years 1998 and 1999: $B=0.82$, $P=0.001$; $B=0.71$, $P=0.002$, respectively), and the only study year in another two leks: Daganzo and Valdehornos (year 2000: $B=1.07$, $P=0.003$; and year 1998: $B=1.09$, $P=0.003$, respectively; Fig. 3).

We were interested in checking whether the low copulation rate observed in our study could be sufficient to fertilize all females in our population. We extrapolated the 4 effective copulations and 38 copulation attempts recorded during the 509 observation hours of our marked males to the 7-week mating period, computing 10-h display activity per day and assuming that 45% of the 301 males counted in the population in year 2000 (Alonso et al. 2003) succeeded in mating. The resulting figures were 4,970 copulation attempts plus 523 effective copulations.

Phenotypic correlates of male display behavior and estimated mating success

The first and second principal components of male behavior (PC1 and PC2) were extracted from a PCA of 12 behavioral traits (Table 1). Loadings on PC1 were high and negative for time displaying (phases D1–D3), mean duration of display bouts, and time spent on full display, so we interpreted PC1 as an index of display effort. Loadings on

PC2 were high and positive for the date a male started displaying as single in the season and negative for number of days spent on solitary display through the season, and for daily percent time spent on solitary display, so we interpreted PC2 as an index of time a male spent on solitary display, i.e., separated from other males of the lek.

We explored the relationships between male behavior and male age, weight, and size through simple correlation analysis. Age was strongly correlated with PC2 ($r=0.67$, $P<0.001$, $n=23$), which means that older males spent a longer period both through the season and through the day displaying as solitary individuals, detached from the male flock in the lek. Age was also correlated with PC1 ($r=-0.41$, $P=0.05$), indicating that older males displayed more. PC1 and PC2 were not correlated with either weight or body size (weight vs. PC1: $r=0.07$, $P=0.75$; weight vs. PC2: $r=0.19$, $P=0.38$, $n=23$; wing length vs. PC1: $r=-0.19$, $P=0.39$; wing length vs. PC2: $r=0.33$, $P=0.12$, $n=23$). Figure 4 shows how the main variable defining PC2 (number of days displaying as a solitary male through the mating season) increased almost linearly with age, at least up to the age of 9 years. The longest period was recorded in a 9-year-old male who spent 62 days displaying as a single male, from late March, when first copulations started, until late May. The increase in the extent of this solitary display period was due to both, an advance in the starting date, and a delay in the ending date (correlation between period length and starting date, $r=-0.69$, $P<0.001$, $n=41$; ending date, $r=0.54$, $P<0.001$). Extreme cases were those of two old males, aged respectively 8 and 9 years, who started as singles on 23 rd March, compared with two younger males, aged 3 and 4 years, who started solitary display as late as 20th and 24th April, respectively.

We explored through simple correlations which behavioral features contributed to increasing mating success. Both principal components of behavior were correlated with the estimated mating success ($r=-0.50$, $P=0.01$; $r=0.41$, $P=0.04$, $n=23$, respectively). The results were the same testing with the individual variables defining the principal components: males starting displaying as singles earlier in the season, those prolonging the daily percent time as singles, and those performing longer full displays obtained higher estimated mating success ($r=-0.51$, $P=0.017$, $n=22$; $r=0.42$, $P=0.033$, $n=26$; $r=0.67$, $P<0.001$, $n=25$, respectively).

The combined effects of age, weight, and body size on the estimated mating success were examined through partial correlation analysis. Using either only data from the capture year or average values for all years, the results showed partial effects of age and weight, but not of body size (Table 2). Finally, the results of a logistic regression showed that the probability of a male to be successful in mating was positively related to his age, weight, and

