



THE MOST EXTREME SEXUAL SIZE DIMORPHISM AMONG BIRDS: ALLOMETRY, SELECTION, AND EARLY JUVENILE DEVELOPMENT IN THE GREAT BUSTARD (*OTIS TARDA*)

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ABSTRACT.—The Great Bustard (*Otis tarda*) is one of the heaviest flying birds and the most sexually dimorphic living bird. Adult males weighed 2.48× more than females, and their linear measurements were 18–30% larger. Weight increased between the pre-breeding and breeding seasons by 16% in females and 20% in males. Sexual size dimorphism emerges very early in development and explains why growth in males is so costly. Weight and central toe length were hyperallometric when related to wing length in males but isometric in females and varied more in males, as compared with females and with other male traits. Although hyperallometry and high variability have frequently been used to invoke sexual selection as a driving force, our results support different functional hypotheses for the evolution of each trait. Male–male competition is intense in this lekking species, and high rank among males and access to females are weight-dependent. Thus, sexual selection has likely pushed male weight close to the limit imposed by powered flight. Because Great Bustards are mostly cursorial, the hyperallometry of the central toes of males in relation to wing length most likely evolved for support and balance. Received 14 November 2008, accepted 30 March 2009.

Key words: allometry, body size, Great Bustard, *Otis tarda*, sexual selection, sexual size dimorphism.

El Mayor Dimorfismo Sexual en Tamaño entre las Aves: Alometría, Selección y Desarrollo Temprano del Dimorfismo en los Jóvenes de *Otis tarda*

RESUMEN.—*Otis tarda* es el ave con mayor dimorfismo sexual y una de las de mayor peso entre las que conservan la capacidad de vuelo. Los machos adultos capturados en España fueron 2.48 veces más pesados que las hembras y sus medidas lineales un 18–30% mayores que las de las hembras. Entre finales del invierno y la estación reproductiva el peso medio aumentó en un 16% en las hembras y en un 20% en los machos. El dimorfismo sexual se manifiesta en los pollos de esta especie a edades muy tempranas, lo que implica que los machos han de sufrir un mayor costo durante el crecimiento que las hembras. El peso y el dedo medio mostraron en los machos un desarrollo hiperalométrico en relación con la longitud alar, mientras que estas medidas fueron isométricas en las hembras. Además, dichas medidas fueron las que presentaron mayor variabilidad fenotípica de entre todos los caracteres biométricos medidos en los machos, siendo éstas también más variables en los machos que en las hembras. Aunque la hiperalometría y una mayor varianza han sido frecuentemente utilizadas como argumento para apoyar la selección sexual como fuerza evolutiva, nuestros resultados sugieren que el peso y el dedo medio han sufrido procesos evolutivos diferentes. La competencia sexual entre machos es muy marcada en esta especie, y un mayor peso facilita el acceso a las hembras. Por ello, la selección sexual ha debido favorecer un incremento del peso hasta el límite impuesto por el beneficio derivado de seguir conservando la capacidad de vuelo. Por otro lado, como *Otis tarda* es un ave poco propensa a volar y que se desplaza fundamentalmente caminando, la hiperalometría del dedo medio ha debido desarrollarse por selección natural, como respuesta al enorme peso, para cumplir adecuadamente la función de soporte y mantenimiento del equilibrio.

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ALTHOUGH SEXUAL SIZE dimorphism (SSD) may have evolved by natural selection through niche divergence processes, agonistic and epigamic sexual selection are probably the main mechanisms leading to sex differences in size. The common view at present is that sexual segregation in different niches may help maintain SSD, rather than being the driving force underlying it (Ruckstuhl and Neuhaus 2005, Fairbairn et al. 2007).

The best way to estimate the influence of sexual selection on a male trait is by measuring lifetime multivariate selection on the trait in natural populations. Because this is generally difficult, experimental manipulation of the trait or study of static allometry is often used to infer selection. Using verbal models, several authors have suggested that allometric coefficients in excess of those expected by isometry (hyperallometry) would evolve in traits subject to sexual selection, whereas isometry or hypoallometry would be expected for traits under natural selection (Green 1992, Petrie 1992). However, recent studies have contradicted these assumptions, and the issue remains controversial (Bonduriansky and Day 2003, Eberhard 2006, Bertin and Fairbairn 2007).

Here, we present data on SSD and scaling among body weight and various linear morphometric traits in the Great Bustard (*Otis tarda*). This species is a good candidate for investigating the selective pressures that potentially lead to sexual differences in size, for at least four reasons. First, it is one of the largest flying birds: the male's maximum weight of ~15 kg is similar to that of other large bustards, such as the Kori Bustard (*Ardeotis kori*; del Hoyo et al. 1996). Second, Great Bustards are one of the most sexually dimorphic birds. In a review of SSD in birds, Payne (1984) listed the Great Bustard as the second most dimorphic in wing length in the family Otididae. Third, Great Bustards mate in leks, and less than half the males on a lek may copulate; weight and age strongly contribute to rank in the male hierarchy and to mating success (Magaña 2007). Males show their status and body condition through their secondary sexual traits (whiskers and neck development and color) and fight by gripping each other with their bills and shoving and jostling breast-to-breast, sometimes for >1 h. In captivity, weight increases in spring have been reported for three large bustards, though samples were small: Australian Bustard (*A. australis*; Fitzherbert 1981), Great Bustard (Carranza and Hidalgo 1993), and Kori Bustard (S. Hal-lager pers. comm.). If a spring weight increase occurs in the wild, it could confer vital physiological and fighting advantages during the long period the birds spend on leks. Fourth, male and female Great Bustards live in separate flocks all year round, which raises the possibility that their extreme sexual dimorphism evolved through niche specialization.

