

RESEARCH PAPERS

Differential Migration by Sex in the Great Bustard: Possible Consequences of an Extreme Sexual Size Dimorphism

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Abstract

We explored migration patterns in Great bustards (*Otis tarda*), a species that shows strong sexual selection and the most extreme sexual size dimorphism among birds. The aim was to explain differential migration, examining whether Great bustards fulfil the main predictions of bird migration theory hypotheses and sexual segregation theory hypotheses. We radio-tracked the seasonal movements of 65 males and 68 females in central Spain. We found four main sexual differences. First, the proportion of migratory males was higher than that of migratory females (86% vs. 51%). Second, males abandoned the leks immediately after the mating season (late May to early Jun.), whereas females remained there for another 3–7 mo. Third, 54% of the migratory males used two different post-breeding areas, the first located northwards at 82 km from the breeding sites in summer, and the second southwards at 50 km in autumn–winter. Migratory females used only one area in autumn–winter which coincided geographically with that of males. And fourth, males returned to the breeding areas earlier (between Sep. and Mar.) than females (between Jan. and Apr.). These results show that the Great bustard is a differential migrant by sex in central Spain and support the weather sensitivity hypothesis (males were less tolerant to summer heat) and the specialization hypothesis (exclusive maternal care of the brood by females). Sexual differences in migratory behaviour are probably ultimately determined by the strong sexual selection in this species.

Introduction

The term differential migration was coined to describe the situation where migration routes, migratory periods and/or the location of wintering grounds differ among distinguishable classes of individuals (ages, sexes or races) in a bird population (Gauthreaux 1982; Terrill & Able 1988). Some pioneer studies in birds had shown that particularly among short-distance and medium-distance migrants males often migrate shorter distances than females, and adults migrate shorter distances than juveniles

(see Schüz et al. 1971; Ketterson & Nolan 1985). In a recent review, Cristol et al. (1999) found that 91% of 160 bird species examined were either confirmed or candidate differential migrants. They concluded that differential migration is much more widespread than previously reported and indeed may be considered as the norm among migratory birds. However, the factors responsible for the evolution and maintenance of differential migration are not clearly understood (Cristol et al. 1999; Berthold 2001; Jenkins & Cristol 2002). Differential migratory behaviour may indeed have different causes in different species. It

may serve to reduce intraspecific competition among age or sex classes at the resting areas by segregating them spatially, enable a certain class an earlier arrival at the breeding areas, or balance the relationship between migration cost and overwinter mortality among classes (Berthold 2001).

Four hypotheses have been proposed in bird migration reviews to explain differential migration: (1) the behavioural dominance hypothesis, which predicts that intraspecific competition forces individuals of the subordinate age class or sex to migrate further (Gauthreaux 1978, 1982); (2) the body-size/physiological hypothesis, which suggests that individuals of the larger sex winter closer to the breeding range at higher latitudes because they tolerate better low temperatures and food shortage (Ketterson & Nolan 1976); (3) the arrival-time/sexual selection hypothesis, which proposes that intra-sexual selection drives individuals of the sex that establishes breeding territories to winter closer to the breeding area, to arrive earlier to the breeding grounds (Myers 1981a); and (4) the prior residence effect hypothesis, which states that residence of early arriving individuals might make these birds dominant over those arriving later (Nolan & Ketterson 1990). However, these hypotheses are not mutually exclusive. Moreover, body size, dominance and arrival time are generally correlated with each other, and with sex, which makes the proposed hypothesis hard to test (Cristol et al. 1999; Catry et al. 2005).

