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Sexual Traits as Quality Indicators in Lekking Male Great Bustards

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Abstract

We studied the development of two sexual traits, whiskers and neck plumage, in relation to sexual selection in 41 free-living great bustard, *Otis tarda*, males radio-tracked at nine leks in central Spain in 1998–2001. During the pre-breeding male–male competition period (Feb.) prior to female arrival, number and length of whiskers correlated with weight, but not with body size or age. Whiskers may thus have evolved as an intrasexual indicator of weight, which in the absence of other weapons in this species is decisive in male–male combats. Signalling through whiskers contributes to minimizing dangerous aggressive interactions in the lek. During the mating period (Apr.), both whisker and neck development were correlated with weight and age. Males reaching higher expression of both traits exhibited higher display intensity, a more prolonged display period through the mating season, and a higher estimated mating success. Moreover, interannual changes in a male's expression of both traits were associated with changes in its display intensity and estimated mating success. Our results resolve earlier debates and contradictory results from previous authors, suggesting that these two secondary sexual traits, whiskers and neck, may function as reliable indicators of age and weight, the two main factors determining social rank of males in great bustard leks, during both rival assessment and mate choice. Their dual functions provide support for the pre-existing trait and redundant signal hypotheses and suggest that multiple ornaments functioning as redundant signals might be more widespread than previously acknowledged.

Introduction

Sexual selection models and numerous empirical studies suggest that many secondary sexual traits develop in proportion to the phenotypic condition or age of the male, making these traits possible candidates for an indicator function (Manning 1985; Andersson 1994; Cotton et al. 2004). In long-lived species, the expression of some sexual traits often increases with age, apparently obscuring honesty in sexual advertisement, i.e. the correspondence between genotype (male 'quality') and phenotype (sexual traits) (see Kokko 1997). For example, in some birds, ornamental feathers increase in size for 5–10 yr (Davison 1981; Smith 1982; Alatalo et al. 1988; Manning 1989), or males go through several subadult plumages that condition their social rank and mating success (McDonald 1989). However, this age-dependent expression of secondary sexual traits may also be a useful indicator of male viability, as it allows females to choose males that have survived longer (age indicator mechanism, Trivers 1972; Halliday 1978; Manning 1985; Kokko & Lindstrom 1996; Kokko 1997, 1998). Life history theories also predict a gradual development of sexual secondary traits after reaching sexual maturity, in parallel with an increase in the yearly reproductive effort with age, at least over the first breeding seasons, as secondary sexual traits are subject to similar selection pressures and constraints as the reproductive effort (Partridge & Endler 1987; Stearns 1992; Andersson 1994). For example, in some species, the ornaments are fully expressed at an age of several years beyond sexual maturity (e.g. 7–8 yr in the lyrebird, Smith 1965; see also Alatalo et al. 1988). Recent theoretical and empirical investigations have renewed interest in the evolution of mating preferences based on age, and it is still unknown how male age is assessed by prospecting females (Brooks & Kemp 2001).

Lekking species have often been selected as study subjects and have produced important insights into sexual selection theory (Bradbury & Gibson 1983; Balmford 1991; Wiley 1991; Johnsgard 1994), in part, because in these species, the two main sexual selection mechanisms, male–male competition and female choice, occur at the same place, the lek. But the mechanisms and consequences of sexual selection and the functions of morphological sex ornaments in many of these species still remain poorly understood. One of these lekking species is the great bustard (*Otis tarda*), a vulnerable bird (IUCN 2010) with more than half its world population in the Iberian Peninsula (Palacín & Alonso 2008). From Jan. on, males gather at traditional lek sites to which they remain faithful through their lives, and where they fight and display to establish or confirm their hierarchy until late Mar., usually in the absence of females (Palacín et al. 2009). Once migratory females have arrived, these and sedentary females concentrate at lek sites in Apr., and most males disperse and display to gain matings in an exploded lek system (Hidalgo & Carranza 1991; Magaña 2007). This species is a good candidate for investigating condition and age dependence of sexual traits, for several reasons. First, it is the most sexually size-dimorphic species among birds, which suggests strong sexual selection for large male size (Alonso et al. 2009). Second, mating success is strongly skewed in great bustard leks, with less than half the males having access to females, and most copulations being gained by a few individuals (Magaña 2007; Alonso et al. 2010). Third, males are long-lived (up to 14–15 yr, own unpubl. data), showing a marked lifetime lek-site fidelity (95–100%, Morales 2000; Magaña 2007), which should favour a hierarchical dominance rank among lek mates. Fourth, besides a large size, males develop each spring two characteristic sexual traits, the whiskers and a colourful plumage pattern at the neck. As both traits (1) show an increase in their average expression with age of the male through at least 8–9 yr (Alonso et al. 2006) and (2) they are exhibited in both, male–male encounters during the phase of hierarchy establishment in Jan.–Mar., and male–female encounters during the mating period in Apr. (Gewalt 1965; Hidalgo & Carranza 1990; Magaña 2007), their functions (condition vs. age indicators) and evolutionary origin (intra- vs. intersexual selection) are uncertain. The usual view under Darwinian sexual selection is that traits used as weapons in male agonistic interactions have evolved through intrasexual selection, while visual traits such as conspicuous colours or feathers are the result of intersexual selection (Bradbury & Davies 1987; Andersson 1994). A very recent study investigated the function of another plumage signal used by great bustard males to increase mating opportunities, namely the uplifted white vent and undertail coverts (Olea et al. 2010). However, several authors have suggested that some male signals may serve a dual function, both as status indicators in male–male contest and quality indicators used for mate choice by females (Borgia 1979; West-Eberhard 1979; Berglund et al. 1996; Panhuis & Wilkinson 1999). Alternatively, multiple male traits may function as redundant signals to improve the accuracy of mate assessment (back-up or redundant signal hypothesis, Moller & Pomiankowski 1993), or serve different functions in male–male competition and female mate choice (Candolin 2003, 2005; Delaney et al. 2007).