This paper accomplishes three objectives. First, we present body measurements of a large sample of free-living Great Bustards of both sexes. This is the first detailed account of SSD and of seasonal weight changes for any of the extremely large and dimorphic bustards. Second, we discuss the allometric constants, presenting various body measurements in relation to what might be expected from sexual and natural selection. Third, we explore the extent to which the allometric relationships and SSD of adults are present in juveniles and compare our results with published data on other, less dimorphic birds to infer whether the growth rate of males is limited by energy requirements.

METHODS

Data collection and variables analyzed.—We analyzed the biometry of a sample of 767 Great Bustards (155 adult males, 51 adult females, 286 juvenile males, and 275 juvenile females) captured in Spain between 1987 and 2007. Adults were captured at several leks or foraging areas between early January and early April, 1993–2004, mostly in central Spain using rocket nets. Great Bustards live in flocks at this time of year, so captures were not selective with respect to age, size, or social status and should be a random sample of the population. Because birds were captured for behavioral ecology studies, we released them within a few minutes to minimize capture stress; thus, for many birds we measured only weight and wing arch. Immature males (i.e., those in their third calendar year or younger; Gewalt 1959, Alonso et al. 2006) were excluded from the sample. Females reach sexual maturity at age two (much earlier than males), and year-old and older females cannot be distinguished, so our sample of females may include some year-old birds. Dependent young were captured between 1987 and 2007 in Madrid, Zamora, Navarra, and several Andalusian provinces in the second half of July, when they were 30–80 days old, and released within 20 min after capture. In all cases, they were soon rejoined by their mothers. We sexed all birds through discriminant analysis of their body measurements and some also with molecular techniques. The ages of young birds were estimated with second-order polynomial growth curves for body mass using a sample of 317 males and 294 females reared in 1981–2007 at the breeding station in Buckow, Germany (H. Litzbarski and T. Langgemach pers. comm.). To check for possible errors when calculating SSD values of young birds because of potential sex-bias in capture success, we used the subsample of 21 sibling pairs wherein one chick was female and the other was male. Our morphological measurements are defined in Table 1. Weight was measured to the nearest 50 g using 10-kg or 20-kg Pesola scales. Wing arch, wing chord, and tail lengths were measured to the nearest 1 mm, and all other measurements were measured to the nearest 0.1 mm. All measurements were made by J.C.A.

Statistical analyses.—To test for possible seasonal variation, we divided our adult sample into two groups: pre-breeding birds (captured before 15 March) and breeding birds (captured after that date). Great Bustards are globally endangered and are strictly protected in Spain, so our breeding sample is small, because most trapping occurred in winter to avoid interfering with breeding. We analyzed seasonal and sex differences using two-sample Student's *t*-tests on log-transformed variables. For sibling pairs, we used Wilcoxon's matched-pairs test. We used principal component analyses (PCA) and Pearson *r* correlation matrices for both adults and juveniles to explore the general biometric patterns within sexes and differences between the sexes. We used STATISTICA, version 6.0 (StatSoft, Tulsa, Oklahoma), for these analyses, and all tests were two-tailed.

To analyze sex differences in allometric scaling, we regressed $\log(Y_i)$ on $\log(\text{wing arch})$, where Y_i represents our various morphological measurements; males and females were analyzed separately. We used wing arch as our measure of body size because it loaded heavily on the first principal component (PC1) and because we had many wing-arch measurements. We used reduced major-axis regression (RMA) because it is preferred over least-squares regressions in scaling studies where *X* and *Y* variables have different units

TABLE 1. Weight (kg) and linear measurements (mm) of adult and juvenile Great Bustards taken in the present study.

Wing arch	Maximum distance between carpal joint and tip of the longest primary, 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 lower edge of the last complete scale before the toes diverge
Central toe length	Distance between distal end of tarsus and central toe tip excluding the claw, with the toe stretched
Head length	Maximum distance between the occipital end of the head and the tip of the bill
Head width	Maximum width of the skull behind the eyes
Bill length 1	Distance between the posterior end of bill commissure and bill tip
Bill length 2	Distance between the anterior end of nostrils and bill tip
Length of whiskers	Length of the longest whitish barbs that arise from each side of the chin, measured from the bill tip on the right side (measured only in adult males; these feathers develop much less and only occasionally in adult females)
Number of whiskers	Number of true barbs, which can be distinguished from the rest of the chin feathers by their characteristic morphology (Gewalt 1959), counted on the right side (in adult males)
Weight	Measured in kilograms

such as length and mass (Harvey and Pagel 1991). Observed slopes were compared with those predicted from allometry to identify characters that had hyperallometric scaling. For linear measurements regressed on wing arch, the expected allometric constant should be 1.0, and for mass it should be 3.0 (Schmidt-Nielsen 1984).

