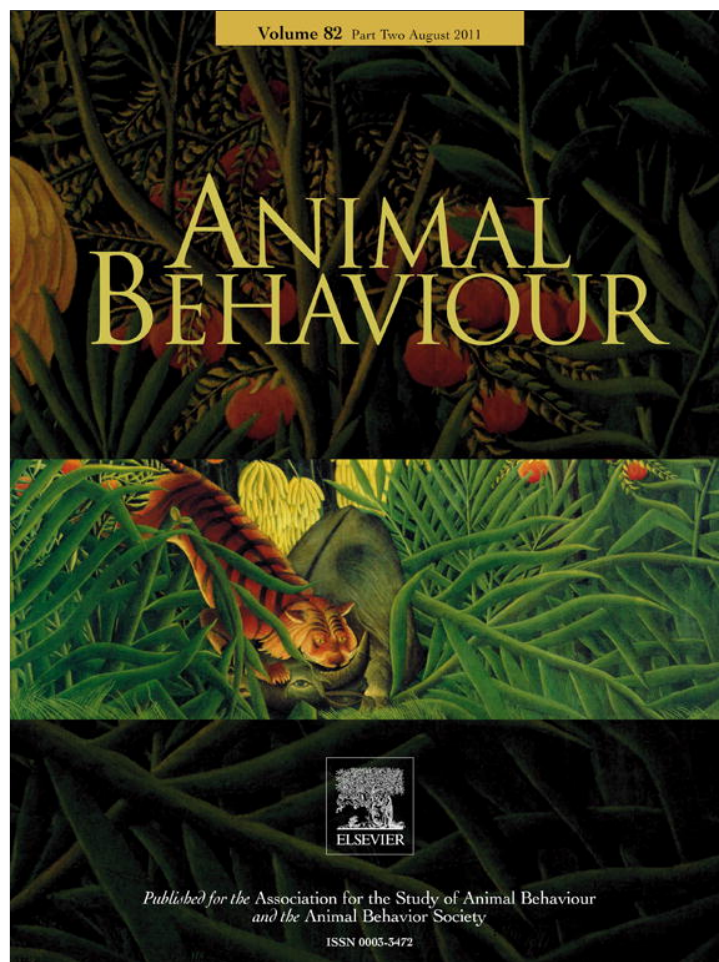


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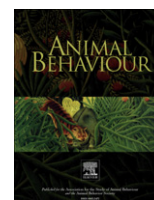
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# Animal Behaviour

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## Age-related dominance helps reduce male aggressiveness in great bustard leks

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Stable dominance hierarchies have evolved in many socially living animals to reduce the negative consequences of agonistic interactions. To evaluate whether established dominance relationships reduce aggressive encounters among males during the mating season, we studied aggressive behaviour in lekking male great bustards, *Otis tarda*. This sexually dimorphic bird species is potentially subject to strong sexual selection operating through intramale competition. The strongly skewed mating success of males is mainly determined by their age and weight, which are reliably signalled through plumage traits. We observed that adult males lived in stable groups at traditional leks to which they remained faithful throughout their lives, a prerequisite for the establishment of stable dominance hierarchies. Males substantially reduced aggressive interactions during the mating period. Males involved in more aggressive interactions during the premating period had weakly expressed sexual traits and low courtship success, which suggests the existence of an age- and possibly also weight-determined lek hierarchy. This is supported by the increase with age in a male's dominance index, and the absence of aggressive interactions at advanced ages. During the mating period, older males and those with higher courtship success were involved in fewer aggressive encounters, suggesting that other males respected their status. Subdominant males disrupted other males' copulation attempts, perhaps to reduce their success or to gain copulations themselves. Our study supports the hypotheses that social dominance is largely age determined in the great bustard and that established dominance relationships help reduce intramale aggression during the mating period.

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Intrasexual competition among males is particularly strong in polygynous species (Orlans 1969; Emlen & Oring 1977; Wittenberger 1979). Together with female mate choice, this is a major sexual selection mechanism creating the high skew in male reproductive success typical of polygynous mating systems. The relative importance of male competition seems to be higher in mammals, most of which have developed armaments and/or strong sexual size dimorphism. In birds, in contrast, evolution of male ornaments and displays to attract females suggests that female mate choice is a more extended behavioural process (Bradbury & Gibson 1983; Shuster & Wade 2003; Saether et al. 2005). Males of many polygynous mammals, and some birds, compete intensely or even fight fiercely with each other to gain access to females during short mating seasons (Clutton-Brock et al. 1982; Geist 1986; Gosling et al. 1987; Festa-Bianchet et al. 1990; Johnsgard 1994; Komers et al. 1994; Mysterud et al. 2005; Hsu et al. 2006). Aggressive encounters are costly and dangerous, and may lead to serious injury or death of combatants, or reduce their survival after breeding (Müller 1979;

Van Rhijn 1991; Stevenson & Bancroft 1995; Toigo & Gaillard 2003; Stevenson et al. 2004).

To reduce the negative consequences of these interactions, stable male dominance hierarchies have emerged in many socially living animals (e.g. Lill 1976; Müller 1979; Foster 1981; Appleby 1982; McDonald 1989; Piper 1997; Widemo 1997; McElligott et al. 1998; Jennings et al. 2006; Pelletier & Festa-Bianchet 2006; DuVal & Kempenaers 2008). In most lekking species, these dominance relationships probably determine the spatial arrangement of male display territories. Dominant males usually occupy central positions at the lek, often permanently within and between consecutive breeding seasons (Höglund & Alatalo 1995). In all well-studied lekking birds, despite a well-established territorial organization, disruption of courtship or copulation has been found to affect 2–68% of observed mating attempts (Bradbury & Gibson 1983; Trail 1985; Höglund & Alatalo 1995; Saether et al. 1999). In these species, this form of interference among adult males when they try to mate is indeed associated with their aggregation at the lek, and constitutes an important mechanism controlling mating success. In fact, the frequency of disruptions and other forms of male aggression have been suggested to increase with the degree of male clustering. Disruptions would thus be one of the main factors favouring the evolution of the exploded lek mating system, in which displaying

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males of many species disperse over a large area, compared to the more clumped classical leks (Foster 1983).