Whiskers of male great bustards are thin, 15–20-cm-long feathers that grow in tufts at both sides of the lower mandible, and have no apparent function other than being exhibited as sexual ornaments. They grow every winter in males older than 1 yr, starting in Dec., reaching maximum length in spring, and disappearing in July–Aug. (Gewalt 1965; Alonso et al. 2009). During display, they are raised upwards in front of the eyes, showing off their length and abundance. The neck and breast plumage of mature males turns through a partial moult, from uniform grey in Dec. into a colourful pattern with contrasting dark chestnut at the base and ivory-white at the throat in Apr. At the start of the mating season, the neck also increases notably in thickness because of an extraordinary development of the subcutaneous tissue and of two profusely irrigated lobes, which may reach 1 kg weight (Gewalt 1965). Breast feathers also reach double the length they are in summer–autumn, also contributing to confer the adult male neck a remarkably thick and powerful appearance (Gewalt 1959). At this time, two blue grey stripes of bare skin are visible from the lower ear-coverts down the neck. These stripes are exposed and greatly enlarged when the gular pouch and oesophagus are inflated during full display (see Gewalt 1959; Glutz et al. 1973 for a detailed description, function and development of these structures).

Gewalt (1959) stated that the expression of these two sexual traits increased with age of the male beyond maturity. This assertion was transcribed in ornithological reviews (Glutz et al. 1973; Cramp & Simmons 1980), but was only recently investigated with males captured as chicks and radio-tracked through up to 10 yr (Alonso et al. 2006). Previous studies had obtained contradictory results; e.g. while Carranza & Hidalgo (1993) found age correlated only with length of whiskers and weight with number of whiskers and neck development in a small sample of captive males, Morales et al. (2003) obtained a correlation between age and neck development in wild birds, but the role of age in whisker growth could not be unambiguously established. To date, the relationships between sexual trait expression, weight, size, age, and display and mating behaviour have not been investigated in great bustards.

In this paper, we explore the idea that these two sexual traits of male great bustards might convey information on male condition (weight, size) and age to other males and females of the lek. The results of our study are based on a large sample of individually marked, free-living adult males radio-tracked through several years. Because of the vulnerable status of the species, experimental manipulation of captured birds was not possible. Instead, we aimed at inferring whether sexual traits are favoured by intra- or intersexual selection by analysing the relationships of trait expression with weight, size and age during both the male contest period, when females are usually far away from males, and the mating period. Also, in order to assess their indicator function, we investigated (1) whether males with more developed sexual traits showed more marked sexual display activity, or obtained higher mating success, and (2) whether changes in the expression of sexual traits between consecutive years were associated with changes in display or mating behaviour.

Methods

This study is based on morphometrics and displays behaviour of 41 great bustard adult males captured at 9 lek sites in Madrid province, central Spain (36 captured as adults in 1998–2001, five as chicks in 1995–1997), and radio-tracked during 1–3 mating seasons each. Body measurements from another 45 adult males captured in other Spanish provinces in 1994–2001 were also included in the analyses.

Trapping, Morphometrics and Age Estimation

Adult males were captured with rocket nets in Jan.–Feb., 32 mo before the peak mating season. Young birds were captured in July, when they were 3–10-wk old, by chasing them down. 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. Each captured bird was fitted with a backpack radio-transmitter (TW3 model; Biotrack Ltd., Wareham, Dorset, 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 yr in the 2 × AA transmitters (60 g) used for juveniles and up to 7–8 yr 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 behavioural alteration of the birds as a result of marking. After release, we located all radio-tagged individuals by triangulation using TR2-TS1 scanner-receivers from Telonics, Mesa, Arizona, USA, several days before starting behavioural 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, Wichita, Kansas, USA).

The following morphometric measurements were taken during handling: weight (±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; wing chord: minimum distance between carpal joint and tip of the longest primary feather (unflattened wing length); tail length: length of the longest tail feather, pushing the bottom of the ruler gently against the base of the middle pair of rectrices while the tail is folded naturally; 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); head length: maximum distance between the occipital end of the head and the tip of the bill (±0.1 mm); head width: maximum width of the skull behind the eyes (±0.1 mm); bill length 1: distance between the posterior end of bill commissure and bill tip (±0.1 mm); bill length 2: distance between the anterior end of nostrils and bill tip (±0.1 mm).

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 yr between 1987 and 1999 (Alonso et al. 2006). In that study, we improved the ageing techniques proposed by Gewalt (1959). We established five estimated adult age categories (4–8 yr, covering the average longevity of great bustard males, estimated at approx. 8–9 yr according to a large sample of marked birds; own unpubl. data), based on the following criteria: (1) a gradual increase in the extent and brightness of the white colour of the upper neck, (2) the contrast between this and a progressively more intense chestnut brown at the neck base, (3) the front shape of the chestnut collar which in birds aged 7–8 is open, with the white of the upper neck reaching the lower breast, (4) a bare skin streak that is visible below the chin along both sides of the neck in birds aged 7–8 yr and (5) the length of breast feathers. We used these details to estimate the age of the 41 males in the present study. Such age estimation is of course subject to some uncertainty that could be guessed at ±1 yr (see details in Alonso et al. 2006; Fig. 1b). To maximize the reliability of our age assignment technique, we continued ageing our males during 2–6 yr after ending the present study.