Table 1 Eigenvectors of a principal component analysis of great bustard male behavior at leks

| Behavior | PC1 (display effort) | PC2 (solitary display) |
|---------------------------------------|----------------------|------------------------|
| % Time full display | -0.97 | 0.01 |
| Mean duration full display bout | -0.81 | -0.34 |
| No. full display bouts | -0.29 | 0.43 |
| Time displaying (phase D3) | -0.93 | 0.02 |
| Time displaying (phase D2) | -0.74 | 0.41 |
| Time displaying (phase D1) | -0.77 | 0.28 |
| Daily % time of solitary display | -0.27 | -0.64 |
| First date of solitary display | 0.33 | 0.71 |
| Period (no. days) of solitary display | -0.25 | -0.82 |
| % Time feeding | 0.30 | 0.52 |
| % Time vigilant | 0.71 | -0.41 |
| % Time aggression | -0.17 | 0.44 |
| Eigenvalue | 4.56 | 2.77 |
| Percent of variance explained | 38.0 | 23.1 |

Observations were conducted during the breeding season (late March to mid-May) during 1998–2001. Principal components loadings >0.6 are in bold-face. A PCA with data from only the first (capture) year for each male gave identical results

display effort (Table 3). Weight and display effort were included in all three models selected as best subsets using $\Delta\text{AIC} < 2$, and age and the solitary display component of behavior in one of these models each (Table 4).

Discussion

Body size, body mass, and age

The increase in wing length up to an age of at least 8–9 years shows that body size increases in great bustard males after reaching sexual maturity, which occurs at ca. 4 years (Gewalt 1959; Glutz et al. 1973; Magaña 2007).

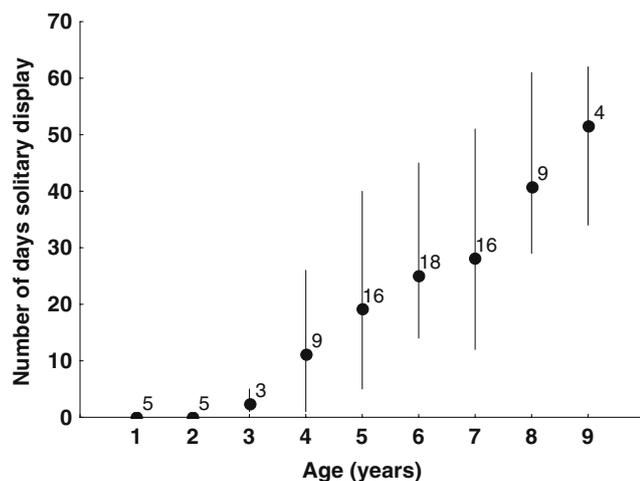


Fig. 4 Increase in the number of days of solitary display throughout the mating season (the variable with highest loading in PC2 of behavior; see Table 1) with age in great bustard males. Means, intervals (minimum – maximum) and sample sizes are given. The increase is significant (Kruskal–Wallis analysis of variance, $H=59.99$, $df=8$, $P<0.001$)

This is remarkable among birds, where final body size is usually attained before age of first reproduction (Ricklefs 1968; Gochfeld 1987; Stamps 1993; Teather and Weatherhead 1994) and resembles more the pattern found among dimorphic mammals, where asymptotic growth continues after reaching adulthood (reviewed in Stamps 1993; Fairbairn et al. 2007). Tarsus length did not increase with age. In an earlier study, we found that tarsus reaches final adult size during the first year of life, i.e., much earlier than other body measurements. We interpreted this early growth of the tarsus as an adaptation to facilitate rapid body growth in this mainly cursorial bird (Alonso et al. 2009). Unlike body size, weight seemed to increase only up to an age of 5 years, i.e., essentially during the immature period. Up to that age, weight was correlated with several linear measurements like wing, head, or central toe length (Magaña 2007; Alonso et al. 2009), but later, in fully sexually mature birds, it fluctuated between years probably depending on body condition. In a small sample of eight captive great bustard males aged 5–13 years, weight showed also no correlation with age (Carranza and Hidalgo 1993), although no information was provided for younger ages or variation with body size. These relationships between body growth, weight, and age had not previously been investigated in wild great bustards.