Similarly, in most polygynous ungulates with established male dominance hierarchies, intense agonistic interactions for access to females often persist during the mating period, thus questioning the usefulness of hierarchies to reduce male–male aggression during mating (Clutton-Brock & Albon, 1979; Appleby 1982; McElligott et al. 1998). An obvious consequence of established dominance hierarchies is that dominant males should suffer fewer interruptions than average individuals (Alexander 1975; Borgia 1979), but in their seminal review of mate choice at leks, Bradbury & Gibson (1983) found no evidence to support this idea. Since then, few studies have reported reduced aggression among high-ranking males (e.g. Widemo 1997; DuVal & Kempnaers 2008; Willisch & Neuhaus 2010). A common feature of these species seems to be that strict dominance hierarchies are established long before the mating period, so that both sexual selection processes, male–male competition and female choice, are separated in time (Widemo 1997; DuVal & Kempnaers 2008; Willisch & Neuhaus 2010).

Willisch & Neuhaus (2009) specifically argued that to show conclusively that dominance hierarchies contribute to minimizing the costs derived from agonistic encounters, a reduction in intramale interactions during the mating period compared to the pre-mating period should be observed. In a recent study with Alpine ibex, *Capra ibex*, they confirmed their prediction by showing that the establishment of stable and strictly binding dominance relationships among individual males during the prerutting season made fighting for access to females unnecessary (Willisch & Neuhaus 2010). Subdominant males were never observed to disturb mating attempts by dominant males. They avoided fights they were likely to lose, based probably on the outcomes of earlier interactions with their opponents (Hsu et al. 2006; Taillon & Coté 2006). This strict adherence to established dominance relationships benefited the energy budget of males and enhanced their subsequent survival during winter (Willisch & Neuhaus 2010). Species living in stable social groups are even able to draw sophisticated inferences about their own dominance status relative to that of strangers that they have observed interacting with known individuals (i.e. transitive reasoning, Paz-y-Miño et al. 2004).

In the present study we investigated agonistic relationships in great bustards, *Otis tarda*, a lekking species showing the most extreme sexual dimorphism among birds, and thus potentially subject to similar strong sexual selection mechanisms to those operating in highly dimorphic ungulates (Alonso et al. 2009a). From October, male great bustards returning from the postbreeding migration arrive on their traditional lek site, where they join together and remain as a single male flock until late March. Between late December and late March they fight and display in the absence of females (Gewalt 1959; Hellmich 1991; Hidalgo & Carranza 1991; Magaña 2007). Intrasexual competition is intense, and may end in fierce duels between combatants with the loser sometimes being unable to fly (J. C. Alonso, personal observation). Male mortality is highest after mating, confirming the strong selection pressure of the intrasexual competition phase (Martín 2008, unpublished data). Females concentrate at lek sites in April, when adult males disperse and display solitarily to gain matings in an exploded lek system (Hidalgo & Carranza 1991; Magaña 2007).

During these two clearly distinct periods (male–male competition or pre-mating period in December–March, and mating period in April), males perform the same display and exhibit the same secondary sexual traits (whiskers and neck plumage). However, the durations of the three phases, which end in the balloon display characteristic of this species, differ between the pre-mating period and the mating period. Briefly, the three phases are: D1: neck vertical, gular pouch 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 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 undercoverts; D3: like D2 but neck completely inflated and reclined over back, whiskers vertical and bird moving sideways or shivering, usually when females are present. Hidalgo & Carranza (1991) observed that what they called 'aggressive' display, with longer durations of the first two phases, was performed mainly during the pre-mating period among males of the flock, whereas the 'sexual' display, with longer D3 phases, was more frequent during the mating period and served to attract females. This was later confirmed by other authors (Morales 2000; Magaña 2007). The following results are also relevant to the present study. First, the two sexual traits, whiskers and neck plumage, are reliable indicators of the age and weight of males, and their development, together with display effort, is a significant predictor of male mating success (Alonso et al. 2010a, b). Second, males attaining higher expression of these traits were able to detach from the male flock earlier in the season, enabling them to display as solitary males and attract females during a more prolonged period (Alonso et al. 2010b). Only males with the highest trait expression, that is, older and heavier males, were allowed by their flockmates to leave the flock, whereas other males were as a rule rapidly reincorporated into it after a ritualized communal free-for-all run (Magaña 2007; Alonso et al. 2010a). This is a kind of communal chase in which, following the initiative of one or a few males, the whole flock typically runs towards a detached male in aggressive attitude (i.e. pointing to it with neck stretched in oblique position), frequently ending with the detached male again absorbed by the flock, after a ritualized free-for-all or plucking dance. This behaviour was first described by Gewalt (1959) and later also reported by various other authors, who did not give a reasonable explanation of its possible function (Glutz et al. 1973; Hidalgo & Carranza 1990; Morales 2000). In an earlier study (Alonso et al. 2010a), we suggested that the function of this behaviour is to prevent males leaving the flock and displaying by themselves early in the mating season. Finally, mating success is strongly skewed in great bustard leks, with fewer than half the males having access to females, and most copulations being gained by a few of the oldest and heaviest individuals (Magaña 2007; Alonso et al. 2010a).

