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ORIGINAL PAPER

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Field determination of age in male great bustards (*Otis tarda*) in spring

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Abstract During a long-term study of individually marked, free-living male great bustards captured as chicks and radio-tracked through several years in Spain, we studied the development with age of two secondary sex traits, the moustachial feathers and the neck plumage pattern. Juvenile males acquired full adult plumage between their fourth and seventh years. The main changes occurred at the neck, coinciding with the onset of sexual maturity. The grey colour typical of immature males turned to ivory white around the fourth to fifth spring, and a gradual increase was appreciated in adults in the brightness of the white colour of the upper neck and in the contrast between this and a progressively more intense chestnut brown at the neck base. Based on these changes, we proposed four neck plumage patterns that can be used to differentiate male age classes during the mating period. The development of moustachial feathers showed more interindividual variability and was not as useful as the neck plumage to estimate male age.

Keywords Great bustard · *Otis tarda* · Plumage development · Secondary sex characters

Introduction

Male great bustards (*Otis tarda*) develop in spring two characteristic plumage traits, the moustachial feathers and a colourful plumage pattern at the neck and breast, which are exhibited during sexual display. The moustaches or whiskers are thin, 15- to 20-cm-long feathers that grow in tufts at both sides of the lower mandible. They grow every winter in males older than 1 year, starting in December, reaching maximum length in spring and disappearing in July–August. 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 molt starting in December and ending up in April, from uniform grey during the non-breeding season into a colourful pattern with contrasting dark chestnut at the base and ivory white at the throat. At the start of the mating season, the neck also increases notably in thickness due to 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 length than in summer–autumn, also contributing to confer the adult male neck a remarkably thick and powerful appearance (Gewalt 1959). At this time, two bluish-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 sex traits increases with the age of the male and proposed three neck patterns to differentiate age classes in males. Each year, the length and number of moustachial feathers and the intensity of the neck plumage pattern would grow up. This assertion, based probably on some captive-bred individuals, was transcribed in later ornithological reviews, without giving further details (Glutz et al. 1973; Cramp and Simmons 1980). However, in a more recent study with a small sample of captive males, no correlation was found between age and number of moustachial feathers or development of neck plumage (Hidalgo and Carranza 1990; Carranza and Hidalgo 1993). These authors concluded that the number of moustachial feathers and the neck plumage pattern could be indicators of the male condition, whereas the length of the moustachial feathers could reflect the age of the male. Finally, in a recent study with a small sample of free-living males, we found neck development to be

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correlated with age, contradicting the results obtained with captive males (Morales et al. 2003).

In the present paper, we describe the development with age of moustachial feathers and neck plumage pattern in Iberian great bustards during the mating season, based on a long-term study of a larger sample of individually marked, free-living male great bustards captured as chicks and radio-tracked through several years.

Methods

In this study, we used 31 males captured as chicks at an age of 20–70 days (10 in Villafáfila, NW Spain, between 1987 and 1993, and 21 in Madrid region between 1995 and 1999). We captured them while they were still dependent on their mothers (body mass 1–3.7 kg) and marked them with PVC patagial tags for visual identification and backpack harness-mounted radio-transmitters TW3-2xAA (Biotrack Ltd., UK). We used elastic harness to prevent affecting their body growth, particularly in the case of juvenile males. The birds were released within 15–20 min after capture, and in all cases, we confirmed that they were soon rejoined by their mothers (more details of the marking procedure in Alonso et al. 1996). We sexed the birds using a discriminant biometric index (Martin et al. 2000). Battery life of the transmitters averaged 3–5 years, which allowed us to track the birds throughout their juvenile–immature dispersal period (first 2–3 years of life, see Alonso et al. 1998). Once established as adults, males could be located by sight and identified through their patagial tags. However, the initial sample size of 31 decreased in subsequent years due to the death or disappearance of some individuals, transmitter failure and long-range movements of some birds, which made them difficult to locate and radio-track during the juvenile dispersal phase. To increase our sample of birds marked as chicks for ages ≥8 years, we used another 5 males captured with rocket nets as adults in Madrid in 1997 (1 bird), 1998 (2 birds) and 1999 (2 birds) and tracked throughout 5–7 years. We studied their plumage traits from their forth tracking spring on, i.e. when they were of ages 8 years or more.

Gewalt (1959) proposed three neck patterns to distinguish the following age classes in males during spring: 1–2, 3–6 and >6 years. Based on these and on our own experience from a preliminary study with marked birds at Villafáfila (Alonso and Alonso 1992), we established the following four moustache development categories:

Moustaches 0
: No moustachial feathers.

Moustaches 1
: Poorly developed, exceeding a few centimetres the rear end on the bill gapes.