RESULTS

Weight and other measurements of adult birds.—Adult males were much larger than adult females in all morphometric variables, with no overlap between the ranges of both sexes for any measure

(Table 2). There were significant seasonal weight increases in both sexes (Table 3). These increases were equivalent to 20% of the pre-breeding weight in males, and 16% in females. These seasonal differences have to be considered when reporting mean weights for this species and comparing them with values for other species. For example, in our study, where the pre-breeding and breeding sample sizes differed markedly, a more representative mean weight for male Great Bustards would be 10.64 kg, the average between the pre-breeding (9.65 kg) and breeding means (11.62 kg). This average is notably higher than the overall mean given in Table 2. As for the male whiskers, it is well known that they start growing in

TABLE 2. Weight (kg) and linear measurements (mm) of adult Great Bustards. All sexual differences were highly significant ($P < 0.001$). Coefficients of variation (CV) and sexual-size-dimorphism values (SSD, expressed as male:female) are also given.

Measure	Males					Females					SSD
	Mean	SD	Range	CV	<i>n</i>	Mean	SD	Range	CV	<i>n</i>	
Weight ^{a,b}	9.82	1.18	7.0–13.0	12.06	155	4.35	0.47	3.30–5.20	10.86	51	2.26 ^a
Length of whiskers	215.1	26.1	150–270	12.12	97	—	—	—	—	—	—
Number of whiskers	14.5	4.8	7–30	32.80	74	—	—	—	—	—	—
Wing arch	628.0	19.2	570–685	3.05	92	491.5	16.3	435–525	3.31	28	1.28
Wing chord	566.9	14.7	535–610	2.59	50	444.7	14.7	400–470	3.30	19	1.27
Tail length	265.0	12.0	240–295	4.53	46	224.7	8.0	210–240	3.57	10	1.18
Tarsus length	152.7	7.3	138–176	4.81	59	120.0	5.6	112.5–129.5	4.63	14	1.27
Central toe length	69.9	4.3	58.5–79.2	6.22	48	53.7	1.6	49.5–55.6	3.06	15	1.30
Head length	151.1	4.8	134.5–160.5	3.20	54	122.3	3.3	115.5–129.7	2.71	18	1.24
Head width	54.7	1.8	51.3–58.5	3.37	44	46.0	1.6	44.6–48.4	3.40	5	1.19
Bill length 1	88.9	3.6	80.5–98.6	4.01	44	73.9	4.5	68.0–78.7	6.03	5	1.20
Bill length 2	34.4	1.4	31–37	4.18	45	27.8	1.6	24.4–29.8	5.68	10	1.24

^aMean annual weights calculated by averaging means of the pre-breeding and breeding samples were identical to the overall means given in this table for females (4.35 kg) but were notably higher in males (10.64 kg), resulting in an SSD value of 2.45 (SSD pre-breeding = 2.40, SSD breeding = 2.48; see text).

^bA 19-kg male found dead on 3 February 2009 in southeastern Spain was reported to us by S. Villaverde, Centro de Recuperación de Fauna de Albacete (not included in the analyses of the present study).

TABLE 3. Seasonal changes in weight (kg) of adult Great Bustards ($***P < 0.001$).

	Pre-breeding				Breeding				Difference
	Mean	Range	SD	<i>n</i>	Mean	Range	SD	<i>n</i>	<i>t</i> -test
Males	9.65	7.00–12.00	1.03	141	11.62	9.50–13.00	1.20	14	6.19***
Females	4.02	3.30–4.45	0.35	26	4.68	3.85–5.20	0.30	25	6.86***

December, increase in number and length up to the peak mating season in late April, and are lost during the prebasic molt (Gewalt 1959, Alonso et al. 2006, Magaña 2007). Linear measurements of size did not change with season.

Controlling for seasonal variation by considering separately the pre-breeding and breeding samples and excluding whisker length and number, weight was the measure that showed the highest interindividual variability in adults of both sexes, with higher values for males than for females (coefficient of variation [CV] = 10.70% and 10.16% in males and 7.50% and 6.93% in females in the pre-breeding and breeding samples, respectively). Central toe and tarsus length were the next most variable traits in males, more variable than in females (Table 2). In young birds of both sexes, weight and tail length showed the highest variability, and head length and head width the lowest (Table 4).