Based on Hidalgo & Carranza's (1991) and our results described above, we hypothesized that during the intrasexual contest period in December–March great bustard males establish or confirm a pre-existing dominance hierarchy within the flock, mainly through displaying their sexual traits. Aggressive interactions would be used mainly by socially subdominant males to challenge a higher rank. This hierarchy is later respected during the mating period, as described for other species with clearly separated male competition and female mate choice periods (DuVal & Kempnaers 2008; Willisch & Neuhaus 2010). Specifically, we predicted that if a pre-established and stable dominance relationship exists among members of the male flock at the time of mating, based on pre-mating male–male interactions, (1) overall male aggressive interactions should be reduced during the mating period compared with the pre-mating period. Second, if rank is based on honest signalling through reliable sexual traits, and these serve to minimize costly aggressive interactions (Alonso et al. 2010b), (2) males with higher expression of secondary sexual traits (i.e. older and heavier males) should be involved in fewer aggressive encounters than other males during the mating period. Moreover, since great bustard males are long-lived birds that live in stable groups at traditional leks (Morales 2000; Magaña 2007), the existence of stable dominance relationships is very likely, and the rank of the oldest and heaviest males should be known and generally respected by flockmates across successive years. Thus, (3) males obtaining



higher courtship success (i.e. older and heavier males) should be involved in fewer aggressive encounters not only during the mating period, but also during the pre-mating male–male contest period, showing that their status is not questioned by other males. Finally, as predicted for these dominance relationships to have an adaptive value, (4) we examined whether males, particularly adult individuals, remained faithful to their leks between years.

## METHODS

This study is based on behavioural observations of agonistic interactions of 18 great bustard males radiotracked during one to four mating seasons (late March–early May 1998–2001) each at seven leks in Madrid province, central Spain (16 captured as adults and two as chicks 1995–2001). Aggressive interactions were also obtained during the pre-mating season (December–March) at the two leks, Camarma and Ribatejada-Valdetorres, with the best observation conditions and with the most marked birds. Interannual lek fidelity and seasonal changes in mean flock size were studied in the 18 males plus another 32 males that were not intensively radiotracked (36 captured as adults in 1996–2001, 14 as chicks 1995–1997).

### *Trapping, Morphometrics and Age Estimation*

Adult males were captured with rocket nets in January–February and young birds were caught in July, when they were 3–10 weeks old and still dependent on their mothers, by chasing them down. After one or two flights the chick usually separated from its mother, lay down and remained motionless, hidden when possible in the ground vegetation, trying to go unnoticed. After marking it, we released the bird in the same spot where we had caught it to facilitate its rejoining its mother as soon as possible. Adults were immediately immobilized using specially designed jackets and their heads, like those of the chicks, covered to minimize capture stress. All birds were released once processed, within 20 min after capture. The average weight  $\pm$  SE at capture was  $2743 \pm 0.14$  g, range 2100–3700 g,  $N = 14$ ; birds weighing less than 1 kg were released unmarked. Each captured bird was fitted with a backpack radiotransmitter 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. The tags were of PVC (Gravoply), 70–65 mm long and 1.5 mm thick. Each tag had a different design using various colours and symbols, to allow visual identification with a telescope. The tags were attached to the wing patagium using special pliers (Allflex). The total weight of tag plus rivet was ca. 12 g. The tags were covered with thin brown paper painted black, imitating the plumage design of the birds to reduce as much as possible the visibility of the tag to predators. The paper usually fell off after a few days. The transmitters (Biotrack Ltd, Dorset, U.K.) were TW3 2-AA backpack-mounted units (60 g). We used elastic harness material to allow the harness to expand as the young grew. The total weight of transmitter plus harness did not exceed the recommended limit of 3–5% of the bird's weight (Kenward 2001). After release, and once we checked that birds behaved normally, we located them using TR2-TS1 scanner-receivers (Telonics, Mesa, AZ, U.S.A.). All adult birds were weighed and their age was 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; see also Alonso et al. 2010a, b for more details). To avoid disturbing the birds, we did not recapture them for the only purpose of weighing them each year. Thus, we could only use the capture-year weight in the correlations. To corroborate correlation results with weight, we used values of whisker development, a sexual trait that is positively correlated with weight ( $P < 0.001$ , Alonso et al. 2010b). Whiskers are thin feathers, 15–20 cm long, that

grow in tufts at both sides of the lower mandible, and have no apparent function other than being exhibited as a sexual ornament (Gewalt 1959; Alonso et al. 2009a, 2010b).

### *Sexual Trait Development and Male Rank*

We assessed the development of the two main sexual characters of great bustard males, whiskers and neck, both through measurements taken during capture and through repeated visual ranking when scan sampling male behaviour at leks throughout the study period. We established three categories to quantify whisker development (1: a few moustache feathers exceeding the rear end of the bill gape by a few centimetres; 2: an intermediate amount of moustache reaching the nape outline; 3: an abundant moustache clearly exceeding the nape outline) and neck plumage development and thickness (1: thin neck with brown lower half and light grey upper half; 2: thicker, with chestnut-coloured base, creamy yellow intermediate band and whitish upper band; 3: bulky neck with well-developed breast feathers, narrow intense chestnut band at the base, and broad intense ivory-white upper band; see Alonso et al. 2010b for details and definitions of these categories, which are slightly modified from those used by Carranza & Hidalgo 1993 and Morales 2000). In our previous study (Alonso et al. 2010b), we suggested that whiskers function as a good indicator of weight during male–male interactions in the pre-mating period, and that the neck is an indicator of age for both males and females during the mating period. In the two leks for which we had a reasonably large number of marked males (five in each), we also explored the relationships between aggressive behaviour and sexual trait expression of males. We assigned a phenotypic rank to each of these males by ranking all marked males of the same lek according to their average neck and whisker rank values: the male with phenotypic rank 1 was the male showing the highest mean value calculated with both whiskers and neck values, and giving priority to the neck value for scores tied among two males.