Differential migration can also be examined from the perspective of sexual segregation theory (Selandier 1966; Morton 1990; reviewed in Catry et al. 2005). One of its main hypotheses, the specialization hypothesis, suggests that males and females segregate spatially because of differential tolerance to ecological factors such as extreme temperatures, or sex-specific constraints arising from role specialization and competitive pressures in reproduction (Catry et al. 2005). In relation to extreme temperatures, some authors have proposed the weather sensitivity hypothesis to explain habitat segregation in a large number of sexually dimorphic species (Jackes 1973; Young & Isbell 1991; Conradt et al. 2000). Sexual size dimorphism (SSD) is probably a major cause of these and other sex differences in many behavioural and ecological patterns (Ruckstuhl & Neuhaus 2000; Ruckstuhl & Clutton-Brock 2005). For example, recent comparative studies have shown that the degree of SSD is related to the amount of sexual segregation outside the breeding season in ungulates (Mysterud 2000; Ruckstuhl & Neuhaus 2002). However, the main hypotheses put forward to explain

sexual segregation in mammals have not yet been adequately tested in birds, although sexual segregation in flocks can be found in some of the most dimorphic game bird species, suggesting a causal relationship between sexual SSD and sexual segregation (reviewed in Catry et al. 2005). In birds, SSD is related to the intensity of sexual selection (Møller & Birkhead 1994; Owens & Hartley 1998; Dunn et al. 2001), and has also been recently found to be related to the timing and sex differences in spring migration (Kissner et al. 2003; Rubolini et al. 2005).

Here, we present the results of a study on differential migration in the Great bustard, one of the vertebrate species showing highest SSD (males' weight is 2.4 times that of females; Alonso et al. 2004a), and therefore in principle a good candidate to test the above mentioned hypotheses. The Great bustard is a globally threatened species (IUCN 2006) with a 60% of its world's population found in Spain (Palacín & Alonso 2008). Males and females live all year round in sexually segregated flocks, and the species exhibits a dispersed lek mating system (Hidalgo & Carranza 1990; Morales 1999; Magaña 2007). Females nest on the ground and rear alone their usually single precocial chick during 6–12 mo (Alonso & Alonso 1992; Martín 1997, 2001; Alonso et al. 1998). Previous studies based on marked birds of both sexes in NW Spain showed that Great bustards behave there as partial migrants, with sedentary and migratory individuals coexisting in the same population (Alonso et al. 2000; Morales et al. 2000). The small sample of migratory birds radio-tracked in that study suggested that males migrated to post-breeding areas located at farther distances from the lek than females (males, 7–20 km; females, 2–15 km). However, up to date no study has investigated in this species the migration patterns of both sexes in the same population with adequate sample sizes of marked birds. The results presented here are based on a radiotracking study of a large sample of marked birds. We aimed to examine whether Great bustards fulfil the main predictions of the various hypotheses posed to explain differential migration between sexes or sexual segregation. Considering the extreme SSD, strong sexual selection between males and marked sexual segregation in this species (Glutz et al. 1973; Cramp & Simmons 1980; own unpubl. data), one should expect also clear sexual differences in their migration and distribution patterns in the non-breeding season. Specifically, we tested if males spent the winter closer to the breeding areas than females (body size hypothesis), if males arrived earlier at the leks (arrival-time/sexual

selection hypothesis), and if females were forced to migrate further (behavioural dominance hypothesis). We also discuss whether spatial segregation between males and females during the non-breeding season could be explained by sex differences in role specialization during reproduction, or by differential tolerance to ecological factors such as temperatures (weather sensitivity hypothesis).

Methods

Study Area

The study was carried out in central Spain (see Fig. 1). We studied the migratory behaviour of Great bustards breeding in Madrid province, which holds approx. 1400 birds (for details see Alonso et al. 2003). Great bustards live there in open, flat to gently undulated areas with an average altitude of 650 m a.s.l. The land is mostly cultivated with cereal (mainly wheat and barley). Some minor crops are legumes, olive trees and vineyards. The Mediterranean climate of the area is characterized by dry, hot summers and cold winters with moderate rainfall (approx. 500 mm/yr). During the last decades, a marked development of urbanizations and associated infrastructures has taken place around the capital city of Madrid, which is causing a decrease and fragmentation of the habitat suitable for the species (Alonso et al. 2004b; Palacín et al. 2004).

