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# Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*

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Factors responsible for individual variation in partial migration patterns are poorly known, and identifying possible causes of these changes is essential for understanding the flexibility in migratory behavior. Analyzing 190 life histories of great bustards *Otis tarda* radio-tagged in central Spain, we investigated the changes in migratory tendency across lifetime in this long-lived bird, and how migratory flexibility is related to individual condition. In females migratory behavior was not fixed individually. For every age class there was a fraction of ca 15–30% of females that changed their migratory pattern between consecutive years. Migrant females tended to remain sedentary in years when they had dependent young to attend. These findings show that the female migratory tendency is a behaviorally flexible, condition-dependent trait. Immature females usually acquired their migratory behavior by learning from the mother in their first winter or by social transmission from other migratory females in their second winter. As for immature males, their summer migratory behavior was not related to mother–offspring transmission, but learned from adult males. We found that their age-related increase in migratory tendency was associated to a greater integration in flocks of migrant adult males. These results show that within the partial migration system, cultural transmission mechanisms, either mediated by kin or not, and individual condition, may contribute to shape the migratory tendency. Our study reinforces the view that the migratory behavior is an evolutionary complex trait conditioned by the interaction of individual, social and environmental factors. Particularly in long-lived species with extended parental care, the inherited migration program may be shaped by mother–offspring and social transmission of migratory patterns.

Partial migration occurs when not all individuals of a breeding population move to a non-breeding area (Gauthreaux 1982). This system represents an evolutionary transition between residency and complete migration (Berthold 1999, 2001), and modern reviews have revealed that it is much more widespread than previously reported and may be considered as the norm amongst migratory birds (Cristol et al. 1999, Berthold 2001, Newton 2008). When partial migration is fixed at the individual level it has been termed 'obligate', to distinguish it from 'facultative' partial migration, used to describe situations in which individuals may change their migratory tendency over their lifetime depending on certain conditions (Terrill and Able 1988). In obligate partial migrants, an individual's migratory behavior is primarily determined by the genetic make-up of its parents (Lundberg 1988) and thus, age- and sex-related biases in migratory tendency are in principle not expected. In facultative partial migrants, migratory decisions are subject to tradeoffs influenced by environmental factors and individual condition (Lundberg 1985, 1987, Smith and Nilsson 1987, Adriaensen and Dhondt 1990, Schwabl and Silverin 1990, reviewed in Newton 2008).

Although various hypotheses have been proposed to explain partial migration (Ketterson and Nolan 1976, Cristol et al. 1999, Newton 2008), the selective pressures that favour this system and the proximate mechanisms which affect migratory tendency remain largely unresolved (Ogonowski and Conway 2009). Factors responsible for individual variation in the timing of migration are poorly known, and identifying possible causes of these changes is essential for understanding the flexibility in migratory behavior (Bêty et al. 2004, van Noordwijk et al. 2006, Pulido 2007, Brodersen et al. 2008, Jonker et al. 2010, Marques et al. 2010).

In short-lived species such as many small passerines, experimental studies have shown that among-population differences in migratory behavior are mostly genetically determined (Berthold 1996, 2001, Pulido 2007). However, other studies have revealed that non-genetic variance components, such as environmental factors, or individual condition and experience, may also be important (Pulido and Berthold 2003, van Noordwijk et al. 2006, Pulido 2007, Ogonowski and Conway 2009). In contrast, in several long-lived species with extended parental care periods such as some geese, swans, storks or cranes, migratory behavior seems to be transmitted from parents to offspring, or migratory flocks may be guided by the oldest, most experienced individuals, rather than merely inherited (e.g. common cranes *Grus grus*, Alonso et al. 1984; sandhill cranes *Grus canadensis*, Drewien et al. 1999; greater snow geese *Anser caeruslescens*, Bêty et al. 2004). Experimental work involving translocation, cross-fostering or training captive-bred juveniles has shown that migration routes can be artificially modified (Ellis et al. 2003), and migratory behavior induced in individuals from non migratory populations (reviewed in Newton 2008). This flexibility in migratory behavior, and the phenomenon of cultural transmission of migratory traits have been poorly studied. In a recent review, Pulido (2007) concluded that in long-lived species we should expect different dynamics in phenotypic changes in migration than in the classical model species. He claimed future research should include new species and study areas different from the small passerines studied in earlier years, to fully understand adaptations in migration and their evolutionary change.

