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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.

Intrasexual competition among males is particularly strong in polygynous species (Orians 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 & Kempenaers 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 & Kempenaers 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 premating 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 premating 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 premating 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 under coverts; 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 premating 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 & Kempenaers 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 premating male–male interactions, (1) overall male aggressive interactions should be reduced during the mating period compared with the premating 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