Capturing and Tracking Birds

Between Jan. and Apr. 1995–2004, we captured 43 adult male and 43 adult female Great bustards at their leks using rocket nets. Another 22 young males and 25 young females were captured in the second half of Jul., when they were 3–10 wk old and still dependent on their mothers. Each bird was fitted with a harness-mounted backpack radio-transmitter (Kenward 1980) using Teflon – only in adults marked in the first 2 yr – or elastic band as harness material to allow the harness to expand as the young grew. The transmitters (Biotrack Ltd., Dorset, UK) were TW3 2× AA units (60 g), which we used to tag juveniles and adult females, or TW3 3× AA units (95 g), which we used to tag adult males. The total weight of transmitter plus harness did not exceed the recommended limit of 3–5% of the bird's weight (Kenward 2001). In addition, juveniles of both sexes and adult females were provided with patagial tags. The tags were of PVC (Gravoply),

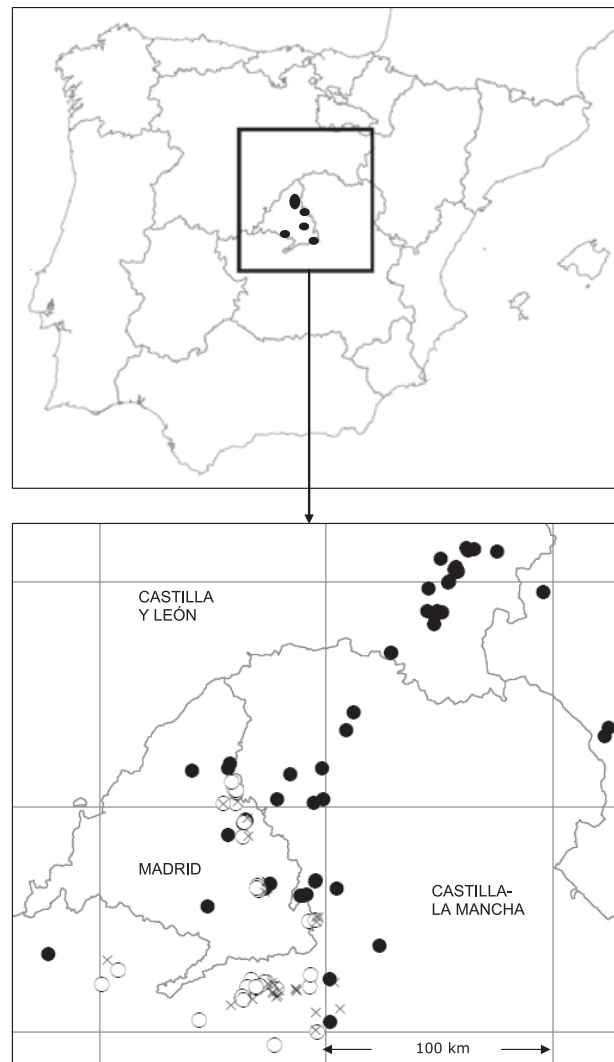


Fig. 1: Map of the study area showing the breeding sites (black areas in small square within the Iberian Peninsula, above) and the distribution of the post-breeding areas of migratory females (white circles) and males (black circles, first post-breeding areas; crosses, second post-breeding areas) (bottom square).

70 × 65 mm large and 1.5 mm thick. Each tag had a different design to allow visual identification with telescope. The tags were attached to the wing patagium using special pliers (Allflex). The total weight of tag plus rivet was approx. 12 g. Adult males were provided with dorsal tags of PVC (70 × 65 mm large and 3 mm thick) glued to the backpack transmitters. Wing or dorsal tags also enabled location of marked birds after transmitter batteries were exhausted (battery life was 4 yr in the 2× AA battery transmitters used for juveniles and adult females, and up to 6 yr in the 3× AA model used in most adult males). We