In the present study we explore partial migration patterns in a long-lived species with extended parental care, the great bustard. This species shows a highy variable migratory behavior across populations: Asian and Russian populations are obligate winter migrants due to snow and freezing temperatures at their breeding areas, as recently confirmed through satellite tracking (Watzke 2007, Kessler 2010); central European populations are facultative winter migrants in response to extreme weather conditions in some years (Streich et al. 2006); and Iberian populations are partial migrants, both in winter and summer, and differential migrants by sex, with variable proportions of both sexes that migrate following sex-specific patterns (Alonso et al. 2000, 2001, Morales et al. 2000, Palacín 2007). Our aims in this study were twofold: first, we investigate the development of partial migratory tendencies in young and immature individuals of both sexes, under the hypothesis that these traits are learned from the mother or from adult conspecifics. The long maternal dependence period of young great bustards (6–12 months), and their dispersal behavior, suggest that the migratory patterns of chicks could be based on movements performed during the period of maternal dependence (Alonso et al. 1998, Morales 1999, Martín 2001, Martín et al. 2008). Alternatively, the marked gregariousness of great bustards might favour social transmission of the migratory patterns. Second, we hypothesize that one of the main factors conditioning the migratory tendency of adult females would be their maternal care duties. The low productivity of this species, and the high cost in which breeding females incur (Alonso et al. 1998, 2003, Martín 2001, Magaña 2007) suggest that rearing offspring might be an important factor potentially affecting the migratory behavior of families. Moreover, the early development of an extreme sexual size dimorphism in this species (Alonso et al. 2009a) might determine differences in the migratory behavior of families with offspring of different sex. Our study is based on continuous monitoring of a large sample of great bustards radio-tracked through several complete annual cycles from their juvenile to adult age. Recent reviews have claimed the need for studies with marked individuals in the wild, to provide convincing evidence for the existence of facultative responses to variable conditions, and for the prevalence of culturally transmitted patterns over the inherited migration program in some species (Pulido 2007, Newton 2008).

# Methods

## Study area and species

The study was carried out in central Spain. Great bustards were marked at the breeding sites in Madrid province and surroundings (Fig. 1). The Mediterranean climate of this area is characterized by dry, hot summers and cold winters with moderate rainfall (ca 500 mm yr$^{-1}$). Breeding sites are located at 530-785 m a.s.l. The habitat used by great bustards is mainly flat to slightly undulated low-intensity, dry cereal farmland with interspersed vineyards, olive groves and fields planted with legumes in some areas. Spain holds ca 60% of the species' world population (Palacín and Alonso 2008) and Madrid region holds ca 1600 great bustards distributed in 14 leks. Approximately 1100 of these birds (9 leks) are found in the north-eastern part of the province, in a Special Protection Area for Birds (SPA) 139 'Estepas Cerealistas de los Ríos Jarama y Henares' (40°45′N, 3°30′E, 331 km$^2$), the rest in smaller areas south and southeast of the province (Alonso et al. 2003).

The great bustard is a long-lived bird (up to 14 yr, unpubl.), lekking species in which strong sexual selection has favoured an extreme sexual size dimorphism, with males weighing 9–13 kg and females 4–5 kg (Alonso et al. 2009a). Males and females occur as a rule in separate flocks. After mating in April, females nest in May and take over all breeding duties. Offspring have a long maternal dependence period, young males being independent at an earlier age

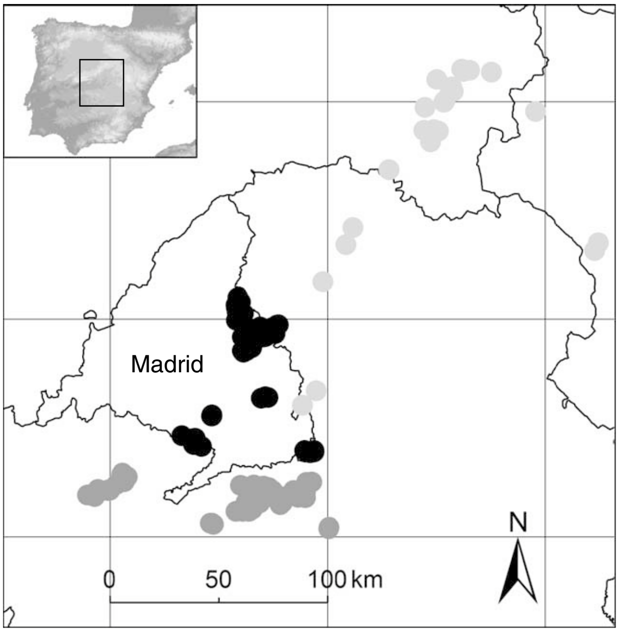

Figure 1. Location of the study area in the Iberian Peninsula showing the breeding sites of the studied population (black areas), the wintering sites of migratory females (dark shaded areas) and the summering sites of migratory males (light shaded areas).