Measuring Sexual Trait Development

We assessed the development of the two sexual characters studied, whiskers and neck, as follows. During the peak male contest period (Feb.), we measured the number and length of the whiskers on the right side of the head when handling the birds after capture. Whiskers can be distinguished from the rest of the chin feathers by their characteristic morphology (Gewalt 1959). Their length was measured from the bill tip to the rear end of the longest whisker. These ornamental feathers are known to reach maximum development in spring (Gewalt 1959; Glutz et al. 1973), and in a recent study, we quantified the increase between Feb. and Apr. as ca. 2.2% in length of the longest feather and ca. 26% in number of feathers (Feb.: length = 213.4 mm, range = 150–270, n = 86; number = 14.3, range = 7–30, n = 69; Apr.: length = 218.0 mm, range = 200–265, n = 11; number = 18.0, range = 15–24, n = 5; Alonso et al. 2009).

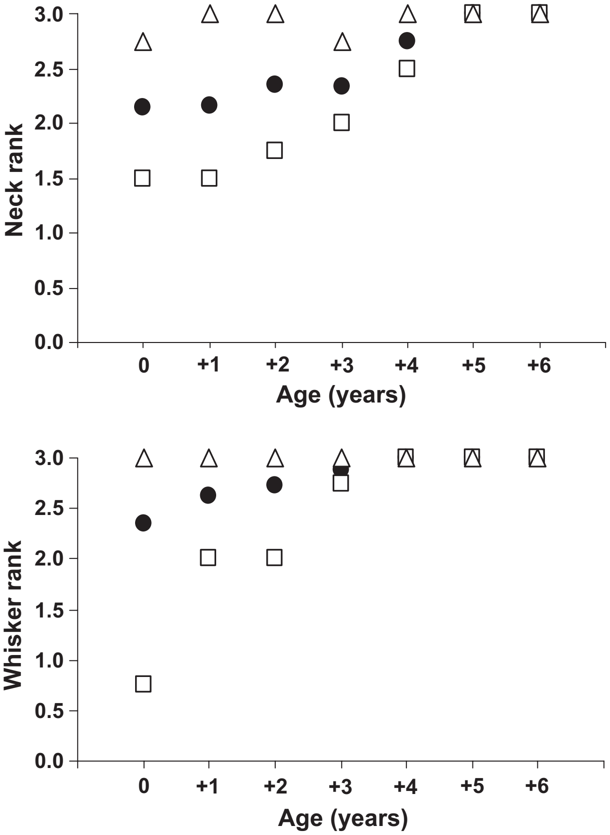

Fig. 1: The expression of sexual traits (neck and whisker ranks, see Methods) increased with age in the sample of males captured as adults, even if they were not aged with criteria given in Alonso et al. 2006. To prevent possible inaccuracies of our age estimation criteria, this graph was constructed by entering sexual trait ranks for 'unknown ages' for each male through the study period plus 2–6 additional years after study termination: 0 = age when captured, +1, +2, … +6 = 1, 2, …6 yr later. Mean (black dots), maximum (triangles) and minimum values (squares) are given. Sample sizes decreased with years (respectively, 29, 31, 12, 6, 3, 3, 1) depending on capture and death dates of each male.

During peak mating in Apr., as well as in consecutive years, we obviously did not try to recapture our marked birds for the only purpose of taking new measurements, as this would have caused excessive disturbances. Instead, we established the following categories (slightly modified from those used in previous studies, see Carranza & Hidalgo 1993; Morales 2000; Morales et al. 2003; Magaña 2007) to rank the development of whiskers and neck during scan-sampling male behaviour at leks (*Behavioural observations*): Whiskers 1: poorly developed, exceeding a

Table 1: Correlations (Pearson) between whisker length (WL) and number (WN) and body measurements in adult males during the period of male contests in Feb.

		WN	W	WAL	WCL	TL	TRL	CTL	HL	HW	BL1	BL2
WL	r	0.62***	0.56***	0.43***	0.41*	0.18	0.27	0.04	0.56***	0.09	0.22	0.44*
	n	69	86	76	37	35	44	36	41	34	34	35
WN	r		0.39**	0.32*	0.16	0.52	0.26	0.08	0.29	0.17	0.33	−0.01
	n		69	59	20	18	27	19	24	18	17	18

W, weight; WAL, wing arch length; WCL, wing chord length; TL, tail length; TRL, tarsus length; CTL, central toe length; HL, head length; HW, head width; BL1, BL2, bill lengths 1 and 2 (see Methods for definitions). *$p < 0.05$, **$p \le 0.01$, ***$p \le 0.001$, after Benjamini & Hochberg's FDR correction for multiple tests.

few centimetre the rear end on the bill gapes; Whiskers 2: viewing the head from the side, the moustaches reach the nape outline; Whiskers 3: the moustaches clearly exceed the nape outline. These categories accounted simultaneously for both, length and number of whiskers, as both are highly correlated (see Table 1). The categories for neck were the following: Neck 1: somewhat thicker than that of 1-yr-old males, with a brown wide band at the lower half and grey at the upper half, of lighter shade than in 1-yr-old males. Neck 2: notably thicker, with wide brown, chestnut-coloured band at the base, a broad intermediate creamy yellow band, and upper neck of a whitish to light greyish colour that reaches the grey colour under the lower mandible. The three fringes of the neck, lower, intermediate and upper are approximately of the same height. Neck 3: a thick, substantially bulkier neck, with well developed, hanging breast feathers, intense chestnut-coloured basal band, not as wide as in previous category, bordered upwards by a narrow creamy yellow fringe, above which there is an intense ivory to pure white upper neck reaching the chin. Intermediate situations between those described above were given values of 1.5, and 2.5. All marked males were ranked using these whisker and neck categories. We described the details and drew possible modifications of each particular male on previously drawn sketches of the neck. We repeated this procedure several times through the whole mating period to check for possible changes in rank values assigned because of variable light conditions or bird postures. We also took photographs of some birds, but these proved to be no better than sketches to categorize sexual traits. After several visits to every male, we obtained for each bird a mean annual value for neck and whisker development. To test how reliable our observed neck and whisker rank values were, a sample of 18 birds had been previously categorized by four different observers, reaching a 95% agreement calculated through Kendall's concordance coefficient (Lehner 1996; Siegel & Castellan 1988). Therefore, we consider that our estimated observational neck and whisker ranks were accurate enough to detect differences between individuals.