Morphometric patterns: Sex and age differences.—In adults, the correlation matrices of both sexes were very similar. The main sexual differences among adults were in central toe, tarsus, and tail lengths. In males, central toe length was highly correlated with weight, tarsus, head, and both measures of bill length (respectively, $r = 0.43, 0.45, 0.38, 0.39,$ and $0.33; n = 44$ males), whereas in females central toe length was correlated with tail length ($r = 0.71, n = 10$ females) but clearly not with weight, tarsus, and head lengths (respectively, $0.10, -0.05, 0.23; n = 14$ females). Tail length showed few correlations with other measurements in males (only with wing chord: $r = 0.32, n = 47$) and in females (with central toe and bill length 2: respectively, $r = 0.71, r = 0.80; n = 10$). Tarsus length was correlated only with central toe and bill length 2 in males (respectively, $r = 0.45, r = 0.30; n = 45$) and with head length in females ($r = 0.59, n = 14$). In young birds of both sexes, the correlations between all body measurements were highly significant ($P < 0.001; P < 0.01$ in the subsample of 21 sibling pairs, values not shown).

The results of principal component analyses confirmed these relationships and showed similar morphometric patterns between adults and juveniles (Table 5). PC1 was defined by strongly negative values for all linear measurements and weight in adults and in both samples of juveniles, thus reflecting the overall size of the birds. This factor explained most of the variance, in both adults and juveniles.

Sexual size dimorphism in adults and juveniles.—Both juvenile and adult males were much larger in all body measures than females (Tables 2 and 4). Adult and juvenile males showed significantly higher values of PC1, the factor reflecting overall body size (adults: $F = 420.89, df = 1$ and $49, P < 0.001$; all juveniles: $F = 268.56, df = 1$ and $539, P < 0.001$; subsample of 21 juvenile sibling pairs: $F = 32.93, df = 1$ and $40, P < 0.001$). In adults, SSD was greatest for weight, with males weighing $2.26\times$ more than females (Table 2). Weight dimorphism was even higher when the pre-breeding and breeding samples were analyzed separately (males:females pre-breeding = $2.40,$ males:females breeding = 2.48 ; Table 3). High SSD values in adults also were found in central toe, tarsus, and wing arch and chord, all of which were 27–30% longer in males. Tail length showed the lowest SSD values (Table 2).

In young birds, all dimorphism coefficients were somewhat smaller, but general trends were similar to those for adults, with highest values in weight and central toe and tarsus lengths (Table 4). All body parts grew quickly in juveniles, reaching, at

TABLE 4. Weight (g) and linear measurements (mm) of young Great Bustards. All sexual differences were highly significant ($P < 0.001$). Sexual-size-dimorphism values (SSD, expressed as male:female) are also given.

Measure	Males						Females						SSD			
	21 sibling pairs			All juveniles			21 sibling pairs			All juveniles			21 sibling pairs	All juveniles		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV			n	
Weight	2,160.7	445.4	20.6	2,135.4	608.9	28.5	286	1,383.1	247.1	17.9	1,392.2	332.2	23.9	275	1.56	1.53
Wing arch	429.4	47.5	11.1	430.7	50.2	11.6	282	376.8	35.6	9.4	381.9	37.5	9.8	271	1.14	1.13
Wing chord	384.1	42.6	11.1	387.7	45.1	11.6	282	342.0	31.3	9.2	347.8	34.4	9.9	270	1.12	1.11
Tail length	187.5	27.7	14.8	186.5	32.1	17.2	286	174.1	21.1	12.1	175.4	22.8	13.0	274	1.08	1.06
Tarsus length	120.0	10.2	8.5	121.8	13.8	11.4	283	103.7	8.0	7.7	106.9	10.1	9.4	273	1.16	1.14
Central toe length	57.9	4.3	7.4	58.7	5.2	8.9	281	48.0	3.1	6.5	49.5	3.6	7.4	273	1.21	1.19
Head length	111.4	7.1	6.4	112.2	7.6	6.8	284	98.2	4.5	4.6	99.8	5.8	5.8	271	1.13	1.12
Head width	41.2	2.7	6.6	41.4	2.7	6.5	282	37.0	1.7	4.6	37.5	1.9	5.1	272	1.11	1.10
Bill length 1	64.4	4.6	7.1	65.5	5.4	8.2	282	56.0	3.2	5.7	57.6	4.0	7.0	272	1.15	1.14
Bill length 2	22.6	2.1	9.3	22.8	2.3	10.0	284	20.1	1.3	6.2	20.7	1.7	8.0	271	1.12	1.10

TABLE 5. Results of the principal component analyses (PCA) of morphometric measurements in adults (45 males and 10 females), juvenile sibling pairs (21 males and 21 females), and all juveniles (275 males and 266 females). Only values for the first principal component (PC1) are given; all other factors had eigenvalues <1.