did not observe any harm in the plumage or behavioural alteration of the birds as a result of marking. We located all radio-tagged individuals (65 adult males and 68 adult females in total, including the birds caught as juveniles) by triangulation (using TR2 receivers-TS1 scanners from Telonics, Mesa, USA) and subsequent visual observation with 20–60× telescopes between one and four times per month. The location of each bird was determined with a GPS receiver (Garmin 12) and a maximum error of 100 m. In the few cases, when a bird was located through radio but not contacted visually its position was determined through triangulation of two or more bearings taken from distant vantage points (White & Garrot 1990). When a marked bird was not found from the ground, we used small aeroplanes (E-24 Bonanza, Beechcraft). During this study, we have spent >1000 flight hours searching for birds over central Spain. Aerial tracking enabled us to obtain breeding and post-breeding locations of all marked birds, thus avoiding the bias derived from emigration outside the study area in dispersal and migration studies (see Koenig et al. 1996). Each bird was radio-tracked for an average 3.7 (range 2–6) consecutive years. In total, we obtained 12 929 locations of our marked birds (13.7 locations per bird and year).

Data Analyses

For each bird, we calculated the activity centre for its *breeding area* (observations between Apr. and mid May) and *post-breeding area* (rest of the year, once the bird had abandoned the breeding area; for some males we defined *first* and *second post-breeding areas*, used respectively in summer and autumn–winter, see below). We classified a bird as migratory if at any time during the non-breeding season it used a post-breeding home range (minimum convex polygon of its locations; Mohr 1947), that did not overlap with its home range during the breeding season (usually mid Mar. to mid May in males, Apr. to Aug. in females). All other birds were considered sedentary. The minimum convex polygon was calculated using ARCVIEW 9.1 (ESRI 2005) and the software extension Hawth Tools (Beyer 2004). We also calculated the *outward migration date* (mean of the last observation at the breeding area and the first at the post-breeding area) and the *return migration date* (mean of the last observation at the post-breeding area and the first at the breeding area in spring). To calculate these migration dates and the activity centre of the breeding and post-breeding

locations of our marked birds, we selected for each individual the year with more locations. This resulted in 19.3 (± 7.2) locations per bird and year (2568 locations in total). Before, we had checked that there were no significant differences in the sites used by individual birds on different years (Great bustards are very faithful to their breeding and post-breeding areas, Alonso et al. 2000; Morales et al. 2000; Palacín 2007), and departure dates did not differ between years (Kruskal–Wallis test, $H_4 = 2.38$, $p > 0.1$ in males, $H_4 = 3.75$, $p > 0.1$ in females). We estimated the interannual fidelity to breeding and post-breeding areas as the percentage of birds using the same areas in consecutive years. We considered annual breeding or post-breeding areas (minimum convex polygons containing all locations for each season and year) to be the same if they overlapped. The proportions of birds migrating and remaining sedentary were compared with chi-squared test. Sex differences in latitude, altitude and distance between breeding and post-breeding areas, and migration dates were calculated with Mann–Whitney U-tests. The preferred migration direction was established after performing a Rayleigh test of uniformity and sex differences were tested with the Watson–Williams F-test. We set the significance level at $p = 0.05$. The software SPSS 14 (SPSS 1999) was used for all statistical analyses, except those related to migration directions, which were analysed with ORIANA software (Kovach Computing Services 2004).

Results

Sex Differences in Migration Tendency

Of the total sample of 65 males radio-tracked, only eight behaved as sedentary individuals, remaining at their breeding areas all the year round. All other males (86% of the 65 males) abandoned the leks after the mating season to spend either the summer or the summer and winter at post-breeding areas. The proportion of migratory females was significantly lower than that of males (56% of the 68 females radio-tracked, chi-square test: $\chi^2 = 18.50$, $df = 1$, $p < 0.001$). Thirty (54%) of the migratory males (46% of all males including sedentary ones) used two different post-breeding areas, the first in summer and the second in autumn–winter. All migratory females visited only one post-breeding area in autumn–winter, which practically coincided geographically with the second post-breeding area used by males (Fig. 1).