Finally, as intra- and intersexual selection processes (i.e. male–male competition for access to females and mate selection by females) occur within a lek, we explored the relationships between phenotypic rank and display and mating behaviour among all marked males within a given lek. We used the males of the three most intensively studied leks (five males in lek Ribatejada-Valdetorres, six males in lek Talamanca-Valdetorres and six males in lek Camarma). We assigned a *phenotypic rank* to each of these males by ranking all marked males of a given lek according to their average neck and whisker rank values: male with phenotypic rank 1 was the male showing the highest mean value calculated with both, whiskers and neck, and giving priority to the neck value in case of tied scores among two males.

Display Rates and Mating Success Estimates

Marked males were tracked during 2–3 days per week over 1–3 mating seasons following capture (from the last week of Mar. to the second week of May). Observations were carried out from dawn to 13:00 h, as activity in general, and particularly sexual activity, is much reduced during midday when birds usually lay down and rest (Hidalgo & Carranza 1990; Hellmich 1991; Martínez 2000; Morales 2000; Morales et al. 2003; pers. obs.). Observations were made from ground vehicles at 1–3 km from the focal bird using 20–40 × and 60–90 × Leica APO Televid 77 HD and Swarowski ATM 65 HD 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 (62–1373 min per bird and season, and 210–2650 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 & Bateson 1993) of all significant behaviours and the duration (to the nearest second) of each behavioural bout of the focal bird. We considered the following behaviours: *display*: we distinguished four display phases (for details see Alonso et al. 2010), from *D0* (tail spread out, showing the conspicuous white under coverts) to *D3* (neck completely inflated and reclined over back, whiskers vertical, and bird moving sidewards or shivering, usually when females are present). We defined as a *full display* bout the total time spent on continuous D3 plus interspersed short D0 bouts just to change position, usually when females are close. From these time budget observations, we calculated mean activity rates 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 *exhibition period* (days from first to last date). All males of a given lek are usually aggregated in a single flock (sometimes 2–3 flocks if the lek is large) in winter. From late Mar. 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).

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 & 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 is 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 (a fact that was also highlighted by all researchers who studied its mating behaviour, e.g. Gewalt 1959: p. 79; Hidalgo & Carranza 1990: p. 193; Hellmich 1991: p. 141; Morales 2000: p. 91; Morales et al. 2003: p. 53; Magaña 2007: p. 138). In the present study, we only saw four copulations of marked males plus four of non-marked males, a number clearly insufficient for statistical analyses. Therefore, as a statistically more practical parameter, we used the *estimated mating success* calculated for each male in Alonso et al. (2010), by adding observed effective copulations plus true copulation attempts, defining these as strictly only those instances when a male was seen full-displaying in very close proximity to one or more females (<3 m), and the latter showed obvious pre-copulatory behaviour, i.e. by approaching him and turning around him to inspect his plumage, ending up pecking his cloacal region (see detailed description of copulation behaviour in Hellmich 1991). Observation times of less than 200 min were discarded for calculating mating success of a male. To support the reliability of this copulation attempt rate as an estimate of mating success, we had previously tested that the rates of effective copulations and copulation attempts were positively correlated in a larger sample of males ($r = 0.33$, $p = 0.020$, $n = 48$ marked males combining samples of the present and a previous study where only five copulations were recorded in 1279 observation hours, Morales et al. 2003). Finally, we also defined a *male attractiveness* index, as the mean hourly number of females approaching the displaying male at <100 m. Male attractiveness indices have also been used in previous studies with a number of lekking birds (Höglund & Robertson 1990; Hidalgo & Carranza 1991; Fiske & Kålås 1995; Rintamäki et al. 1995a,b; Gibson 1996; Jiguet 2001; Morales et al. 2003), as they have been shown to correlate with copulation rate in a number of species (Andersson 1992; Rintamäki et al.1995a).

Statistical Analyses

In order to reduce handling time and so minimize capture stress, not all measurements were taken in all birds. In addition, observation difficulties at some leks prevented us from getting adequate estimates of various behavioural parameters for some birds. These two facts generated variable sample sizes (only 22 birds with all morphometric and behavioural variables), which prevented us from using a single multivariate technique to analyse all morphometric and behavioural data. Instead, we used simple and partial correlation analyses. We used simple Pearson correlation analysis to study univariate relationships between body measurements and whisker length and number, and between these and mating behaviour parameters in the year of capture, after appropriate transformation of all variables. Spearman rank correlation was used to test univariate relationships between whisker and neck rank estimates in Apr. and whisker and body measurements taken in Feb. Partial correlation analysis was used to investigate the simultaneous effect of weight, body size and age on sexual traits, using only data from first years for each male. As a measure of body size, we used its best indicator, the wing arch length (see Alonso et al. 2009). In all cases, we applied Benjamini & Hochberg's False Discovery Rate (FDR) correction for multiple tests (Benjamini & Hochberg 1995; Verhoeven et al. 2005). To study how changes in the rank values of sexual traits were associated with changes in display and mating behaviour parameters between consecutive years, we used Fisher's exact probability tests. Finally, after checking that phenotypic ranks among marked males of a given lek did not change through the observation period (1998–2001), we compared the phenotypic rank of the different males with their mean dates of first solitary display and mean mating success values calculated through the 1–3 study seasons, using non-parametric tests (respectively, Kruskal-Wallis test and Spearman rank correlation, Siegel & Castellan 1988). All statistical analyses were performed with STATISTICA 6.0 (Statsoft Inc., Tulsa, OK, USA), assuming two-tailed tests.