	Adults PC1	Juveniles (sibling pairs) PC1	All juveniles PC1
Weight	-0.915	-0.926	-0.640
Wing arch	-0.948	-0.955	-0.958
Wing chord	-0.950	-0.944	-0.951
Tail length	-0.789	-0.832	-0.854
Tarsus length	-0.894	-0.962	-0.956
Central toe length	-0.885	-0.913	-0.906
Head length	-0.944	-0.979	-0.973
Head width ^a	—	-0.956	-0.939
Bill length 1 ^a	—	-0.962	-0.954
Bill length 2	-0.903	-0.910	-0.851
Eigenvalue	6.55	8.74	8.16
Percent variance	81.88	87.37	81.58

^aThese variables were omitted in the principal component analyses of adults because of the small sample size of females (see Table 2).

the age of 70 days, 77.7–100% of the adult linear measurements and 34.8% (males) to 46.3% (females) of the adult weight (Table 6). At that age, all measures were smaller in young females but represented higher percent values of the adult values than those of young males. All measures had higher CV values in young males (Table 4). In both sexes, central toe and tarsus were the body parts that reached the highest percent value of the adult measure (Table 6). These were also the traits reaching highest SSD at the age of 70 days. The growth curves followed a similar pattern for all body measures (see Fig. 1 for an example). The growth rate was only slightly higher for juvenile males between hatching and the age of ~40 days but later tended to diverge between sexes, when female growth rate began to decline. The central toe represents an

TABLE 6. Weight (g) and linear measurements (mm) of young Great Bustards at age 70 days, as predicted from second-order polynomial growth curves adjusted to the sample of all juveniles. The values are the measurements of juvenile birds expressed as percentages of adult values.

	Males		Females	
	Measured at 70 days	Percentage of adult value	Measured at 70 days	Percentage of adult value
Weight	3,157	32.1	2,003	46.0
Wing arch	501.2	79.8	424.3	86.3
Wing chord	447.2	78.9	388.9	87.5
Tail length	226.8	85.6	207.7	92.4
Tarsus length	140.9	92.3	121.1	100.0
Central toe length	65.3	93.3	53.0	98.7
Head length	123.8	81.9	107.8	88.1
Head width	45.3	82.7	40.1	87.2
Bill length 1	73.8	83.0	63.5	86.0
Bill length 2	25.9	75.2	22.9	82.2

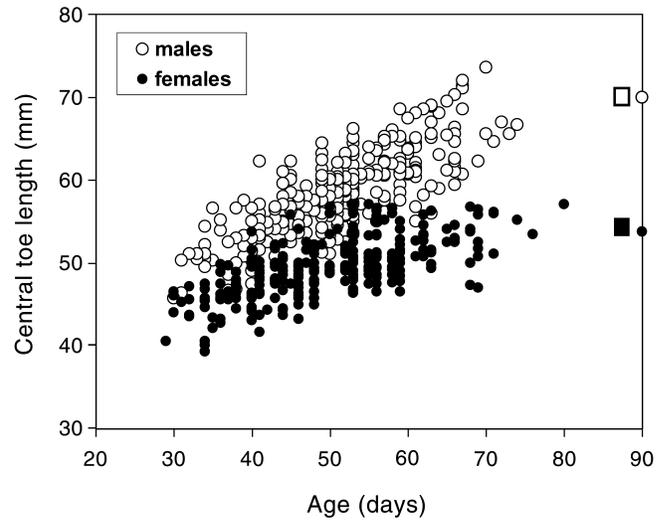


FIG. 1. Growth of central toe with age in Great Bustards 30–80 days old (sample of all juveniles: 281 males and 273 females). Squares on the right are the mean weights of adult birds (males: open square, females: black square).

extreme case of fast growth, with female and male chicks having reached, at the age of 50 days, 94.1% and 82.3% of the adult values, respectively (Fig. 1).

Scaling in adult birds.—When related to wing chord as an index of body size, weight and central toe length were hyperallometric in males (Table 7). In adult females, no measure deviated significantly from isometry, but sample sizes for females were small. More importantly, the slope of weight was 3.05 in females, practically equal to that expected under isometry (3.0). For all measures except bill length 1 and 2, the allometric slope was more positive in males than in females, though sex differences did not reach statistical significance.

DISCUSSION

Maximum weights of adult males.—The maximum weight we recorded for male Great Bustards was 13 kg, which is notably lower than the highest values cited in the literature for Iberian and central European Great Bustards, 17–20 kg (Trigo de Yarto 1971) and 16–18 kg (del Hoyo et al. 1996), respectively. However, a male found dead in Albacete, southeastern Spain, on 3 February 2009 weighed 19 kg (S. Villaverde, Centro de Recuperación de Fauna de Albacete, pers. comm.). Gewalt (1959) cast some doubt on the veracity of several old references reporting maximum weights of up to 21–24 kg and suggested that “weights over 15 kg are probably found only occasionally and under very favorable conditions.” Although mean or maximum weights may have decreased during the past century as a result of food availability or global warming (e.g., Yom-Tov 2001), we think that most old references close to or exceeding 20 kg should be considered exaggerations from hunters either in central Europe or in Iberia. On the other hand, we should allow for a further small seasonal increase of the maximum weights recorded in our sample up to the peak of the mating

TABLE 7. Scaling of morphometric measures against body size (wing chord), by sex, of adult Great Bustards. The reduced major-axis regression (RMA) slope expected under isometry is 3 for weight and 1 for all other variables (* $P < 0.05$).