(6–12 months) than young females (8–15 months; Alonso et al. 1998, Martín 2001). The productivity is low in this species, with an average 0.11 young birds survived per female up to September in our study area (unpubl.). In the study area the species behaves as a partial migrant and has a differential migration pattern by sex (Palacín et al. 2009). The proportion of migrants is higher in males than females. Most males abandon the lek-site between early May and late June, and migrate to summering areas located up to 180 km northwards, whereas females remain at the breeding areas for another 3–7 months, and ca 50% migrate in November to wintering areas located up to 110 km southwards. Migrant males use two different post-breeding areas (summer and autumn), and migrant females use one (winter). Males return to the lek-sites earlier (September–March) than females (January–April).

### Capturing and tracking birds

We used a total of 190 life histories of 81 adults (38 males and 53 females) captured between January and April 1995–2004, and 109 juveniles (62 males and 47 females) captured in July 1995–2006, when they were 1–3 months old and still dependent on their mothers. The sex of young birds was determined by size dimorphism in late summer. All birds were marked with Biotrack radio-transmitters and located at least once per month throughout their lives using Telonics TR2-TS1 telemetry receivers. The total weight of transmitter plus harness did not exceed the recommended limit of 5% of the bird's weight (Kenward 2001). In addition, juveniles of both sexes and adult females were provided with wing-tags, and adult males with dorsal tags. The tags were of PVC (Gravoply), 70 × 65 mm large and 1.5 mm thick. Each tag had a different design to allow visual identification with telescope. The wing-tags were attached to the wing patagium using special pliers (Allflex). The total weight of wing-tag plus rivet was approximately 12 g. Dorsal tags (same size, 3 mm thick) were glued in a vertical position on the top of the backpack transmitters, showing the same symbol to both sides. Wing or dorsal tags also enabled location of marked birds after transmitter batteries were exhausted (battery life was 4 yr in the 2 × AA units, and up to 6 yr in the 3 × AA units). We did not observe any harm in the plumage or behavioral alteration of the birds as a result of marking.

We located all radio-tagged individuals by triangulation 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 and Garrot 1990). When a marked bird was not found from the ground, we used aeroplanes. 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 migration outside the study area in dispersal and migration studies (Koenig et al. 1996). Each bird was tracked for an average $3.8 \pm 2.3$ consecutive years. In total, we used in this study 8926 locations of our marked birds. The recorded range comprising all sightings of marked birds extends from male summering areas located 180 km north of Madrid, to the southern limit of the wintering area, 110 km south of the province (Fig. 1).

Families integrated in female flocks by October, long before winter migration started. From that moment on it was difficult to identify the mothers of marked juveniles, except in the few cases when mothers were also marked. This made it hard to recognize the family as a unit, which was only possible when offspring clearly followed their mother and there was some interaction among them, e.g. when a young bird received an occasional feeding from her, or when the whole family remained at a certain distance, or temporally isolated, from the rest of the flock. These cases were unequivocally recorded as families. Within winter flocks, other associations of one or two marked chicks with an adult female where the latter assumed a clearly leading or vigilant role were also interpreted as families.

### Data analyses

An individual was considered migrant when it performed a regular seasonal movement between separate breeding and post-breeding areas (Newton 2008). For each bird, we determine the annual breeding and post breeding area, defined as the minimum convex polygon (Mohr 1947) encompassing all locations during the breeding season (observations from mid March–mid May in males, April–August in females) and post breeding area (rest of the year), respectively. The minimum convex polygon was calculated using Arcview 9.1 (ESRI) and the software extension Hawth's tools (Beyer 2004). We estimated the inter-annual 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 to be the same across years if the minimum convex polygons containing all locations for each season and year overlapped. We defined migratory tendency of the population as its percentage of migrant birds. The proportions of birds migrating and remaining sedentary were compared with chi-squared test and Fisher's exact probability test. Sex and age differences in distance between breeding and post-breeding areas were assessed with ANOVA test after log-transformation of the data. We set the significance level at $p = 0.05$. The software SPSS 15 (SPSS 2006) was used for all statistical analyses.