Results

Body Size, Weight and Sexual Traits

During the period of male contests in Feb., the number of whiskers was correlated with whisker length, and both variables were correlated with weight and various body measurements (Table 1). Controlling for the effect of body size through partial correlation, number and length of whiskers were significantly correlated with weight, whereas controlling for the effect of weight, whisker length and number were not correlated with body size (Table 2). This suggests that during the male contest period, whiskers were good indicators of weight, but not of the overall body size of males.

Whisker rank estimated during the mating period in Apr. was correlated with length and number of whiskers measured in Feb. (respectively, $r_S = 0.48$, $p = 0.009$, and $r_S = 0.41$, $p = 0.029$, $n = 29$ males) and also with neck rank estimated in Apr. ($r_S = 0.440$, $p = 0.017$, $n = 29$). Both rank values were correlated with weight (respectively, $r_S = 0.49$ and $r_S = 0.59$, $p < 0.01$, $n = 30$), but not with the main body measurements (wing length-whisker rank: $r_S = 0.28$, $p = 0.150$, $n = 28$, wing length-neck rank: $r_S = 0.29$, $p = 0.128$, $n = 28$, tarsus length-whisker rank: $r_S = -0.25$, $p = 0.382$, $n = 14$, tarsus length-neck rank: $r_S = -0.41$, $p = 0.147$, $n = 14$). Controlling for the effect of body size, whisker and neck ranks were still significantly correlated with weight (Table 2). But controlling for weight, rank values were not correlated with body size. This suggests that during the mating period, the development of whiskers and neck was a good indicator of weight but not of body size of males.

Age, Body Size and Sexual Traits

We also used partial correlation to explore whether variability in sexual trait expression was because of age or weight. Controlling for age, heavier males had longer and more abundant whiskers during the male contest period and also higher whisker and neck ranks during the mating period (Table 3). Controlling for weight, age was correlated with both whisker and neck ranks during the mating period, but not with whisker length and number during the male contest period. This suggests that during the contest period, whisker development is a good

Table 2: Partial correlations of sexual traits with weight and body size in adult males during the peak male contest period (Feb.) and peak mating period (Apr.)

		Feb.						Apr.					
		Whisker length			Whisker number			Whisker rank			Neck rank		
Independent variable	Controlled variable	r	p	n	r	p	n	r	p	n	r	p	n
Weight	WAL	0.42	<0.01**	76	0.25	0.05*	59	0.57	<0.01**	30	0.46	0.01*	30
WAL	Weight	0.16	0.36	76	0.13	0.62	59	0.02	0.92	28	0.18	0.37	28

Wing Arch Length (WAL) was used as the best indicator of body size (see Alonso et al. 2009), but the regression values were similar using tarsus length in Apr., and all other body linear measurements in Feb. *p < 0.05, **p ≤ 0.01, ***p ≤ 0.001, after Benjamini & Hochberg's FDR correction for multiple tests.

Table 3: Partial correlations of sexual traits with weight and age in adult males during the male contest period (Feb.) and the peak mating period (Apr.)

		Feb.						Apr.					
		Whisker length			Whisker number			Whisker rank			Neck rank		
Independent variable	Controlled variable	r	p	n	r	p	n	r	p	n	r	p	n
Weight	Age	0.31	0.05*	44	0.34	0.03*	40	0.52	<0.01**	30	0.42	0.02*	30
Age	Weight	0.19	0.25	40	−0.03	0.84	40	0.44	0.02*	29	0.83	<0.01***	29

*$p < 0.05$, **$p \le 0.01$, ***$p \le 0.001$, after Benjamini & Hochberg's FDR correction for multiple tests.

indicator only of male weight but not of age, and during the mating period, both traits may be indicators of weight and age, although neck seems a better indicator of age and whiskers a better indicator of weight. Figure 1 shows how the mean expression of both traits increased with age.

The absence of a significant correlation between whisker development and age in Feb., while both are correlated in Apr., suggests that the final growth of whiskers that occurs between Feb. and Apr. varies among adults of different weights or ages. To explore this, we extracted the residuals of the regression of whisker rank in Apr. vs. whisker length in Feb. These residuals were significantly correlated with both weight and age (Table 4), i.e. males being either heavier or older in Feb. showed higher whisker growth until Apr. However, the effect of weight and age differed between age classes. Among <6- yr-old males, whiskers grew more in heavier individuals, whereas in ≥6- yr-old males, whiskers grew more in older individuals.

Interannual Variability in Sexual Trait Expression

Normally, the whisker and neck rank values of a male increased between consecutive mating seasons. Among all interannual comparisons in our sample of marked males, whisker rank decreased only in two cases (of two different birds) and neck rank in six cases (five birds). Rank values remained unchanged in another two comparisons for whiskers and three comparisons for neck (Table 5). We found a significant correspondence between both sexual traits in the number of cases when they increased *vs* remained unchanged or decreased ($p = 0.04$, Fisher's exact probability test).

Table 4: Correlations of weight and age with the amount of growth of whiskers from Feb. (male contest period) to Apr. (mating period)

	r	p	n
All males			
residuals *vs* weight	0.58	0.001	28
residuals *vs* age	0.55	0.003	28
Males < 6 yr			
residuals *vs* weight	0.57	0.035	14
residuals *vs* age	0.40	0.153	14
Males ≥ 6 yr			
residuals *vs* weight	0.38	0.179	14
residuals *vs* age	0.56	0.039	14

This growth was estimated as the residuals of the regression between whisker length in Feb. and whisker rank in Apr.

Rank changes between years were associated with changes in the display behaviour and mating success of males. The correspondence was significant for neck rank ($p = 0.015$ and $p = 0.033$, respectively, for comparisons with % time spent in full display and mating success, Fisher's exact probability test) and marginally significant for whisker rank when compared with mating success (Fisher's exact probability test, $p = 0.067$). When we compared interannual increases in both traits *vs* decreases in any of them, the correspondence was significant with both display rate and mating success (respectively, $p = 0.008$ and $p = 0.010$).