Location and Altitude of Post-Breeding Areas with Respect to Breeding Areas

The preferred outward migration direction to the first post-breeding area of males was 57° northeast (Rayleigh test of uniformity: $p < 0.001$), significantly different from that preferred by females (180°, Rayleigh test, $p < 0.001$; Table 1, see also Fig. 1). The distances between breeding and post-breeding areas of females ($\bar{x} = 49.8$ km, range 10–110) were shorter than those between breeding areas and the first post-breeding areas of males ($\bar{x} = 82.2$ km, range 8–172) (Table 1, Fig. 2). The mean latitude also differed between sexes (Table 1). The mean altitude of the first post-breeding areas of males was nearly 200 m higher than that of females (Table 1, range for males, 590–1184 m; for females, 493–794 m). However, sexual differences in migration direction, distance and latitude disappeared when we compared the post-breeding areas of females with the second post-breeding areas (autumn–winter areas) of the 30 males which used two post-breeding areas (Table 1). The second post-breeding areas of males were only slightly higher in altitude (31 m) than the post-breeding areas of females.

Migration Dates

Males started the outward migration between 10 May and 13 Jun. ($\bar{x} = 29$ th May, Julian date = 149, Table 1). Females abandoned the breeding areas four to five mo later, between 7 Sep. and 30 Dec. ($\bar{x} = 10$ th Nov., Julian date = 314). The sex difference in mean outward migration date was highly significant (Fig. 3 and Table 1). Males also returned to their breeding areas significantly earlier than

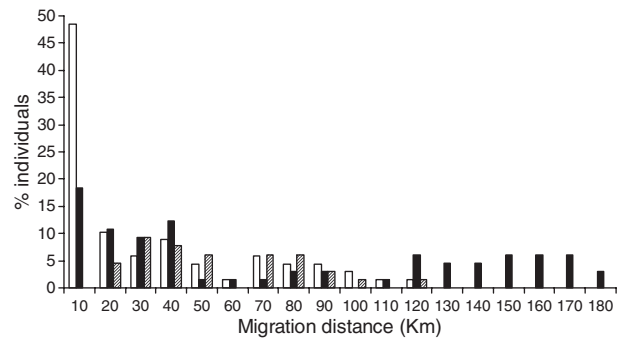


Fig. 2: Migration distances in male (black bars, distances to first post-breeding areas; hatched bars, distances to second post-breeding areas) and female (white bars) Great bustards in central Spain. Sedentary individuals are included in the first column; total sample sizes: $n = 65$ males, 68 females.

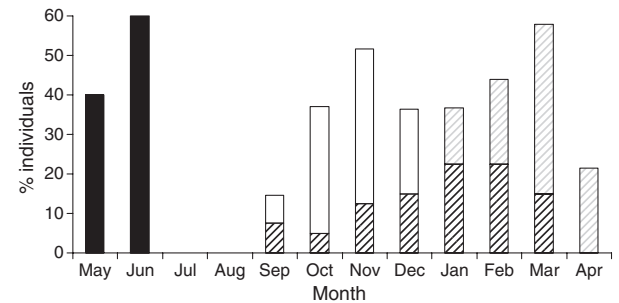


Fig. 3: Timing of migration: monthly frequency distribution of departures and returns from/to the breeding area by sex. Black bars, males' departures; white bars, females' departures; black-hatched bars, males' returns; and grey-hatched bars, females' returns.

females (mean for males: 17th Dec., SD = 61 d, range 2 Sep. to 25 Mar.; mean for females: 7th Mar., SD = 28 d, range 18 Jan. to 18 Apr.; Mann–Whitney