### *Behavioural Observations*

Marked males were tracked 2–3 days per week over one to three mating seasons (from late March to mid-May). Observations were carried out from dawn to midday, when activity in general, and particularly sexual activity, is much reduced. Each observer tracked one male per day from a ground vehicle at 1–3 km from the focal bird using 20–40 $\times$  and 60–90 $\times$  telescopes. After we discounted periods of bad weather or when birds were disturbed or not visible from our observation points, our total sample was 177 useful days and 267 useful observation-hours of males displaying alone in the exploded lek. We recorded each aggressive interaction of a focal bird with any other male or group of males of the lek, its duration to the nearest second, whether the focal bird was the aggressor or victim, and the outcome of the attack, that is, who was the winner and the loser. For each male we calculated a relative dominance index, as the difference between the raw counts of dominant and subordinate actions divided by their sum (Paz-y-Miño et al. 2004). We recorded the distance at which contestants started an attack, and counted the other males and females in the immediate vicinity.

We considered the following types of aggressive interactions: threat walk (a male intimidated a nearby displaying lek mate by walking or running towards him in aggressive attitude, with neck stretched in oblique position) and displacement (a male ran or flew directly to the position of another displaying male, forcing him to move or fly away). These two types do not usually imply physical contact between contestants. However, they sometimes end with the aggressor attacking the rival's face with the bill, or with both

(occasionally three and rarely even four) combatants engaging in a duel (by gripping each other with their bills and shoving and jostling breast to breast sometimes for more than 1 h, until eventually the loser abandons the fight). Threat walks, displacements or attacks were usually intended to interrupt another male's display, or displace him from his displaying position, but could also be frequently directed towards a male courting a female during the precopulatory phase, in which case we defined the behaviour as copulation disruption.

Given the low number of effective copulations typically recorded in this species and also seen during our study, as a statistically more practical parameter we calculated for each male an estimated courtship success per 10 h, by adding observed effective copulations plus copulation attempts, defining these as only those instances when a male was seen displaying very close to one or more females (<3 m) when these showed obvious precopulatory behaviour (see details in Alonso et al. 2010a, b). To support the hypothesis that the courtship success correlates positively with mating success, we had previously compared the rates of effective copulations and copulation attempts and found that they 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).

#### Ethical Note

We found no evidence of adverse effects of the marking method on the survival of our radiomarked birds (Martín et al. 2007). Thus, we assumed that our marking method did not negatively affect the birds, as has also been shown or assumed for similar radiotagging methods with other species (Rohner & Hunter 1996; Combreau et al. 2001; Grant 2002). Short-term effects of handling and tagging did not differ in relation to chick body mass, which suggests that marking did not affect lighter individuals disproportionately (Martín et al. 2007).

Capture permits were obtained, for a limited number of individuals per year, from the conservation authorities of the regional government of Madrid Community. Because of this, and since priority was always given to the welfare of animals, sample sizes were kept to a minimum acceptable for analysis, and observation methods were designed to minimize disturbance to the birds.

Our research was carried out under the supervision of the Ministry for Science and Technology, to which our institution, the Museo Nacional de Ciencias Naturales – Natural History Museum (Consejo Superior de Investigaciones Científicas – Spanish High Research Council) belongs.

#### Data Analyses

For each marked male, we first calculated a mean annual value of aggressive interaction rate (number of interactions per 10 h) and estimated courtship success. To increase the significance of mean

values for each individual, we later obtained overall mean values for each male, after confirming that there were no significant differences between years (see also Alonso et al. 2010a, b). Similarly, after checking that phenotypic ranks among marked males of a given lek did not change between consecutive years through the observation period, we compared the phenotypic rank of the different males with their rate of aggressive interaction. Seasonal changes in mean flock size and mean aggression rate were analysed through repeated measures ANOVA since the data were taken from the same individuals across multiple years and through the season within a year. We used Spearman rank correlation to explore relationships between mean individual interaction rate, estimated courtship success, age, weight, sexual trait expression value and phenotypic rank of males, and the chi-square test to assess whether interaction rate was related to the presence of nearby females. All statistical analyses were performed with Statistica 6.0 (Statsoft Inc., Tulsa, OK, U.S.A.).

## RESULTS

### Male Fidelity to the Lek

A large majority of great bustard males remained faithful to their leks between consecutive years, and fidelity increased with age up to the 8th calendar year, when it was 100% (Table 1). Also, three of eight males that dispersed after breeding returned to their original lek after 1 year displaying at a different lek (Table 1). These results confirmed our fourth prediction (see Introduction).

### Seasonal Changes in Flock Size and Aggressiveness

There was a significant seasonal variation in male flock size, with highest values between February and March (repeated measures ANOVA:  $F_{7,497} = 42.13$ ,  $P < 0.001$ ; Fig. 1). From late March on, adult males progressively left the flock to display as solitary individuals in April. Simultaneously, the frequency of aggressive interactions among lekking males increased between early December and early March, reaching a maximum of 35.7 interactions/10 h, and later decreased through the mating period (repeated measures ANOVA:  $F_{7,155} = 9.783$ ,  $P < 0.001$ ; Fig. 2). This result confirmed our prediction (1).