Copulation frequency and mating skew

Although the number of effective copulations was apparently very low (4 in 509 h, or an average 0.08 copulations per male in 10 h), this figure was similar to that found in a previous study in northern Spain (0.05 copulations/10 h; Morales 2000; Morales et al. 2003). Some authors have cited sporadic matings during full-moon nights (e.g., Gewalt 1959; also for the Indian great bustard *Ardeotis*

Table 2 Partial correlations of estimated mating success with age, weight, and wing length in great bustard males

| | Multiple regression parameters | | | | Age | | Weight | | Wing length | |
|----------------|--------------------------------|------|------|-------|------|-------|--------|-------|-------------|-------|
| | R | F | df | P | r | P | r | P | r | P |
| Capture year | 0.65 | 4.63 | 3,19 | 0.013 | 0.49 | 0.026 | 0.42 | 0.033 | -0.33 | 0.116 |
| Mean all years | 0.65 | 4.54 | 3,19 | 0.015 | 0.47 | 0.025 | 0.41 | 0.043 | -0.27 | 0.179 |

Weight and wing length correspond to the year of capture. Since males were not recaptured every year, analyses were performed, first, using only data from the capture year and, second, using mean data from all years for each male

nigriceps, Ali and Rahmani 1984), but most authors refer to early morning and late evening as the main mating periods (Gewalt 1959; Glutz et al. 1973, Hidalgo and Carranza 1990; Hellmich 1991; Morales 2000), and no matings were recorded during occasional night observations in our study population (Magaña 2007).

The 523 copulations extrapolated from our observed four matings were enough to inseminate 65% of the 800 adult females in the population (assuming one copulation per female, which seems common among lekking Tetraonidae; see Birkhead et al. 1987). To complete insemination of the remaining 35% adult females, just a 5.6% of the recorded copulation attempts would need to be successful. These figures suggest that the effective copulation rate recorded in this species (Morales et al. 2003; present study), although apparently very low, could reasonably reflect the real mating frequency.

The estimated mating success figures are among the most strongly skewed values reported for lekking birds (reviews in Halliday 1983; Andersson 1994; Johnsgard 1994; Höglund and Alatalo 1995). Since we only saw three birds actually copulating, the skew was probably much higher than that reflected using our estimated mating success parameter, which included copulation attempts. The three males seen copulating were those with highest estimated mating success scores in their respective leks (see

Table 3 Results of the logistic regression for estimated mating success (successful vs. unsuccessful) of 23 great bustard males

| Variable | χ^2 | P |
|------------------------|----------|-------|
| Age | 4.90 | 0.027 |
| Weight | 3.87 | 0.050 |
| Wing length | 0.06 | 0.800 |
| PC1 (display effort) | 9.41 | 0.002 |
| PC2 (solitary display) | 1.69 | 0.194 |

PC1 and PC2 are the first and second principal components of male behavior extracted from a PCA of 12 behavioral traits (see Table 1). Mean data for the overall tracking period were used in this analysis. An analysis using data only from the capture year gave the same results

Fig. 3). This supports the validity of the estimate used in our study as a proxy of the real mating success.

Correlates of male mating success

Our results show that age, weight, and display effort were all significant and independent predictors of male mating success in great bustards. The higher display effort involved longer full display bouts, which resulted in a longer percent time devoted to full display (first component of male behavior). Display effort is the most common correlate of mating success in most lekking birds studied before (reviewed in Johnsgard 1994; Höglund and Alatalo 1995) and thus could have also been expected to show a significant effect in great bustards. Perhaps the most interesting finding of our study was that age is a determinant of male mating success in great bustards. Although the positive effect of age might be ultimately attained through female preference for older males, males also actively contributed to such age-related effect via a second component of their behavior. We found that age was strongly correlated with PC2, i.e., older males spent longer seasonal and daily periods on solitary display. To get independent from the male flock is, however, not an easy task, since any individual trying to detach from the flock, particularly when this happens early in the season, is as a rule rapidly reincorporated to it as described below. Following the initiative of one or a few males, the whole flock typically runs toward the detached male in aggressive attitude, frequently ending up with the detached male again absorbed by the flock, after a ritualized free-for-all or plucking-dance. This behavior was first described by Gewalt (1959) and later also reported by various other authors, without giving a reasonable explanation of its possible function (Glutz et al. 1973; Hidalgo and Carranza 1990; Morales 2000).