Table 1: Differences between post-breeding areas of females and first and second post-breeding areas of males. Departures and arrival dates refer to the lek, except in the case of the second post-breeding area of males, where the departure date is when males left the first post-breeding area

| | Females | | | Males 1st post-breeding area | | | Sex difference | | Males 2nd post-breeding area | | | Sex difference | |
|----------------------------------|-----------|------|----|------------------------------|------|----|-------------------------|--------|------------------------------|------|----|-------------------------|--------|
| | \bar{x} | SD | n | \bar{x} | SD | n | Test value ^a | p | \bar{x} | SD | n | Test value ^a | p |
| Direction (degrees) ^b | 180 | 67 | 35 | 57 | 48 | 56 | 77.29 | <0.001 | 168 | 54 | 30 | 1.30 | 0.258 |
| Distance (km) | 49.8 | 29.5 | 35 | 82.2 | 57.2 | 56 | 2.24 | 0.025 | 50 | 27.2 | 30 | 0.17 | 0.86 |
| Latitude (degrees) | 40.55 | 0.34 | 35 | 40.90 | 0.59 | 56 | 5.55 | <0.001 | 40.09 | 0.22 | 30 | -0.93 | 0.350 |
| Altitude (m) | 708 | 71 | 35 | 895 | 136 | 56 | 5.95 | <0.001 | 739 | 67 | 30 | 2.32 | 0.019 |
| Departure date ^c | 314 | 29 | 28 | 149 | 8 | 32 | 6.63 | <0.001 | 277 | 26 | 18 | 3.57 | <0.001 |
| Arrival date ^c | 66 | 29 | 28 | 279 | 23 | 10 | 4.64 | <0.001 | 27 | 29 | 18 | 3.81 | <0.001 |

^aThe tests used were Watson–Williams F for direction and Mann–Whitney Z for distance, latitude, altitude and dates.

^bOrientation of the post-breeding area with respect to the breeding area.

^cJulian date.

U-test: $U = 82.5$, $N_1 = N_2 = 28$, $p < 0.001$, Fig. 3). Males using two post-breeding areas left the first area on average on 4 Oct., 38 d before females left the breeding areas, and arrived to the breeding areas also significantly earlier than females (Table 1). However, there were no sex differences in the average duration of stay at autumn–winter areas (mean stay of males at second post-breeding areas = 114 d, $SD = 34$, mean stay of females at wintering areas = 117 d, $SD = 34$; Mann–Whitney U-test: $U = 230.5$, $N_1 = 28$, $N_2 = 18$, $p = 0.628$).

Fidelity to Migration Pattern and Post-Breeding Area

Only one of the 48 males which were tracked during two or more years changed its behaviour from migratory in 2 yr to sedentary in the third year. This adult bird suffered from intestinal parasitism by the nematode *Heterakis isolonche* and died in Sep., only 14 wk after deciding not to start its outward migration that year. All other males were either sedentary or migratory during the years they were studied. Most of these males (94%) showed a remarkable site fidelity to their post-breeding areas. As for the 48 females for which we could accurately establish their wintering area in two or more years, 79% showed the same behaviour year after year. The remaining 21% changed at least 1 yr their migratory pattern. These changes were significantly associated to the breeding success, as shown by a sample of 13 females with different breeding success in consecutive years. Eight of these females did not change their migratory pattern (six were sedentary, two migratory). The other five changed from migratory to sedentary when they had dependent young. Thus, in years when a migratory female had successfully reared a young there was a higher probability that she would remain at the breeding area through the autumn–winter (Fisher's exact probability test: $p = 0.021$). Most migratory females (88%) showed fidelity to their wintering areas.

Discussion

Our results show that the Great bustard is a differential migrant by sex in central Spain and confirm the partial migration pattern in this species. We found four main differences between males and females. First, the proportion of migratory males was higher than that of migratory females. Second, males abandoned the leks immediately after the mating season was over, whereas females remained there for another 3–7 mo. Third, about half the migratory

males used two different post-breeding areas, the first during summer and the second in autumn–winter, whereas migratory females used only one during autumn–winter. And fourth, males returned to the breeding areas earlier than females.