Sexual Traits and Mating Success

Whisker development attained during the male contest period (Feb.) did not correlate with display behaviour and mating success exhibited 2 mo later (Table 6). However, the rank value of both sexual traits during the peak mating season was positively correlated with various display and mating parameters (Table 6). Males with higher rank value for neck started displaying as single males earlier in the season, spent a longer period displaying as single males through the mating season, performed longer full display bouts and achieved a higher estimated mating success (Table 6). Males with higher rank value for whiskers performed longer full displays, and spent more daily time on display, obtaining a marginally significant increase in estimated mating

Table 5: Correspondence between interannual changes in sexual trait expression and four display and mating behaviour parameters for 14 males radio-tracked two or more years

		Interannual variation in rank value of sexual trait		Interannual variation in display and mating behaviour parameters[a]			
Individual	Years compared	Whiskers	Neck	Exhibition period	Male attractiveness	Full display rate	Estimated mating success
A	1–2	+0.17	−0.25	+8.0	+0.3	−0.5	0.0
B	2–3	m	+0.40	−2.5	−0.8	+1.8	−1.5
C	1–2	+1.0	+0.75	−7.5	−0.6	+0.5	+0.4
	2–3	0.0	+0.13	+26	+0.1	+12.4	+0.7
D	1–2	+0.13	+0.62	+1		+3.7	+0.9
	2–3	+0.37	+0.20		+0.5	+11.8	−0.9
E	1–2	m	+0.33	−0.5	+1.6	+11.1	+0.6
F	1–2	+0.5	+0.25	−2	+3	+7.1	+0.3
	2–3	m	m	+6	+1	−4.4	+8.0
G	1–2	−0.25	0.0	12.5	−2.2	+8.9	−0.7
H	1–2	m	−0.05	−5.0	+0.6	+17.5	0.0
	2–3	m	−0.20	+15.5	−0.5	−10.9	0.0
I	1–2	−0.50	−0.75				
	2–3	+0.75	+0.50		−3.5	+24.1	+2.3
J	1–2	+0.25	0.0	−13	−1.7	−4.9	+0.2
K	1–2	m	+0.75	+10.0			
L	1–2	+0.50	+1.0	0.0	−3.5	+2.5	0.0
M	1–2	0.0	−0.25	−23.0	+2.4	−10.3	−0.9
	2–3	+1	0.0		+4.7	−21.7	−1.6
N	1–2	+1	−0.17	+12.0	+1.0	−0.4	0.0
Means		0.35	0.17	2.34	0.14	2.68	0.43
SD		0.47	0.43	11.89	2.17	11.02	2.10

'm' means that the male already showed maximum rank value (=3.0) for that sexual trait; missing data are as a result of insufficient yearly observation time (<200 min) or inaccurate starting or ending dates of solitary display.

[a] Exhibition period: number of days spent on solitary display through the mating season; male attractiveness: number of females attracted by the displaying male at <100 m; display rate: % time spent in full display; estimated mating success: frequency of effective copulations plus copulation attempts (see Method).

Table 6: Simple correlations between measurements and rank values of sexual traits, and display and mating behaviour parameters of great bustard males

	Feb.						Apr.					
	Whisker length			Whisker number			Whisker rank			Neck rank		
	r	n	p	r	n	p	r	n	p	r	n	p
Estimated mating success	0.11	22	0.63	0.10	22	0.65	0.33	26	0.10	0.55	26	<0.01*
% time full display	0.21	22	0.35	0.08	22	0.71	0.48	26	0.01*	0.44	26	0.02
Mean duration full display bout	0.32	22	0.15	0.23	22	0.31	0.61	26	<0.01*	0.55	26	<0.01*
Number full display bouts	0.09	22	0.68	0.00	22	0.98	0.27	23	0.21	0.45	23	0.03
First date of solitary display	−0.21	27	0.30	−0.05	27	0.81	−0.27	31	0.14	−0.52	31	<0.01*
Exhibition period	0.16	25	0.44	0.26	25	0.21	0.30	29	0.11	0.57	29	<0.01**
Male attractiveness	−0.04	22	0.84	0.02	22	0.94	0.12	26	0.56	0.20	26	0.33

*p < 0.05, **p ≤ 0.01, ***p ≤ 0.001, after Benjamini & Hochberg's FDR correction for multiple tests.

success (Table 6). Analysing these relationships within each lek, males with superior phenotypic rank (expressed as the mean of both, neck and whisker rank values) started displaying earlier in the season and obtained a higher estimated mating success (Figs 2 and 3).

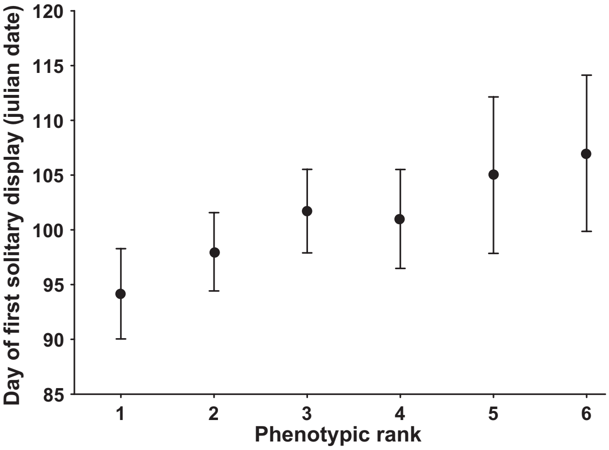

Fig. 2: Relationship between the phenotypic rank of all males marked at each lek and their mean Julian date of first display as solitary males. Values are 1998–2001 means for the three leks studied most intensively (Ribatejada-Valdetorres, five males; Talamanca-Valdetorres, six males; and Camarma, six males). For each lek, male with phenotypic rank 1 was the male showing highest mean rank value of both sexual traits, whiskers and neck, when compared with its lek mates. Vertical bars show 95% confidence intervals. The increasing trend was significant (Kruskal-Wallis test, $\chi^2 = 12.44$, df = 5, p = 0.029).