Our finding that older males are the first to display as singles—both through the mating season and within the day—suggests that the behavior described above may help establishing a social rank order and determine which males should be allowed to detach from the group first. The privilege of being able to display as a solitary

Table 4 Comparison of the 15 logistic regression models with lower Δ AIC examining the effects of male age, weight, wing length, and both behavioral factors on mating success

| Model | Variables | <i>df</i> | AIC | Δ AIC | χ^2 | <i>P</i> |
|-------|-----------------------------|-----------|-------|--------------|----------|----------|
| 1 | Weight, PC1 | 2 | 21.45 | 0.00 | 17.81 | <0.001 |
| 2 | Weight, PC1, PC2 | 3 | 22.01 | 0.56 | 19.26 | <0.001 |
| 3 | Age, weight, PC1 | 3 | 23.23 | 1.78 | 18.04 | <0.001 |
| 4 | Weight, wing, PC1 | 3 | 23.46 | 2.01 | 17.82 | <0.001 |
| 5 | Age, weight, PC1, PC2 | 4 | 23.77 | 2.32 | 19.50 | 0.001 |
| 6 | Weight, wing, PC1, PC2 | 4 | 23.85 | 2.40 | 19.42 | 0.001 |
| 7 | Age, weight, wing, PC1 | 4 | 25.23 | 3.78 | 18.04 | 0.001 |
| 8 | Age, weight, wing, PC1, PC2 | 5 | 25.54 | 4.09 | 19.73 | 0.001 |
| 9 | PC1, PC2 | 2 | 30.20 | 8.75 | 9.07 | 0.011 |
| 10 | Weight, PC2 | 2 | 30.25 | 8.80 | 9.02 | 0.011 |
| 11 | Age, weight | 2 | 30.70 | 9.25 | 8.57 | 0.014 |
| 12 | Weight | 1 | 30.79 | 9.34 | 6.48 | 0.011 |
| 13 | Age, PC1 | 2 | 31.13 | 9.68 | 8.14 | 0.017 |
| 14 | Age, PC1, PC2 | 3 | 31.75 | 10.30 | 9.52 | 0.023 |
| 15 | Weight, wing, PC2 | 3 | 32.00 | 10.55 | 9.27 | 0.026 |

male early in the mating season seems to be reserved to older males, which are probably those ranking high in the lek hierarchy. Having a more prolonged solitary display period—both daily and seasonally—these males may thus benefit from more mating opportunities. The maintenance of such hierarchy from year to year is most likely favored by both the high longevity and strong fidelity of males to their leks typical of this species (Morales 2000; Magaña 2007). A similar system seems to determine male mating success in another long-lived lekking bird, the long-tailed manakin *Chiroxiphia linearis*, where an extended period of male–male interactions appears to predetermine the access of older males (greater than 8 years of age) to females (McDonald 1989). Social rank has also been shown to increase with age, favoring mating success in several mammals (Clutton-Brock et al. 1982; Hass and Jenni 1991; Pelletier and Festa-Bianchet 2006; Zedrosser et al. 2007).

Female preference for older males has been observed in numerous polygynous bird and mammal species and some insects (reviewed in Andersson 1994; Johnsgard 1994; Kokko 1998; Brooks and Kemp 2001; see also Coltman et al. 2002; Pelletier and Festa-Bianchet 2006; Zedrosser et al. 2007; Durães et al. 2008). These studies support the hypothesis that age could be used by females as indicator of male viability because old age is proof of high survivorship (Manning 1985, 1989; Kokko and Lindstrom 1996; Kokko 1997, 1998). Although the validity of these age-based indicator mechanisms has been recently questioned (Beck and Powell 2000; Brooks and Kemp 2001; Beck and Promislow 2007), a new model proposed by Proulx et al. (2002) provides an alternative explanation of why females might prefer older males, based on the idea that older males reveal more information in their sexual

displays. This model suggests that male display and the differences in signalling between quality classes increase with male age, making female choice more effective among older males. Our finding that age, but not weight, is correlated with display behavior suggests that this could be the case in the great bustard.