The first sexual difference refers to the proportion of migratory individuals. Both sexes showed a partial migration pattern, in agreement with the findings from previous studies in other populations in Spain (Alonso et al. 2000; Morales et al. 2000; Palacín 2007), which suggests that partial migration may be the norm in this species, as it is also in most bird species (Lundberg 1988; Cristol et al. 1999; Berthold 2001). In contrast to central Europe, Russia and Mongolia, where females tend to migrate in higher proportion than males (Streich et al. 2006; H. Watzke, cited in Streich et al. 2006), we found that the proportion of migratory males was much higher than that of migratory females. However, excluding males migrating northwards to summering areas and selecting only those males that used an autumn–wintering area (30 males that used a second post-breeding area plus the four southernmost black dots in Fig. 1), the proportion of wintering males (34 of 65, or 52%) was very similar to that of wintering females (51%). The sexual difference in the proportion of migratory birds found in this study is therefore attributable to the fact that in Spain males had a summering area and females did not.

The proportions of migrants vary not only at a large geographical scale through the Palaearctic distribution range of the species, but also between regions in Spain (Alonso et al. 2000; Morales et al. 2000; Palacín 2007), probably because each population is adapted to local ecological conditions. Eastern European and Asian Great bustards are obligate migrants in winter (Glutz et al. 1973; Watzke et al. 2001; Watzke 2007), and some populations in central Europe are facultative migrants in response to extreme weather conditions (Dornbusch 1981; Block 1996; Streich et al. 2006).

The second sexual difference, namely the earlier departure dates in males, can be explained by the differential investment of both sexes in reproduction and is thus consistent with the specialization hypothesis of sexual segregation. In several bird species it has been observed that generally the non-caring parent departs the breeding grounds and initiates migration first (Myers 1981b; Jehl 1990; Owen & Black 1990; Berthold 2001; Ydenberg et al. 2005). Like in these species, male Great bustards are free to abandon the breeding areas as soon as the mating season has finished because they do not take part in

incubation or chick rearing. However, while it is reasonable to assume that females with dependent young would be retained at the breeding areas at least until full flight ability of their offspring is developed, we cannot find an explanation why non-breeding females should be prevented from migrating to summering areas, if these are assumed to be equally beneficial for females as for males. Our results show that the winter migratory behaviour of females is rather flexible, because a significant proportion of migratory females changed to sedentary in years when they had dependent young. Thus, females could have also developed facultative migration behaviour in summer. For this reason, we suggest that males probably obtain higher benefits than females from spending the summer at summering areas (see discussion of third sexual difference below). An early abandonment of the breeding sites by males once most of the females have been mated has also been reported for certain mammal species (Boyd et al. 1998). The departures of Great bustard males were concentrated within a relatively short period (most departures happened in the last week of May and first of Jun.), and the mean departure date (29 May) was a few days before the mean estimated hatching date (3 Jun., own unpubl. data). Mean male departure and hatching dates were positively, though not significantly, correlated in the series of 5 yr of this study (Palacín 2007). This remarkable correspondence suggests that males have adjusted their departures to the end of the period when females may be receptive to late copulations, thus ensuring that they do not leave any unfertilized females, and that the females fertilized by them will not probably copulate with other males.

The third sexual difference was the use of summering areas only by males. Most of these areas were located to northeast and a high proportion far away from the breeding areas (see Fig. 1). All males using these distant areas abandoned them in late Sep. to early Oct., just after the hottest summer months and some returned directly to the breeding areas, whereas others went to their second post-breeding area where they spent the autumn–winter. This second, wintering area practically coincided with the wintering area used by the females, a result that did not support the behavioural dominance hypothesis, which predicts that intraspecific competition forces individuals of the subordinate age class or sex to migrate further. There are two possible explanations for the exclusive summer migrations of Great bustard males. The first is the differential investment of both sexes in reproduction discussed