## Results

### Consistency of migratory patterns in females

To determine whether female migratory patterns varied among age classes, we examined winter migratory tendency and migration distance of 47 juvenile females through their first three years of life, and 43 adult females. Neither tendency nor distance changed with age (respectively, $\chi^2 = 1.57$, $p = 0.666$, $DF = 3$; ANOVA, $F_{3,85} = 0.80$, $p = 0.496$; Table 1).

In all age classes, most females repeated the migratory pattern (sedentary or migratory) across two consecutive

Table 1. Effect of age on winter migratory tendency and migration distance of female great bustards in central Spain.

| | Age | | | |
|---|---|---|---|---|
| | 1st yr (n =47) | 2nd yr (n =43) | 3rd yr (n =35) | adults (n =43) |
| Percent migratory females | 47 | 58 | 60 | 51 |
| Migration distance (mean ±SD) | 45.1 ±34.6 | 50.4 ±36.3 | 35.3 ±25.9 | 48.9 ±30.0 |

winters (Fig. 2). The number of females that changed their pattern was higher in juveniles and immatures (respectively, 33 and 22–31% of the birds) than in adults (16%; $\chi^2 = 13.40$, $p = 0.004$, DF $= 3$; Fig. 2). Twenty-one percent of juvenile females remained sedentary in their first winter, when they were still dependent on their mother, but changed to migratory in their second winter, after becoming independent (Fig. 2).

## Effect of breeding success and offspring sex on the migratory pattern of females

No female abandoned her brood prior to migration from the breeding areas. We could unequivocally identify all members of migrant families in 13 cases (five families of mother and one female chick, six of mother and one male chick, one family of mother and two male chicks, and one of mother and one chick of each sex).

We found a strong significant association between changes in migratory tendency and breeding success ($p < 0.001$, Fisher's exact probability test; Fig. 3). Of 26 females that successfully reared offspring up to the date when migration started, eight changed their migratory pattern. These were all migrants, and the change was always from migratory to sedentary. This suggests that having dependent young forced most migrant females to remain sedentary that year. Comparing the migratory behavior of families with offspring of different sex, we did not find differences in migration tendency (34% in families with male chick, 47% with female chick, $\chi^2 = 1.87$, $p = 0.171$, DF $= 1$). However, families with male chick migrated significantly shorter distances than those with female chick (ANOVA, $F_{1,41} = 5.76$, $p = 0.034$; Fig. 4).

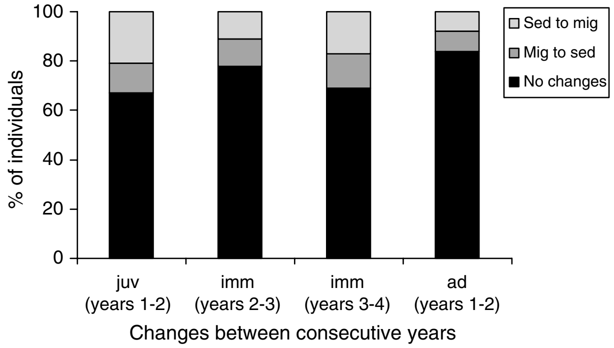

Figure 2. Effect of age on changes in migratory tendency of great bustard females across two consecutive winters. Sample sizes for bars from left to right: 43, 36, 19, 25.

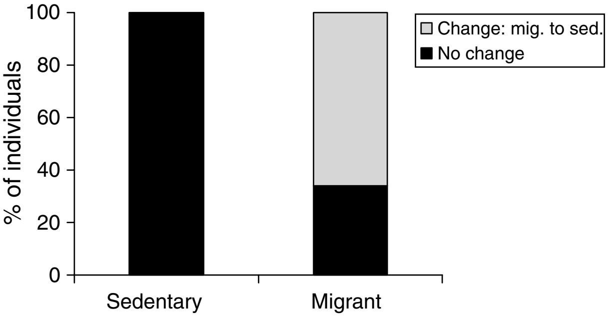

Figure 3. Changes in migratory tendency of successful breeding females across two winters. Sample sizes for bars from left to right: 14, 12.