Moustaches 2
: Viewing the head from the side, the moustaches reach the nape outline.

Moustaches 3
: The moustaches clearly exceed the nape outline.

Moreover, we also established the following four neck patterns:

Neck 0
: Relatively thin, uniform grey spotted with brown at the base, with a slim fringe of brown colour at the neck base on its dorsal face.

Neck 1
: Somewhat thicker, with a brown wide band at the lower half and grey at the upper half, of lighter shade than in the previous category.

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 very light greyish colour that grades to grey under the lower mandible. The three bands of the neck, lower chestnut, intermediate creamy-yellow and upper whitish, are approximately of the same height.

Neck 3
: A thick, substantially bulkier neck, with well-developed, hanging breast feathers, very intense chestnut-coloured basal band, not as wide as in the 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 0.5, 1.5 and 2.5.

Each spring throughout the study period, we assigned values to our marked birds, after observing each individual during two to six periods ranging between 60 and 2250 min in the morning display activity time through the main display phase between late March and early May, using telescopes 20–60× and 60–90×. Based on previously drawn sketches of the neck and breast patterns, we described the details and drew possible modifications of each particular bird and estimated the length of the moustaches. We also took photographs of some birds, but due to their generally poor quality, changing light conditions and variable postures of the birds, pictures proved to be no better alternative to sketches to categorize sex traits. After several visits to every male, we obtained for each bird a mean annual value of moustache and neck categories and plotted the resulting series of values on a graph ranging between ages 1 and 10 years.

Results

Figure 1 shows the development of sex traits with age in male great bustards. Males developed short moustachial feathers already in their second spring after hatching, i.e. during their third calendar year (Fig. 1, left). At the age of 3 years, the moustaches exceeded the nape outline in only one male and just reached it in another male, out of 15 birds. Between the third and sixth springs, the average moustache category increased rapidly with age, reaching maximum values in the seventh spring in most birds. However, interindividual variability was relatively high

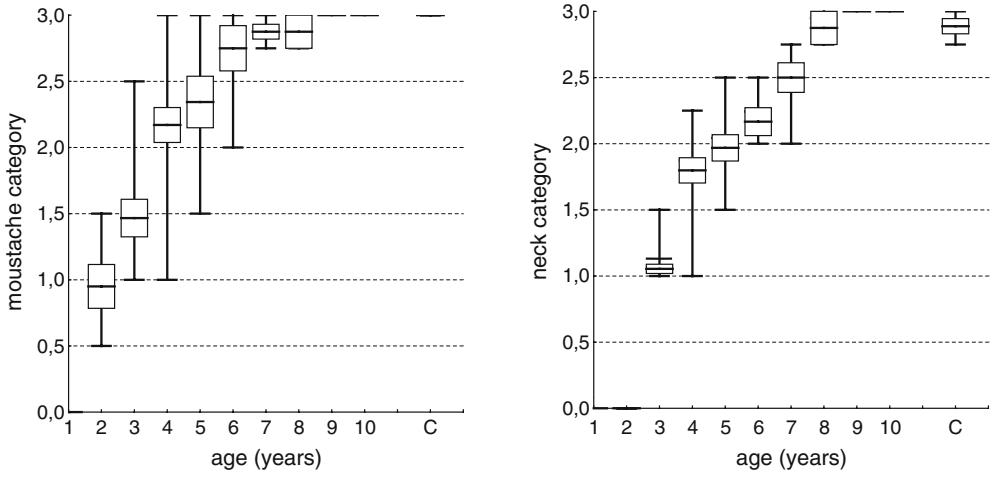

Fig. 1 Development of moustache and neck categories with age in male great bustards. Means±1 S.E., minimum and maximum values of both sex traits during the mating period (late March–early May) are represented. Birds aged 1 were about to be 1 year old that spring, i.e. in their second calendar year. The initial sample size of 31 birds decreased in successive years due to the death or disappearance of some individuals and transmitter failure (n=31, 5, 15, 14, 8, 6, 6, 2, 1 and 1, respectively, for ages 1–10). All 1-year-old birds scored 0 for the moustache category, and all 1- to 2-year-old birds scored 0 for the neck category. To confirm the categories for ages >8 years, for which our sample of birds marked as chicks was too small, we used a control sample of five males captured as adults and tracked throughout 5–7 years. Their mean moustache and neck values for the springs when they were of ages 8 years or more are represented under *C* in both graphs

during this age interval (2–6 years). As for the neck category, it scored 0 in all birds in their first and second springs, increasing to values around 1 in all birds in the third spring (Fig. 1, right). In the fourth spring, only one bird scored 1, most being close to value 2. Between that age and the seventh spring, neck values increased regularly and with lower interindividual variation than in the moustache category. Maximum neck scores were reached in birds aged 8 years or more.