in the paragraph above. A second likely reason is related to the milder temperatures at these places, because they are located at higher altitudes and latitudes than the breeding areas (for more details see Palacín 2007). Males probably tolerate less than females the very hot midday temperatures (approx. 40°C) typical of central Spain in Jul. to Aug., because of their smaller surface area to volume ratio, which increases their heat retention and metabolic efficiency (Kendeigh 1944). For the same reason, males produce almost double amount of metabolic heat than females (Calder & King 1974), and have proportionally more difficulties in dissipating body heat and balancing their water budget (Calder & King 1974; Walsberg & King 1978; Searcy 1980; Dawson & O'Connor 1995). The summering behaviour of male Great bustards thus represents an example of sexual segregation through differential migration that is consistent with the weather sensitivity hypothesis, as in some sexually dimorphic mammals (Jackes 1973; Young & Isbell 1991; Conradt et al. 2000).

Finally, males returned to the breeding areas significantly earlier than females, and many spent the winter already at the lek sites. The sex difference in return date was most obvious in males using only one post-breeding area (almost 5 mo before the females), but also significant in males using the same wintering area as females. Our results were consistent with the basic requirement of the arrival-time/sexual selection hypothesis, namely that early arrival is advantageous in intrasexual competition among males. An earlier return of males to the breeding areas has been reported for many bird species (Myers 1981b; Gauthreaux 1982; Ketterson & Nolan 1983; Butler et al. 1987; Chandler & Mulvihill 1990; Spina et al. 1994; Swanson et al. 1999; Morbey & Ydenberg 2001; Ydenberg et al. 2005), and usually attributed to the importance of early arrival in acquiring good breeding territories (Myers 1981a; Gauthreaux 1982; Kokko 1999) or maximizing the mating opportunities (Morbey & Ydenberg 2001). In contrast to birds that form pairs, in many polygynous species the intensity of mating competition in males is related to the amount of SSD (Webster 1992; Székely et al. 2000; Dunn et al. 2001). Recently, this relationship has also been shown for bustards (Raihani et al. 2006). As for the relationship between sexual selection, SSD and migration dates, recent studies found that species showing higher SSD tend to arrive earlier at the breeding areas in spring (Rubolini et al. 2005), and tend to show higher differences between males and females in

arrival dates (Kissner et al. 2003). These authors proposed that sex differences in both body size and timing of migration are products of the same sexual selection pressure, the intensity of mating competition. Our results on Great bustards are consistent with these ideas. The Great bustard is indeed the bird species showing the highest SSD, the differences in return migration dates between males and females are extreme (males arrive at the breeding areas on average approx. 2.5 mo earlier), and the intensity of intrasexual competition between males is particularly high in this species, with a marked phase of fightings and status-signalling displays at the lek between Jan. and Mar., before females are arrived (Hidalgo & Carranza 1990, Magaña 2007; own unpubl. data). In line with Kissner et al. (2003) and Rubolini et al. (2005), we suggest that the intense sexual selection in male Great bustards has favoured both, an extreme SSD and a marked sexual difference in spring migration dates (mate opportunity hypothesis, Morbey & Ydenberg 2001). If the sex differences in arrival dates had evolved because of the differential susceptibility of both sexes to harsh conditions found at the breeding areas in spring (susceptibility hypothesis, Morbey & Ydenberg 2001; see also arrival-time/sexual selection hypothesis, Myers 1981a), we should expect higher protandry in Great bustard males in northern European latitudes (males tend to arrive only a few days earlier than females in the long-distance migratory Russian population, M. L. Oparin, pers. comm.), than in Mediterranean latitudes (on average approx. 2.5 mo, this study), where weather and food conditions are much milder.

In conclusion, our findings add the Great bustard to the list of documented differential migrants by sex. The main sexual differences found were the much earlier outward migration dates of males from the breeding areas, and their use of summering areas, a behaviour that is absent in females. These differences are probably caused by the differential investment of males and females in reproduction and by their differential sensitivity to weather, two cases of the more general specialization hypothesis proposed to explain the general patterns of sexual segregation in birds. A strong sexual selection is probably the ultimate cause underlying these sexual differences in Great bustard migration patterns.

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