Variable	Males			Females			Sex difference		Test isometry: males		Test isometry: females	
	RMA slope	r	n	RMA slope	r	n	T^a	df	T^a	df	T^a	df
Weight	5.805	0.367	49	3.054	0.617	19	1.244	33	2.113*	46	0.041	16
Tail length	1.732	0.324	47	— ^b	—	—	—	—	1.692	45	—	—
Tarsus length	1.544	0.120	61	1.498	0.150	14	0.045	18	1.460	61	0.615	14
Central toe length	2.020	0.149	49	1.373	0.117	11	0.506	15	2.117*	48	0.416	11
Head length	1.042	0.262	49	0.793	0.561	15	0.466	20	0.127	47	0.438	13
Head width	1.319	0.140	46	— ^b	—	—	—	—	0.806	46	—	—
Bill length 1	1.312	0.209	45	— ^b	—	—	—	—	0.791	44	—	—
Bill length 2	1.351	0.209	46	— ^b	—	—	—	—	0.886	45	—	—

^aThe T statistic has the same distribution as Student's t .

^bThe values for variables with $n \leq 10$ were not significant; they are not given because of low sample size.

season in late April (see below). Therefore, ~15 kg may be the maximum weight of male Great Bustards in Iberia, although some exceptional individuals may reach higher weights.

Seasonal variation in adult weight.—Results in the present study are the first to show a spring weight increase in male and female adult Great Bustards in the wild (Table 3). Carranza and Hidalgo (1993) recorded similar increases in two of eight captive birds. This increase is partly attributable to the development of the subcutaneous tissue and of two profusely irrigated lobes in the neck, which may reach 1 kg weight in spring (Gewalt 1965). We have no weight data for other seasons, but the scarce data from captive birds (Carranza and Hidalgo 1993), the undernourished appearance of males after the mating period, and the higher mortality observed during the post-reproductive period (Martín 2008, J. C. Alonso et al. unpubl. data) suggest that males probably reach minimum weights in summer, as a consequence of the physical strain suffered during male competition and mating (Magaña 2007). We also found a significant weight increase in females between the pre-breeding and breeding seasons, which probably reflects an accumulation of reserves for breeding.

Increases in weight of males in spring have been reported for other large bustards in captivity: up to 47% in Australian Bustard (*A. australis*; Fitzherbert 1981) and 30% in a male Kori Bustard (S. Hallager pers. comm.). In 20 wild male Kori Bustards, no significant increase was observed between the dry season (10.36 kg, $n = 7$) and the wet season, when birds breed (11.65 kg, $n = 14$; T. Osborne pers. comm.). Male weight also increased in spring in both subspecies of the Houbara Bustard (*Chlamydotis u. undulata* and *C. u. macqueenii*; Jacquet 1998).

Are Great Bustards the heaviest flying birds?—Our highest weights did not reach those reported for the somewhat taller Kori Bustards, which could also be somewhat exaggerated: 10.9–19.0 kg (del Hoyo et al. 1996) and 19 kg (reached by a captive male; S. Hallager pers. comm.), but the male Great Bustard cited above, recently reported from Albacete, indeed reached 19 kg. The only sample of wild Kori Bustards taken in recent times yielded a mean weight of 11.5 kg for adult males (range: 7.14–15.2; $n = 19$ adult males in Namibia, 1997–2002; T. Osborne pers. comm.). This weight is higher than our overall mean (9.82 kg, $t = 4.27$, $P = 0.001$), but the mean for the wet season (11.81 kg) was not significantly higher than our breeding-season mean (11.62 kg, $t = 0.37$, $P = 0.85$).

Wild female Kori Bustards were larger and heavier (mean weight = 5.6 kg, range: 4.31–6.73 kg, $n = 37$ adult females; T. Osborne pers. comm.) than our female Great Bustards, considering either the total or only the breeding-season samples ($P = 0.03$ in both cases). Male Kori Bustards seem to be as heavy as male Great Bustards, but Great Bustards are more sexually dimorphic in weight (male:female = 2.48 in the breeding season) than Kori Bustards (male:female = 2.05 in the whole sample, 2.32 in the wet season). Limited data for Great Indian Bustards (*A. nigriceps*; males almost twice as heavy as females [Rahmani and Manakadan 1988]; males ≤ 14.5 kg, females 3.5–6.75 kg [Rahmani 1989, del Hoyo et al. 1996]) and Australian Bustards (del Hoyo et al. 1996) also indicate lower SSD values in these species.

Mute Swans (*Cygnus olor*) and Andean Condors (*Vultur gryphus*) are similar (males: 6.6–15 kg and 11–15 kg, respectively; del Hoyo et al. 1992, 1994; recent sample of Mute Swan males: 8.2–13.4 kg, $n = 314$, BTO 2005), but less dimorphic, than Great Bustards. Other birds with high male:female weight ratios are the Australian Brown Songlark (*Cinchoramphus cruralis*), at 2.17 (Amadon 1977); Capercaillie (*Tetrao urogallus*), at 2.0–2.14 (Milonoff and Lindén 1989); and Muscovy Duck (*Cairina moschata*), at ~2.0 (Fairbairn et al. 2007). Male:female ratios for linear measurements in Kori Bustards varied between maximum values of 1.33 and 1.27 for tarsus width and head length, respectively, and minimum values of 1.08 and 1.17 for tarsus length and tail length, respectively (T. Osborne pers. comm.). Great Bustards were more dimorphic in all measures except head length. In Great Indian Bustards, SSD for linear measurements varied between 1.10 and 1.20 (Rahmani 1989).