### Male–male Interactions during the Premating Period

In both leks where male behaviour was studied during the pre-mating male–male competition period, the rate of aggressive interactions of males was inversely correlated with their phenotypic rank (Camarma:  $r_s = 0.9$ ,  $P = 0.037$ ; Ribatejada-Valdetorres:  $r_s = 1.0$ ,  $P < 0.001$ ;  $N = 5$  males; Fig. 3). At one of the leks, Camarma, males involved in more aggressive interactions during

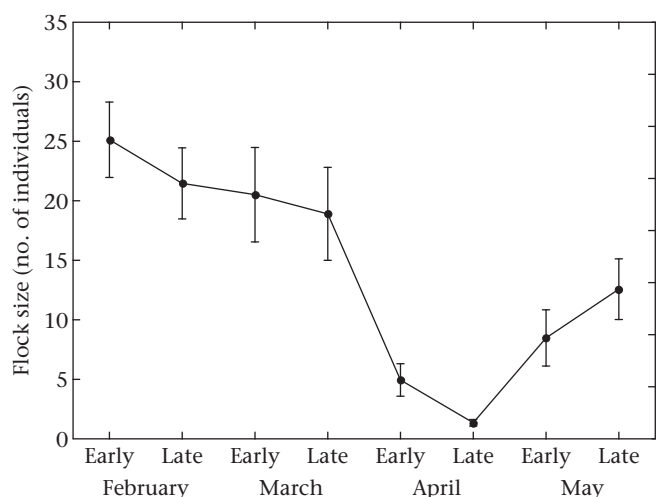
**Table 1**  
Lek fidelity of great bustard males marked in 1997–2001 at different ages and localized each spring until they died

	Age (calendar year)															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16		
Total number of marked males of that age in the study area	14	19	30	37	32	26	19	12	6	5	4	2	2	1		
Total number of males for which their lek is known for that year and the previous year (A)	14	14	17	26	25	25	19	12	6	5	4	2	2	1		
Males that remain at the lek of the previous year (B)		12	15	24	23	25	19	12	6	5	4	2	2	1		
Males displaying that year for the first time (C)	–	2	2	2	2	0	0	0	0	0	0	0	0	0		
Males returning to the original lek after 1 year breeding dispersal*	–	–	1	1	0	1	0	0	0	0	0	0	0	0		
Lek fidelity†		85.7	88.2	92.3	92.0	100	100	100	100	100	100	100	100	100		

Fourteen of these males were of known age (captured as chicks); the age of the other 36 males (captured as adults) was estimated following criteria in Alonso et al. (2006, 2010a, b).

\* These three males are included among the eight males dispersing 1 year before (C).

† Lek fidelity in a given year was defined as the percentage of males remaining faithful to their lek from the previous year  $(B/A) \times 100$ .

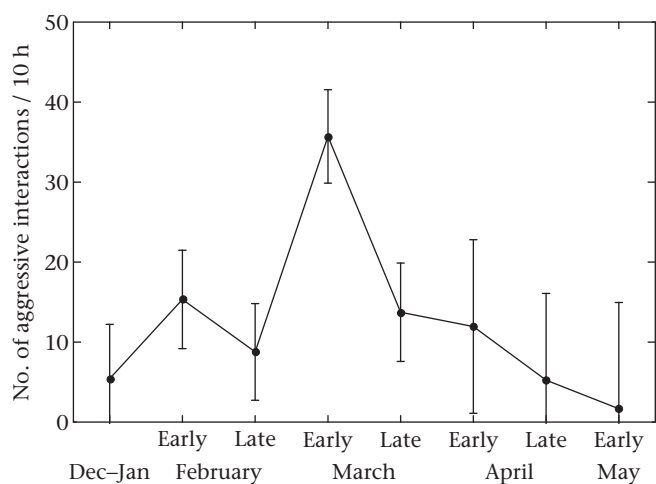


**Figure 1.** Fortnightly changes in mean adult male flock size through the breeding season. The graph shows means and 95% confidence intervals, and includes fortnightly mean flock size values for all marked males ( $N = 50$ ) during the period 1998–2001.

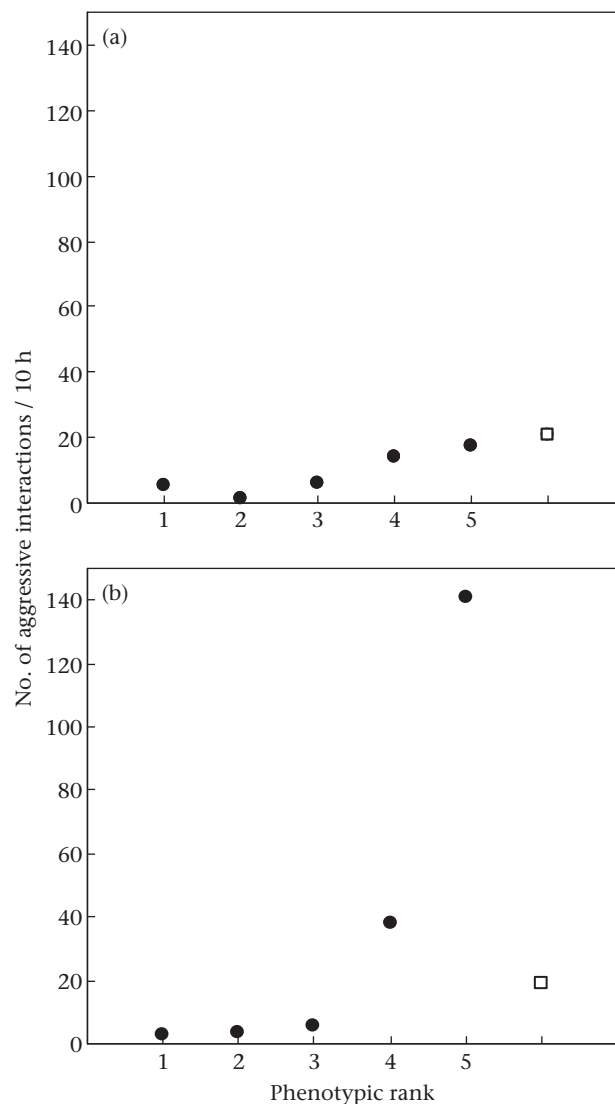
the pre-mating period later had lower courtship success (Camarma:  $r_s = 0.87$ ,  $P = 0.05$ ; Ribatejada-Valdetorres:  $r_s = 0.56$ ,  $P = 0.32$ ;  $N = 5$  males; Fig. 4). The dominance index of adult males tended to be negative at younger ages, shifting later to positive, and zero at advanced ages, when males were usually not involved in aggression during the pre-mating period (Table 2). These results confirmed our prediction (3).