## Consistency of migratory patterns in males

To explore the influence of age on the migratory patterns of males, we examined summer migratory tendency and migration distance of 52 immature and 38 adult males. The summer migratory tendency developed in males from their second year increased significantly with age ($\chi^2 = 8.68$, $p = 0.034$, DF $= 2$; Fig. 5). The distance travelled between breeding and summering areas also increased with age (2nd yr males: 51.9 km, SD $= 44.3$, $n = 34$; 3rd yr males: 60.7 km, SD $= 63.9$, $n = 34$; adult males: 94.7 km, SD $= 59.5$, $n = 38$; ANOVA $F_{2,100} = 6.05$ $p = 0.003$).

We found that the increase in migratory tendency with age was associated to a progressive integration of migrant

Figure 4. Differences in winter migratory distance (mean ±SE) between families with female and male offspring. Sample sizes: 22 females, 21 males.

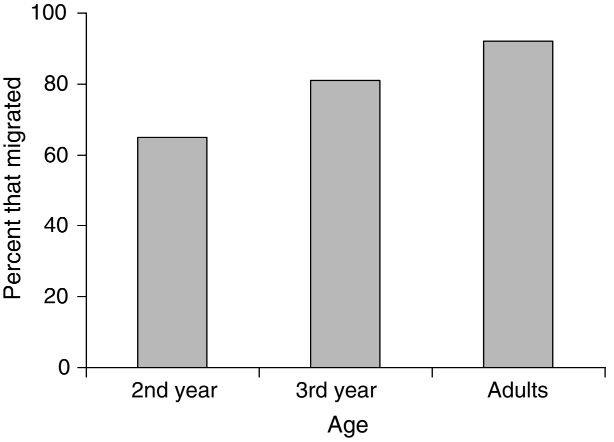

Figure 5. Effect of age on summer migratory tendency of male great bustards in central Spain. Sample sizes for bars from left to right: 52, 42, 38.

immatures in adult male flocks. During their second and third summers, most migrant immature males were already integrated in male flocks, whereas a major part of sedentary immature males were still included in female flocks (p = 0.001 for 2nd yr males, p = 0.01 for 3rd yr males, Fisher's exact probability test; Fig. 6).

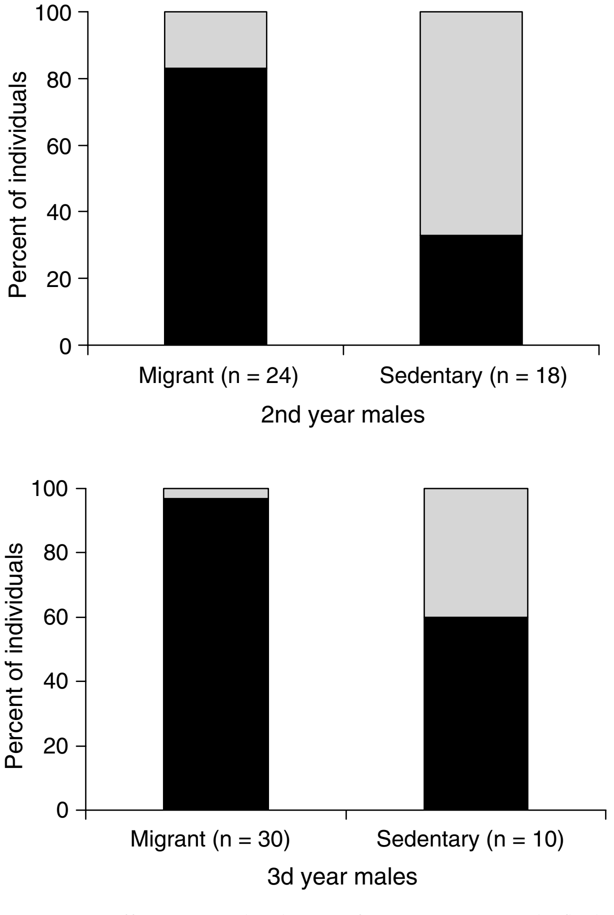

Figure 6. Differences in the degree of integration in male flocks (black colour) and female flocks (grey colour) between migrant and sedentary immature (2nd and 3rd yr) males.