In sum, Great Bustards show the highest sexual dimorphism, in weight and in most linear measurements, known in birds. Among terrestrial vertebrates, the SSD of Great Bustards is surpassed only by the most dimorphic mammals and some reptiles (reviewed in Weckerly 1998, Fairbairn et al. 2007). Male Great and Kori bustards have comparable mean and maximum weights and may be considered the two heaviest flying birds, on the basis of recent samples taken in the wild.

Causes of SSD in adults.—Weight and central toe length were hyperallometric in males but isometric in females and were more variable in males as compared with females and with other male traits. Nevertheless, our results did not support an association between allometry and sexual selection. Although hyperallometry

and high variability are often interpreted as consequences of sexual selection (e.g., Green 1992, Petrie 1992, Pomiankowski and Moller 1995, Eberhard et al. 1998, González-Solís 2004), recent empirical studies and analytical models have shown that some sexually selected male traits may exhibit isometric or hypoallometric scaling; thus, the form of selection operating on traits cannot be reliably inferred from allometry patterns or trait variation (Bonduriansky and Day 2003, Bertin and Fairbairn 2007). Bonduriansky and Day (2003) concluded that sexual selection would result in positive allometry when the marginal fitness gains from an increase in relative trait size are greater for larger individuals than for smaller ones. This may be the case with regard to weight in male Great Bustards, in which, as described below, the higher mating success of heavier and older individuals suggests that sexual selection may have favored heavier weights but not longer central toes.

The allometric coefficient of 5.8 for male weight on wing arch greatly exceeds the expected value of 3.0. In Great Bustards, wing length increases in males until they are 8–10 years old (i.e., well beyond sexual maturity; Magaña 2007). Older males might benefit more than younger males from becoming heavier because increased weight (stored reserves, greater muscle mass, or larger necks) and old age independently contribute to increasing their mating success (Magaña 2007). In several mammals, efficiency of antlers or tusks used in male–male fights increases with body size and weight (reviewed in Andersson 1994). Because male Great Bustards do not have weapons, body weight may be crucial in male–male contests. These combats may be dangerous, given that males often peck their rival's face and eyes (J. C. Alonso et al. pers. obs., using decoys). After such intense fighting, males are sometimes so exhausted that they temporarily cannot fly. Finally, being heavy is not an obstacle in a species that displays on the ground. On the contrary, it probably means more reserves that may be useful during the peak mating season in April, when males spend only 14% of their time feeding. Males that weighed more at the start of the season spent less time feeding ($r = -0.46$, $n = 29$, $P = 0.013$; J. C. Alonso et al. unpubl. data), which allowed them to concentrate on display (Magaña 2007).

The central toe was also hyperallometric in males in relation to wing chord, and central toe and tarsus were the two traits that were the most sexually dimorphic, as well as the most variable among males. The greater SSD of these skeletal structures may be a consequence of being much heavier. Rather than being a result of sexual selection, the development of longer toes and tarsi was probably necessary to allow heavy males to keep their balance, which is important in a species that is mostly cursorial. Central toe length was positively correlated with weight, tarsus, head, and bill lengths in adult males, but not in females. Also, the allometry of central toe length on weight was 0.38, not significantly different from the value of 0.33 expected if the toe length is adjusted to the mass the toes support. We interpret these relationships as sexual selection having favored the extreme SSD in Great Bustards, leading to heavy weights only in males, which have developed strong tarsi and long central toes as adaptations to support their huge weights.

Other authors have found hyperallometric relationships in body parts that are not explained by sexual selection but that are also associated with larger or heavier individuals. Examples

are the tails of newts, which allow a greater propulsive force during swimming (Green 1992); the width of atlas vertebrae of the Caribou (*Rangifer tarandus*), which are hyperallometric because of the relatively greater mass of muscles that has to be supported in larger individuals (Hardy and Stroud 1981); the relatively longer wing-bones in larger birds, which are probably related to lift requirements and size-dependent variation in flight behavior (flapping vs. soaring; Nudds 2007); and the longer legs of larger individual aquatic insects and spiders, which enable locomotion on the water surface (Klingenberg and Zimmermann 1992, Suter and Gruenwald 2000). Likewise, wing dimorphism of some birds has been interpreted as a need to provide aerodynamic compensation for their sexually selected long tails (Andersson and Andersson 1994). These size-required allometric increases describe changes in form required to maintain a given function and, thus, may be interpreted as functional constraints on shape imposed by changes in size ("allometric constraint"; Fairbairn 1997).