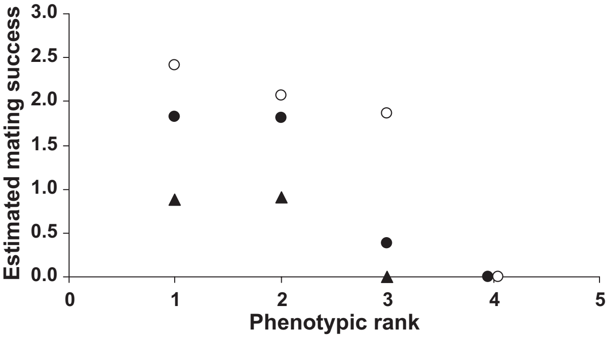

Fig. 3: Relationship between the phenotypic rank of all males marked at each lek and their estimated mating success (=number of effective copulations plus copulation attempts per 10 h). Phenotypic rank calculated as in Fig. 2. Mating success estimates could only be obtained for four males in both, Talamanca-Valdetorres (black dots) and Camarma (open dots), and three males in Ribatejada-Valdetorres (triangles).The correlation was significant in both leks with four males ($r_s = 1$, Spearman rank correlation).

Discussion

In a recent study, we showed that age and weight are two phenotypic features significantly contributing to increase in mating success in great bustard males (Alonso et al. 2010). The results of the present study suggest that the two secondary sexual traits of males, whiskers and neck, may function as reliable indicators of age and weight during both rival assessment and mate choice. During the peak male–male competition period in Feb., when males are already at the leks but females are either not yet arrived, or in the lek areas but far away from the male flock, number and length of whiskers were correlated with weight, but not with body size or age. Whiskers may thus function as a condition-dependent sexual trait, like numerous other ornamental feathers in many bird species (reviewed in Andersson 1994; Johnstone 1995; Cotton et al. 2004). We could not measure neck expression during the male–male contest period in the year of capture, but values from subsequent years suggest that neck rank may also function as age indicator during this period, as it is during mating in Apr. (unpubl. data). In Feb., whiskers are remarkably variable (coefficients of variation = 12.12 and 32.80%, respectively, for number and length, much higher than those of all other body measurements – between 3.05 and 6.22% – and respectively similar and higher than that of weight, 12.06%, Alonso et al. 2009), as would be expected in a sexually selected character (Alatalo et al. 1988; Pomiankowski & Moller 1995; Bonduriansky & Day 2003). The correlative nature of our results does not enable to unequivocally establish causality between sex trait evolution and function under an indicator mechanism. However, the vulnerable status of the great bustard prevented us from performing any experimental manipulation, and the limited number of capture permits allowed us to just get a reasonably large sample to carry out our observational study. In spite of this limitation, we believe the evidences provided are sufficiently strong to allow inferences about the functions of both sexual traits examined, and the role sexual selection has played in their development.

Our results suggest that heavier males probably signal their competitive ability through their whiskers, reducing the frequency of dangerous fights for status in the lek hierarchy. Indeed, during the hierarchy establishment phase preceding the mating period, individuals with more developed whiskers were involved in less aggressive interactions with other males (the correlations ranged from $r_s = -0.90$, $p = 0.037$ to $r_s = -1.0$, $p < 0.001$ for different leks, Magaña 2007). Whiskers may thus be indicators of rank, in a similar way as badges of status of many other bird species (Maynard-Smith & Harper 2003). Elsewhere, we have shown that the main body size measurements are correlated with age and continue increasing at least 3–4 yr after reaching sexual maturity (Magaña 2007; Alonso et al. 2010). Thus, the absence of a correlation between body size and whisker development shown in the present paper corroborates that whiskers do not function as age indicators in male–male contests. Furthermore, the high correlation between both estimates of whisker development, namely their length and number, suggests that these two parameters depend on the same causal factor. It seems less reasonable that they express different characteristics of the male as suggested by Carranza & Hidalgo (1993). The differences found by these authors could have been determined by their small sample size, captivity conditions, or both.

In several mammal species, size and efficiency of antlers or tusks in male–male fights increase with body size and weight (reviewed in Andersson 1994; Schmidt et al. 2001; Weladji et al. 2005). Great bustard males do not have such arms and therefore their body mass, more than their body size or age, may be crucial in fights involving most males of the lek in early spring, or in the less frequent duels where two adult males push each other breast to breast. These combats may be very dangerous, as males often attack the rival's face with their bills, trying to reach the eyes (pers. obs. using decoys). After a period of intense fighting, males may get exhausted and lose temporally their ability to fly (pers. obs.). Finally, a heavier weight represents no obstacle in a species with terrestrial display. On the contrary, it probably means more fat reserves that may be useful for display. During the peak mating period in Apr., males spend only 14% of their time feeding, and we found that males weighting more at the start of the mating season devoted less time to feeding, which allowed them to spend more time on display, and eventually obtain a higher mating success (Magaña 2007).

During the peak mating period in Apr., both sexual traits seem to be reliable and independent indicators of both weight and age. We could not unequivocally assign to each trait a specific indicator function, but the higher partial correlation coefficients of whiskers with weight and neck with age suggest some specificity in their signalling function, namely neck development would be a better indicator of male age to females and whisker development a better indicator of weight. An interesting result was that the final development of whiskers between Feb. and Apr. was determined independently by age and weight, i.e. the highest whisker ranks were shown by males having just reached maturity (<6- yr old; maturity age is 4–5 yr in this species, Gewalt 1959) but having attained a high weight already in Feb., and by older males (≥6- yr old) independently of the weight they had in Feb. This last correlation within the group of oldest males may explain why whisker development was correlated with age in Apr. Older males might compensate a slight weight deficit with their higher age. Alternatively, a possible higher increase in weight in older males between Feb. and Apr. might have been the cause of the partial correlation whiskers age found in Apr.