*Male–male Interactions during the Mating Period*

During the mating period, a total of 53 aggressive interactions were recorded in the 18 marked males when these displayed as solitary males at the lek. Seventeen (32%) of these interactions were threat walks, 19 (36%) were displacements, four (8%) were duels and 13 (24%) were copulation disruptions. The time spent on aggressive interactions represented on average 2.6% of a male's time budget, and 19.2% of the time he spent on mating activities



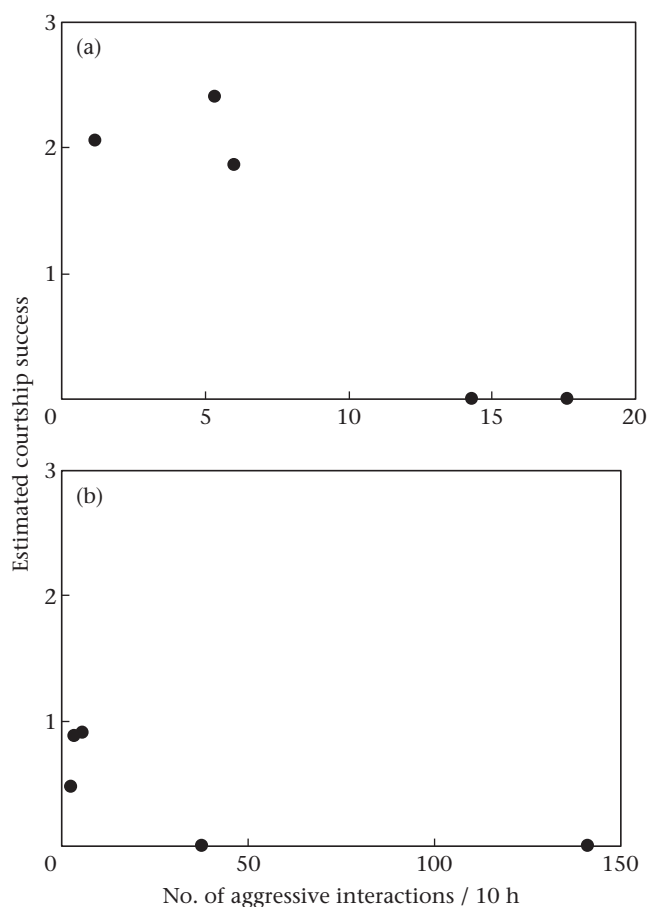
**Figure 2.** Fortnightly changes in mean frequency of aggressive interactions of the 10 males radiotracked in 1998–2001 at the two leks where male behaviour was studied during both the pre-mating and mating periods (Camarma, five males; Ribatejada-Valdetorres, five males). Means and 95% confidence intervals are shown. The pre-mating period extended from December to late March, and the mating period from early April to early May.



**Figure 3.** Relationship between rate of aggressive interactions and phenotypic rank of the 10 males marked at leks (a) Camarma and (b) Ribatejada-Valdetorres during the pre-mating period. Values are 1998–2001 means. For each lek, the male with phenotypic rank 1 was the male showing the highest mean rank value of both sexual traits, whiskers and neck (see Methods), when compared with its lek mates. The square represents the mean aggression rate of all other males in the flock.

(effective copulations plus copulation attempts). Interactions were associated with the presence of females nearby (within 100 m of the focal marked male; 49 of 53 cases; chi-square test:  $\chi^2_1 = 10.95$ ,  $P < 0.001$ ). In most cases (44 of 53), the attacking or victim male or males were also close (within 100 m of the focal marked male) when the aggression started.

The interaction rate of a male was inversely correlated with its age and estimated courtship success (Spearman rank correlation: age:  $r_s = -0.61$ ,  $P = 0.007$ ; courtship success:  $r_s = -0.47$ ,  $P = 0.05$ ;  $N = 18$  males), but showed no correlation with weight or whisker development (weight:  $r_s = 0.16$ ,  $P = 0.53$ ; whiskers:  $r_s = -0.29$ ,  $P = 0.25$ ). Males with less development of the neck sexual trait (an indicator of age, Alonso et al. 2010b) had marginally lower relative dominance indexes ( $r_s = 0.42$ ,  $N = 18$ ,  $P = 0.08$ ), losing a higher proportion of aggressive interactions ( $r_s = -0.51$ ,  $N = 18$ ,  $P = 0.03$ ). Finally, males weighing less and those showing less development of the whiskers sexual trait (an indicator of weight, Alonso et al. 2010b) more frequently disrupted copulations of other lek mates (weight:



**Figure 4.** Relationship between aggressive interaction rate during the pre-mating period and mating success in April, of the 10 males marked at leks (a) Camarma and (b) Ribatejada-Valdetorres. Values are 1998–2001 means.