The alternative hypothesis that SSD in weight and central toe length were selected through sexual segregation seems unlikely. Male and female Great Bustards occur in different flocks year round but use the same areas and habitat types and have similar foraging and locomotion strategies, and apparently they have no significant dietary specializations (J. C. Alonso et al. pers. obs.). Sexual segregation is common in several other game birds, as well as in size-dimorphic ungulates, in which asynchrony in activity budgets caused by sexually selected size dimorphism has been suggested to make group cohesion costly to maintain (Ruckstuhl and Neuhaus 2005). Natural selection may even work against sexual selection for larger male size (a process for which evidence is still sparse; see Blanckenhorn 2005) through mechanisms such as (1) predation pressure against large, less agile males with reduced ability to escape by flying or reduced maneuverability during flight and (2) male vulnerability during food shortages. Finally, we do not think that larger central toes are related to display-agility in a species with ground display (Raihani et al. 2006, Fairbairn et al. 2007), apart from the purely mechanical function of supporting the male's weight. A recent review revealed SSD in birds to be explained most consistently by sexual selection through mating competition, and the relationship of SSD in bustards was the opposite of that predicted by the resource-division hypothesis (Fairbairn et al. 2007).

Early development of SSD in the Great Bustard.—Great Bustards show one of the most extreme cases of early SSD development among sexually dimorphic birds (Teather and Weatherhead 1994, Fairbairn et al. 2007). Our results from a previous study suggested how sexual selection may have favored rapid growth of young males by increasing their competitive ability during the immature period and probably also their fitness as breeding adults (Alonso et al. 1998). Young males that fed at higher rates or received more feedings from their mothers became independent at a younger age, integrated earlier into adult male flocks, and settled earlier at their definitive leks. However, these benefits of rapid growth were counterbalanced by increased mortality (Martín et al. 2007). As in several birds and mammal species, male-biased juvenile mortality resulting from starvation when food is scarce may limit the growth rate of male Great Bustards (e.g., Clutton-Brock 1991, Torres and Drummond 1997). The resulting tradeoff means that males grew more slowly than females when growth rates were

examined in relation to adult size, as has been shown for other dimorphic birds (Teather and Weatherhead 1994). The male:female weight ratio at fledging in Great Bustards and in another highly dimorphic bird, the Capercaillie (1.40 at an age of 40 days in both; fig. 1 in Milonoff and Lindén 1989, present study), is lower than those of other birds with lower adult SSD values (fig. 1 in Teather and Weatherhead 1994) and confirms the main prediction of the energetic-cost hypothesis (i.e., that a reduced male growth rate should be most pronounced in the most dimorphic species). Instead of growing at the fastest possible rate, as predicted by the allometry hypothesis of Teather and Weatherhead (1994), young male Great Bustards continue putting on weight for a longer time (up to 4–5 years; Magaña 2007), a pattern that is widespread among dimorphic mammals (see Teather and Weatherhead 1994). Indeed, for some male characters, asymptotic growth is achieved after sexual maturity (Magaña 2007, J. C. Alonso et al. unpubl. data), a pattern found in many invertebrates, poikilothermic vertebrates, and some highly dimorphic mammals, but rarely in birds (Stamps 1993).

As in adults, the character that exhibited the most SSD in juveniles was the length of the central toe, followed by tarsus length. In males, the central toe grows through the immature period and even in adulthood, but then only in association with weight increases, not the overall body size of the bird as estimated through wing or tail lengths (Magaña 2007). In a smaller sample of adult males for which we could estimate age, tarsus and central toe lengths did not increase with age, unlike wing length or head length and width (Magaña 2007). By contrast, central toe and tarsus in females reach 99–100% of their adult length at age 70 days and are independent of weight or body size in adult females. The early juvenile development of central toe and tarsus has most likely evolved in both sexes through natural selection, to facilitate running and the rapid weight increase of young in this mainly cursorial species.

ACKNOWLEDGMENTS

We are grateful to the farmers in all our study areas for allowing us to work on their properties. We also thank E. Martín, M. Morales, and C. Ponce for their collaboration during field work over several years, H. Litzbarski and T. Langgemach for growth data, S. Villaverde and M. E. Gómez for a male weight from Albacete, and two anonymous reviewers for constructive comments on a previous version of the manuscript. Additional help in the field was provided by C. Alonso, L. M. Bautista, C. Bravo, H. Bustami, C. Caldero, A. Correas, J. A. Cruz, E. Fernández, D. González, I. de la Hera, E. Izquierdo, S. J. Lane, R. Manzanedo I. Martín, C. Martínez, I. Martínez, R. Muñoz, M. A. Naveso, A. Onrubia, P. E. Osborne, N. de la Torre, and the guards from Navarra province. L. M. Bautista helped during RMA analyses. The field work was financed by the Dirección General de Investigación (projects PB87-0389, PB91-0081, PB94-0068, PB97-1252, BOS2002-01543, and CGL2005-04893), the Instituto Nacional para la Conservación de la Naturaleza, and the Direcciones Generales del Medio Natural of Madrid, Castilla y León and Andalucía. The Consejerías de Medio Ambiente of the Madrid Community, Junta de Andalucía, Junta de Castilla y León, Navarra and Aragón, and the provincial delegations of Toledo and Albacete allowed us to capture birds.

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Associate Editor: S. Rohwer