As for weight, although it also contributed significantly to increase mating success, the causal relationships are less clear. We found no behavioral traits that could explain how heavier males gained more copulations. In contrast to older males, who invested more in daily and seasonal display time, weight did not show significant correlation with display effort or time displaying as single. One possibility is that the higher mating success of heavier males is a direct result of female preference for some indicator trait of good body condition, e.g., length and number of whiskers, which indeed correlate positively with weight and body condition (Magaña 2007).

The correlations between age, weight, and secondary sexual trait expression at the start and during the peak mating season support our suggestion that age and weight could independently contribute to increase mating success in great bustard males. Magaña (2007) found that whisker development correlated with weight, but not with age, at the start of the breeding season (male–male competition phase), thus being a good indicator of body condition. Between this phase and the peak mating period in April, whiskers developed further mostly in young males (<6 years old) who had already attained a heavy weight at the start of the season and in old males (>6 years) independently of their weight. This suggests both groups of males, the oldest (independently of their weight) and the heaviest (independently of their age), were able to reach during mating the maximum expression of this indicator trait of body

condition. Also, males reaching higher expression of indicator traits showed higher mating success (Magaña 2007). Another result from aggressive behavior during the mating period supports that older males have a higher social rank within the lek. Older males were involved in a significantly lower number of aggressive interactions (mostly copulation disruptions) than other males (Magaña 2007). This suggests that their status was probably accepted by lek mates, and thus, they could increase their display time, whereas males of younger age but higher weight did not increase display time perhaps to prevent inducing attacks from other males.

Body mass has been found to correlate with male mating success in species with large variation in body size (reviewed in Höglund and Alatalo 1995). These species include several insects, where larger males occupy the sites favored by incoming females; frogs, where spectral properties of male mating calls are associated with body size (but see Friedl and Klump 2005); and, particularly, polygynous ungulates, where body mass is generally considered to be the main determinant of social rank or territorial acquisition (e.g., Uganda kobs, Balmford et al. 1992; fallow deer and bighorn rams, Clutton-Brock et al. 1988; McElligott et al. 2001; Pelletier and Festa-Bianchet 2006; bison, where females prefer to mate with larger males, Bowyer et al. 2007). Body weight is also related to dominance rank and thus an important predictor of mating success in other mammals like feral cats *Felis catus* (Natoli et al. 2007) or brown bears *Ursus arctos* (Zedrosser et al. 2007). The scheme described here for great bustards (see also Magaña 2007) seems particularly similar to that found in bighorn rams, where social rank is a complex trait determined by both age and mass, whose respective influences change over a ram's lifetime, age being the main factor up to an age of 5–7 years and body mass thereafter (Pelletier and Festa-Bianchet 2006).

In contrast to the species mentioned above, among most lekking species, particularly birds, plumage and behavioral traits such as display rate or lek attendance or centrality have been found to correlate more with male mating success than age or body mass (reviewed in Johnsgard 1994; Höglund and Alatalo 1995; see also Beani and Dessi-Fulgheri 1995; Rintamäki et al. 1998; Parker and Ligon 2003; Nooker and Sandercock 2008). In this respect, great bustards represent a particular case among birds. Probably because they are the most sexually dimorphic bird species (Alonso et al. 2009), in many aspects, they resemble more the pattern found among highly dimorphic mammals as described above. As suggested for some of these mammals, the mating behavior of great bustards presented here combined with their extreme size dimorphism between sexes (Alonso et al. 2009) suggests that sexual selection continues to act on sexual size dimorphism in this species.

In conclusion, an advanced age and a high weight, together with a high display effort, seem to exert an important and independent influence on male mating success in the great bustard. The main behavioral mechanism contributing to increase mating success was to perform longer full-display bouts. The two phenotypic traits, age and weight, apparently helped males achieving a higher mating success through different mechanisms, as described for some ungulates. Older males probably were allowed by other males of the lek to display as solitary individuals during longer periods. Heavier males did not make higher display effort, which suggests that they could probably be both, recognized as dominants by other males and selected by visiting females, through direct assessment of their quality via inspection of their secondary sexual traits.

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Ethical standards The procedures followed in this study comply with the current Spanish laws.

Conflict of interest The authors declare that they have no conflict of interest.

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