$r_s = -0.54$ ,  $P = 0.02$ ; whiskers:  $r_s = -0.49$ ,  $P = 0.04$ ;  $N = 18$  males). The frequency of disrupted copulations was not correlated with either age ( $r_s = -0.28$ ,  $P = 0.25$ ) or neck development ( $r_s = -0.08$ ,  $P = 0.76$ ). Overall, these results confirmed our predictions (2) and (3).

**Table 2**  
Changes with age in the dominance index of 10 males (A–J), recorded at two leks (Camarma and Ribatejada-Valdetorres) during the pre-mating period (December–March)

Male	Age (calendar year)							N
	4	5	6	7	8	9	10	
A	-1							8
B	-1	-1	+1					15
C		-1	+1	0	0			5
D			-1					1
E					-0.33			14
F				0	0	0	0	2
G					+1	0	+1	5
H					-1	0	0	1
I				+1	0	0		6
J	+1	+1						7
Modal value	-1	-1	+1	0	0	0	0	

The dominance index was computed as the difference between the raw counts of dominant and subordinate actions divided by their sum (Paz-y-Miño et al. 2004).  $N$  = number of interactions recorded for each male. In all cases, zero values mean that there were no aggressive interactions. Male E showed an exceptionally high interaction rate and low dominance index when he was 8 years old. Soon after the mating period this male died, and its faeces showed an extraordinary amount of parasites, which suggested he was in poor condition that year.

**DISCUSSION**

Great bustard males showed a strong lifetime fidelity to their leks. Breeding dispersal, that is, the change of lek between years, was rare among adults, shifts between leks being observed almost only in immature birds (see also Alonso et al. 1998; Martín et al. 2008). One of the outcomes of this marked lek fidelity was the remarkable stability of the male flock size at each lek in spring across years. Moreover, through the several months males spent at their lek site, most males of a lek also tended to remain aggregated in the same flock (M. Magaña, personal observation). The only exception was during the postbreeding migration, when males mixed with individuals from other leks at summering or wintering areas, to which they remained extremely faithful throughout their lives (Alonso et al. 2009b; Palacín et al. 2009). Such lek faithfulness and the consequent flock stability, both within and between years, fulfilled the prerequisites for the establishment of stable dominance hierarchies (Piper 1997). In several socially living animals, interactions among the same males during a prolonged period of time enable exchange of accurate information about each other's competitive abilities and facilitate the development of efficient dominance relationships (Appleby 1982; Piper 1997; McElligott et al. 1998; Hsu et al. 2006; Pelletier & Festa-Bianchet 2006; Taillon & Coté 2006; Willisch & Neuhaus 2010). Specifically in lekking species, aggregation of the same individuals at leks year after year may lead to stable social dominance structuring (reviewed in Andersson 1994; Johnsgard 1994; Höglund & Alatalo 1995; Widemo 1997).

In accordance with one of our main predictions, male great bustards substantially reduced the frequency of aggressive interactions during the mating period compared with the pre-mating period. The pre-mating period, when great bustard males invest considerable time and effort displaying and interacting in the absence of females, extends through several months, which led authors to emphasize the relevance of this period in modulating social structuring within the male group (N. Collar, cited in Cramp & Simmons 1980; Hidalgo & Carranza 1990, 1991; Morales 2000). Hidalgo & Carranza (1990, 1991) suggested that the main function of pre-mating aggressive displays among males when females are not present is to show their status, although they had no marked birds to support their conclusions. In a recent study with marked birds, we showed that the two main secondary sexual traits of male great bustards, whiskers and neck, function as reliable indicators of age and weight during both rival assessment and mate choice (Alonso et al. 2010b), and that age and weight are positively correlated with mating success (Alonso et al. 2010a). This suggested that both traits might be reliable indicators of rank in this species, in a similar way to badges of status of many other bird species (Maynard Smith & Harper 2003). Sexual traits are thus probably used by older and heavier male great bustards to signal their competitive ability and so reduce their investment in costly and potentially dangerous fights to maintain their status in the lek. In the present study, we showed that, indeed, males with more developed secondary sexual traits were involved in fewer aggressive encounters during the pre-mating period, strongly suggesting that our previous assumptions (Alonso et al. 2010b) about the capacity of these traits to reduce unnecessary aggression are probably right. These results support the hypothesis that dominance hierarchies help to minimize the costs of agonistic encounters (see Willisch & Neuhaus 2009). Most pre-mating aggressive interactions were undertaken by males that would later have the lowest mating success, which suggests that these males were trying to go up in the hierarchy. An additional result supporting the existence of an age-determined social dominance structure in great bustard males is the increase with age in the dominance index, and the absence of aggressive interactions at advanced ages in the males studied during the pre-mating period.



Taken together, our previous and current results support earlier interpretations of male–male interactions during this period, that is, that the function of the long pre-mating interaction period in great bustard males is to establish a largely age- and weight-determined dominance hierarchy or confirm the hierarchy from previous years. Older and heavier males would attain this through displaying, or just because their status is known by other males with no need to get involved in many fights, whereas lower-ranking males would use aggressive interactions to try to get a better position in the lek hierarchy. The fact that some of our marked males were not involved in aggression at older ages in various consecutive years supports our suggestion that their rank would be known and respected by other males of the lek. Social rank and mating success have also been shown to increase with age in other long-lived, lekking birds and mammals with extended periods of male–male interactions (McDonald 1989; Johnsgard 1994; McDonald & Potts 1994; Höglund & Alatalo 1995; Widemo 1997; Wegge et al. 2005), and with weight in sexually dimorphic, polygynous ungulates (Clutton-Brock et al. 1988; Balmford et al. 1992; McElligott et al. 2001; Pelletier & Festa-Bianchet 2006; Bowyer et al. 2007).