Both weight and age are positively related to male quality in a number of other species. A higher weight reflects a better body condition and lower parasite load, and longevity is a sign of experience and survival ability (Andersson 1994; Höglund & Alatalo 1995; Kokko 1998; Brooks & Kemp 2001). Taken together, our previous and current results suggest that great bustard males form a linear hierarchy in the lek that is strongly associated with age, and age is reliably signalled by the neck plumage (Alonso et al. 2006, 2010; Magaña 2007; this study). In addition, mature males of younger ages that have reached high weights may also show their quality through their more developed whiskers. This system, where age and weight are so important, differs from most other bird species, even those breeding in leks, where these characters seem to have lower predictive power for determining mating success than behavioural traits (reviewed in Höglund & Alatalo 1995; Nooker & Sandercock 2008), and resembles more that found in some long-lived and strongly sexually dimorphic ungulates, where social rank is a complex trait determined by both age and mass (e.g. Clutton-Brock et al. 1988; McElligott et al. 2001; Pelletier & Festa-Bianchet 2006). In many of these species, it has been shown that an increase in the expression of the sexually selected trait over several years is an evolutionarily stable strategy under a wide range of situations, so that a correlated preference for old age can emerge through a viability indicator mechanism (Kokko 1997).

During the mating period in Apr., neck and whiskers may not only be used to attract females, but also to signal the own status to other males in the lek. In the exploded lek system typical of this species, the males display at moderate (ca. 200 m modal) distances of each other, and copulation disruption is frequent, occurring in 28% of all copulation attempts, Magaña 2007). Thus, a signalling function of sexual traits to other males may be of high adaptive value, in order to minimize male–male aggressive encounters. Indeed, among 18 males showing aggressive interactions with other males during the mating period, males with higher neck rank were involved in fewer aggressive interactions and those with a lower whisker rank disrupted copulation attempts with higher frequency (Magaña 2007). These results suggest that older males (as indicated by their higher neck rank) tended to be avoided by males initiating aggressive encounters, and that dominant males would signal their attractiveness through their sexual traits with no need to disrupt other males' copulation attempts, whereas copulation disruptions were used by lighter, subordinate males (as indicated by their lower whisker rank) as a secondary mechanism to compete for access to females.

The functions of whisker and neck discussed previously are compatible with other possible functions not investigated in this study. For example, whiskers –and also neck feathers that reach double length during the breeding season (Gewalt 1959) – might have similar effects as moustaches and beards of several Primates, which namely contribute to increase the apparent size of the head and face in male–male ritual displays or combats (Guthrie 1970). Also, whisker length and number could provide females with reliable information on symmetry of their sexual ornaments (e.g. Moller 1990, 1992), or on their vulnerability in male–male contests, as expressed by their completeness (e.g. Alatalo et al. 1991). Males frequently direct their attacks to the face of their opponents and easily cause that some whiskers are damaged or lost. In one case described by Carranza & Hidalgo (1993), the looser of a combat lost 22% of his whiskers compared to the winner who lost <9%. The yellow and chestnut colour of the neck pigmented by carotenoids, which cannot be synthesized but must be ingested may reflect condition or health (reviewed in Griffith et al. 2006; Hill & McGraw 2006). The white colour, which reaches complete cleanness during the mating period, being much duller, greyish-yellowish white during previous months, may be a good indicator of low ectoparasite load (Kose & Møller 1999). These functions can hardly be investigated in great bustards, which because of their threatened conservation status cannot be manipulated as would be required.

Finally, males reaching higher development of both sexual traits exhibited higher display intensity, a more prolonged display period through the mating season, and a higher estimated mating success. Furthermore, the changes in the expression of both sexual traits in a given male between consecutive years were associated with changes in its display intensity and estimated mating success, which strongly suggests that the expression of both traits is condition dependent. The results suggest that the mechanisms used to increase mating success were extending the duration of full displays in males with higher ranks for both, whiskers and neck, and in the latter, also by detaching from the male flock earlier in the season.

As both sexual traits are exhibited during both male–male and male–female interactions, we conclude that they are 'dual function' traits (West-Eberhard 1979; Berglund et al. 1996; Panhuis & Wilkinson 1999). Whiskers are not only used by males as honest indicators of weight and fighting ability to resolve contests, but also by females during mating by enabling them to select the healthiest and oldest males. Our results provide support to (1) the 'pre-existing trait' hypothesis (Borgia 1979; West-Eberhard 1979; Berglund et al. 1996; Panhuis & Wilkinson 1999; Borgia & Coleman 2000; Morris et al. 2007), which proposes that the evolution of signalling traits used in resolution of male–male contests may lead to female preference for these traits as indicators of male quality; and to (2) the redundant signal hypothesis, one of the three hypotheses proposed to explain the evolution of multiple ornaments via mate choice (Moller & Pomiankowski 1993; Johnstone 1996; Coleman et al. 2004; van Doorn & Weissing 2004, 2006). Such a system of multiple ornaments functioning as redundant signals has been reported for many species (Sullivan 1994; Buchanan & Catchpole 1997; Rowe 1999; Candolin 2003; Jawor & Breitwisch 2004; Hebets & Papaj 2005; Loyau et al. 2005; McElroy et al. 2007; Vásquez & Pfennig 2007).

As an applied corollary of our results, we should suggest that the selective hunting of males with long whiskers and big necks practised when hunting was allowed probably removed the most successful individuals and not senescent ones who do not reproduce any more, as often argued by hunters. Trophy hunting can be a strong selective pressure (Fenberg & Roy 2008) that could have altered the social structure, sex ratio and population stability of great bustard populations in the past, as has been shown for several mammal species (Milner et al. 2007; Bonenfant et al. 2009).

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