Discussion

Our results confirmed that average moustache length and neck categories increased with age in male great bustards. We suggest that four post-juvenile age classes can be distinguished through their neck plumage designs in spring (Fig. 2). The first corresponds to 2-year-old birds, which can usually be distinguished from 1-year-old birds (hatched on the previous year) by the more apparent brown spots at both sides of the neck base. First-year males strongly resemble adult females, with whole neck and central chest pale ash-grey and brown only on the lower hindneck, extending to both sides of the upper chest, but spots in the foreneck base usually absent or much less marked than in 2-year-old birds. In addition, none of our marked birds had moustaches when they were 1 year old, whereas all had already grown short moustaches at the age of 2 years. This coincides with the descriptions in Gewalt (1959) and contrasts with those in Cramp and Simmons (1980, p. 667). The differentiation of 1- and 2-year-old males is sometimes difficult even for experienced observers, and behavioural

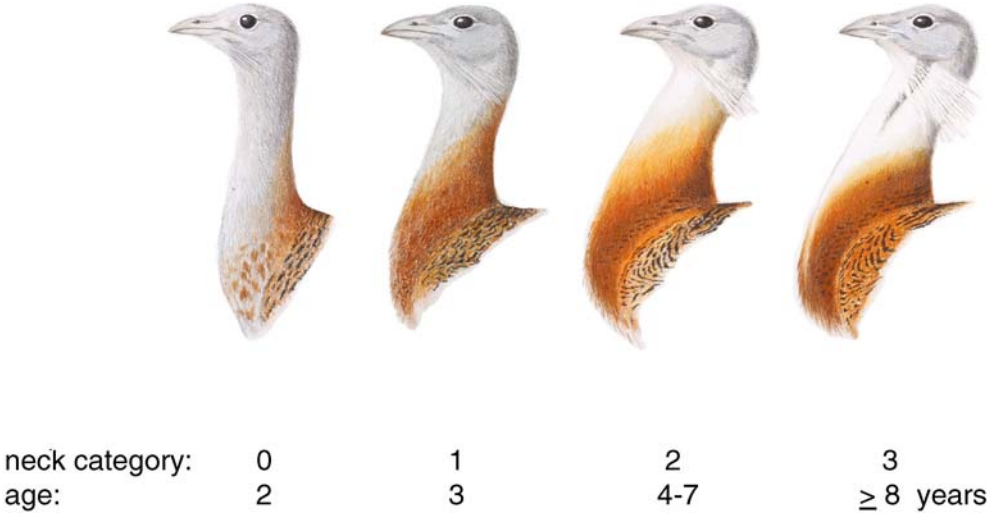

Fig. 2 Development of spring neck plumage with age in post-juvenile male great bustards. The four neck categories proposed in this study are represented, with the approximate corresponding ages (see legend of Fig. 1 for age definition and text for details). (Drawings by J.C. Alonso) (For a detailed colour version of this figure, please contact the authors or see the online version of this journal.)

traits may be helpful in such cases. First-year males are typically associated to females during the spring of their second calendar year, in contrast to 2-year-old males, who tend to aggregate in male flocks with individuals of their same or subsequent immature cohorts.

The second age class that can be recognized corresponds to 3-year-old birds. The upper half of their neck is grey, of a lighter shade than in younger males, but clearly different from the ivory white of older males. The lower half of the neck is chestnut brown, forming at the neck base a collar of much wider extension and notably duller shade than in older males. The chestnut colour of hindneck almost reaches the nape. A key character of this neck pattern is the absence of a creamy-yellow fringe separating the upper grey half from the lower chestnut-brown half. These males are still immature and do not have access to females during the mating period (Magaña 2006, personal observation of display behaviour and mating success of marked birds).

The third age class includes males aged 4–7 years. With the exception of two birds scoring 1 and 1.13, there was no overlap between score ranges of birds aged 3 years and those aged 4 years or more. It is interesting to note that this change in plumage pattern coincides with the acquisition of sexual maturity and access to females (4–5 years, personal observation). Males aged ≥4 years can be distinguished from younger birds by the white throat and upper foreneck and the broad intermediate creamy-yellowish band, which grades to intense chestnut brown on the chest. Each of these three bands, white, yellowish and chestnut, occupy approximately one third of the neck's height, and the chestnut colour is much more brilliant than in neck category 1. The neck base is also bulkier due to the longer, hanging breast feathers, which according to Gewalt (1959) grow after the partial moult in winter to more than double their length of the non-breeding season. This provides the necks of adult males with their typical massive, powerful appearance.