Another main result of our study was that during the mating period dominant males (older birds and those with strongly expressed neck sexual trait and higher courtship success) were involved in fewer aggressive encounters. Our study adds to the few studies reporting reduced aggression among high-ranking males (Widemo 1997; DuVal & Kempenaers 2008; Willisch & Neuhaus 2010), which is an obvious ultimate reason for the existence of established dominance hierarchies (Alexander 1975; Borgia 1979; Bradbury & Gibson 1983). Willisch & Neuhaus (2010) hypothesized that costly intramale interactions are reduced during the mating period in Alpine ibex by the adherence to pre-established and stable dominance relationships, in contrast to most other polygynous ungulates for which agonistic behaviour usually peaks during mating. They explained this apparently atypical behaviour of Alpine ibex as a mechanism to reduce mortality risks associated with energy expenditure and fighting during the rut, to increase the future reproductive potential, given the delayed age of first successful reproduction in this species (9 years) as compared to other ungulates (1–5 years). In the case of great bustards, a bird species similar to some ungulates in many respects, with males showing a very delayed age of successful breeding and one of the most strongly skewed mating success values among lekking birds (Alonso et al. 2010a), and highest mortality after mating (Martín 2008), the ultimate reasons leading to a reduction of the time spent in agonistic interactions during mating could be similar to that hypothesized by Willisch & Neuhaus (2010).

Time spent on aggression during mating was not particularly high (2.6% of a male's time budget), but it was important in two respects. First, some agonistic encounters (e.g. duels) could be dangerous, as males often try to stab the rival's eyes with their bills (M. Magaña, personal observation using decoys). Also, after a period of intense fighting, males may get exhausted and temporarily lose their ability to fly, increasing their vulnerability to predators (J.C. Alonso, personal observation). High energy expenditure and predation rates are probably the main causes of the observed increase in mortality at this time of year (Martín 2008, unpublished data). Second, it represented a considerable proportion (19.2%) of the time a male spent on copulation attempts plus successful copulations. Most aggressive interactions were in fact directed to males displaying very close to females, forcing them to stop display activity (68%), and a significant number were copulation disruptions (25%). The 13 copulation disruptions observed mean that 28.3% of all copulation attempts (four copulations and 42 copulations observed in the 31 marked males, Alonso et al. 2010a) were disrupted. Young males and those with weakly expressed neck trait and lower

courtship success were involved in more aggressive interactions, and specifically for copulation disruptions, males with lower weight and lower expression of the whiskers trait disrupted more copulations. However, even if they were not able to gain copulations from the disruption directly, at least they increased their relative copulation rate, just by lowering the copulation rate of disrupted males.

The decrease in aggressive rate of great bustard males during the mating period was probably favoured by the exploded lek system typical of this species (Magaña 2007; Alonso et al. 2010a). The average distance between solitary displaying males was 264 m (Magaña 2007). This distance could represent a trade-off between the aggregating behaviour and male–male interaction rates, as has been suggested for other lekking birds (Foster 1983; Höglund & Alatalo 1995), and specifically for some bustards displaying in an exploded lek mating system (Hingrat et al. 2008). It would be interesting to explore whether this distance of 264 m could be long enough to allow dominant males to finish some copulations, and short enough to enable subdominants to disrupt copulations of some neighbours, in addition to enabling all the other advantages of lekking for both sexes (i.e. hypotheses of lek evolution, Höglund & Alatalo 1995) to be operative.

The temporal separation of the two main sexual selection mechanisms, namely intrasexual competition among males and female mate choice, has been reported for only a few species, but could occur among more lekking and other polygynous species than previously thought. In ruffs, *Philomachus pugnax*, high-ranking males suffer fewer disruptions, suggesting that rigid dominance relationships exist between males and could have been established prior to the mating period (Widemo 1997). Female great snipes, *Gallinago media*, apparently select particular males rather than particular display sites within leks (Saether et al. 2005). In capercaillie, *Tetrao urogallus*, competition among males occurs off the lek and some males are excluded from holding any territory and thus also from the female selection process (Wegge et al. 2005). In lance-tailed manakins, *Chiroxiphia lanceolata*, male–male competition to obtain alpha status occurs long before females visit the lek, and alpha males rarely interact with each other (DuVal & Kempenaers 2008). Finally, in an ungulate mammal, the Alpine ibex, males spend less time in agonistic interactions during the rut than in the pre-rut, and changes in access between males always occur without fights and are based entirely on pre-established and stable dominance relationships (Willisch & Neuhaus 2010).

In conclusion, our results show that during both the pre-mating male–male contest period and the mating period, a largely age-determined social dominance hierarchy prevails among great bustard males. Most aggressive encounters were provoked by subdominant males, probably as a mechanism to increase dominance status in the lek (male–male contest period) and to increase their mating opportunities (mating period), either by gaining copulations with females whose copulations they disrupted or simply by reducing other males' success. Our study supports the hypothesis that pre-established dominance relationships help reduce costly intramale aggression during the mating period, as has been shown for some other polygynous birds and ungulates. The results also corroborate the importance of male competition as a mechanism influencing mating success in the great bustard, and probably favouring in this species the most extreme sexual size dimorphism among birds. In these respects, sexual selection processes in great bustards resemble those of ungulates and other dimorphic mammals, rather than those of most lekking birds, where mate choice seems to be prevalent.

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