Finally, our fourth age class comprises males aged 8 years or more. The pattern shown by the two males of known exact age was fully corroborated with the sample of five males captured as adults. The white colour of the neck is much brighter at this age than in younger males, particularly at the neck sides, extending approximately over the upper two thirds of the neck height. The chestnut colour of the neck base is also much more intense, and the intermediate yellowish band separating white from chestnut is typically reduced to a thin fringe. This produces a highly contrasting white–chestnut pattern and makes the chestnut collar appear narrower than in younger males. In addition, the chestnut collar is open in the front so that the pure white colour of the upper foreneck reaches the lower breast, notably increasing the overall extent of the white plumage surface. The white colour of the upper neck is most visible when the male is in rest or alert posture and under good light conditions. When males inflate their neck during display, the stretched front neck feathers may show up a more creamy-yellowish colour and appear less white.

Our characterization of the neck pattern of very old males confirms Gewalt's (1959) observation of a sharp change between the white colour of the upper neck and the intense chestnut of the neck base. However, it contrasts with his description of the chestnut neck base collar being more open in younger adults, increasing in width with age and reaching almost half the total height of the neck in very old males (Gewalt 1959, pp. 28 and 39; see also Glutz et al. 1973, p. 651). Furthermore, in males of age-class 3, but not in younger males as indicated in Gewalt's (1959) designs, the bare skin streaks below the chins are visible along the sides of the neck, even when the male is in resting posture. At younger ages, these bare skin stripes are only observable when males inflate their necks during display.

The differences between Gewalt's and our descriptions of the development of the white–chestnut ratio with age in old males might be related to plumage differences between central European and Iberian populations. A recent study has shown that both populations diverged genetically during a complete and long-term separation through the Pleistocene Ice Age (Pitra et al. 2000), and several authors have suggested that the possible existence of two subspecies in Europe should be further investigated (Gewalt 1959; Hidalgo and Carranza 1990). The more intense chestnut-brown neck collar of Iberian males has been accepted by most authors that have studied the species in detail (Gewalt 1959; Kleinschmidt 1938 cited in Gewalt 1959; England 1966; Hidalgo and Carranza 1990, personal observation). The development of these characters with age has not been studied in detail in the Asian subspecies *O. tarda dybowskii* (Glutz et al. 1973).

As for the development categories of moustachial feathers, we found a high interindividual variability throughout most of the age interval studied. Values ranged between 0.5 and 1.5 in 2-year-old birds, between 1 and 3 in 4-year-old birds and between 1.5 and 3 in 5-year-old birds (see Fig. 1). Therefore, although we can confirm Gewalt's (1959) statement that the development of moustachial feathers roughly increases with age, our results show that moustache length is not as good indicator of age as the neck pattern. On a small sample of captive great bustards, Carranza and Hidalgo (1993) found that age was correlated with the length, but not with the number of moustachial feathers. Their results suggested that the number of these feathers could reflect the body condition rather than the age of the birds.

An ongoing study confirmed that not only moustachial feathers but also the neck pattern described for older males may indeed suffer regressive development on certain years with respect to previous springs, associated with less intensive display behaviour and lower mating success, probably due to a poorer body condition on those years (Alonso et al., unpublished data). The white of the upper neck may then be less pure than in springs when males acquire the full expression of secondary sex traits.

In conclusion, our results indicate that juvenile great bustard males acquire full adult plumage between their fourth and seventh springs, instead of between second and sixth or third and sixth springs, as stated in ornithological reviews (Cramp and Simmons 1980; Morales and Martín 2002). Neck development proved to be a better indicator of

the males' age than moustache development, which might depend more on their weight and body condition. The neck design of males in spring plumage changes throughout the first ca. 8 years of life along two lines, which resemble seasonal variation between the non-breeding season and the peak of the mating period (for details of this moulting process, see Gewalt 1959; Glutz et al. 1973): first, changing the grey colour typical of juveniles for a brilliant ivory white, and second, increasing the brightness and contrast between this white and a progressively more intense chestnut brown at the neck base. These changes allowed differentiating four age classes in non-juvenile birds, which may be used to estimate ages of free-living male great bustards only during the mating period, when age differences acquire their maximum expression. Obviously, there is a certain interindividual variability in plumage design, and we are currently investigating an additional variability due to the body condition on particular years (Alonso et al., unpublished data). Although the age estimation method proposed in the present study may entail a certain error due to these sources of variability, we believe it is useful to guess a basic age composition of male flocks at leks during the mating period. Neck design can be used at least to separate the 1-, 2- and 3-year-old birds and the two age classes among adults.

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