## Discussion

Previous studies had shown that sedentary and migratory great bustards of both sexes coexisted in the same population, with a marked constancy in their migratory or sedentary patterns, and a remarkable site fidelity to post-breeding areas in consecutive years (Alonso et al. 2000, 2009b, Palacín et al. 2009). This suggested an obligate partial migration system with two genetically controlled strategies, migrant and resident, whose proportions would be adapted to local environmental conditions (Lundberg 1987, 1988, Berthold 1999, Newton 2008). In the present study we analysed the variation in migration tendency with age, and between consecutive years within individual birds. We concluded that mother–chick transmission mechanisms and individual condition contribute to shape the migratory tendency in great bustards, suggesting a more flexible, condition-dependent migratory behavior not previously described for this species.

Facultative partial migration dependent on food supply, social status or on different priorities related to age and sex (Lundberg 1985, 1987, Smith and Nilsson 1987, Adriaensen and Dhondt 1990, Schwabl and Silverin 1990, reviewed in Newton 2008). In this facultative system, coexisting resident and migrant individuals may not necessarily have equal pay-offs. Indeed, migrants have often been found to be less competitive, 'making the best of a bad job' (Lundberg 1987, 1988, Adriaensen and Dhondt 1990, Gillis et al. 2008). Moreover, in some species the same individual may change its migratory behavior over time, or the behavior of offspring may differ from that of their parents, providing evidence for a condition-dependent individual plasticity component in migratory behavior (Adriaensen and Dhondt 1990, Warkentin et al. 1990, Coppack et al. 2003, Morrissey et al. 2004, Ogonowski and Conway 2009).

In our study we found some evidences for such a condition-dependent migratory behavior in the great bustard. First, we observed changes in migratory tendency with age that were not consistent between sexes, and also differed from patterns found in most species. For example, in contrast to the lower migration tendency of adults compared to immatures predicted by one of the main hypotheses explaining partial migration (dominance hypothesis, Gauthreaux 1982), adult great bustard males were more likely to migrate to post-breeding areas than immatures. Other authors also found results contradicting this hypothesis, as well as the arrival-time and body size hypotheses (Boyle 2008, in white-ruffed manakins *Corapipo altera*; Jahn et al. 2010, in kingbirds *Tyrannus melancholicus*), and concluded that an individual's probability of migrating was associated with a more complex interaction of size, age and sex than predicted by any of these hypotheses. In the case of great bustards, where post-breeding migration represents a valuable adaptation exclusive of males to escape the summer heat of breeding areas (Alonso et al. 2009b), all males should be expected to migrate as soon as they become independent from their mothers. However, young males that feed at lower rates during the early maternal dependence period become independent later and integrate later into adult male flocks (Alonso et al. 1998). A slow development might therefore be the ultimate reason why some males remained up to their third year in female flocks. In fact, this is a quite unnatural situation, since great bustards show a strong sexual segregation, with males and females living normally in separate flocks. Since immature males adopt the migratory behavior of the flock in which they are integrated, if an immature male is able to join a group of migrant adult males he will most probably follow them and become a migrant. This happened in most cases with second year males. In contrast, most sedentary second year males had not yet abandoned the female flocks when males of that population started the summer migration. The prolonged attachment to females was probably the reason why these males remained sedentary. The number of immature males still associated to adult females obviously decreased as they grew older (from their second to third year), and consequently the proportion of migrant third year males was higher than that of second year males. The changes across age classes in male migratory tendency described here may thus be interpreted as a condition-dependent behavior, where only the more competitive immature males would be able to associate with adult males and migrate with them.

As for female great bustards, neither the overall migratory tendency nor the migration distance did change between age classes. This result is in line with our suggestion based on previous studies that for a given population, female migratory tendency and distance are constant, and probably adapted to local conditions. For example, the migratory tendency and distance found for females in central Spain clearly differs from those of females in NW Spain (Alonso et al. 2000, Palacín et al. 2009). The patterns found in Iberian populations also differ from the behavior described at other areas of the species' distribution range (Streich et al. 2006, Palacín 2007, Watzke 2007, Kessler 2010).

We also found changes in migratory behavior of individual birds between consecutive years. In spite of the constancy across age classes in female migratory tendency at the population level discussed above, our results show that the migratory behavior was not fixed at the individual level. For each age class there was always a fraction of ca 15–30% of females that changed their migratory pattern between consecutive years, either from sedentary to migratory or vice versa. This shows that, indeed, females were able to modify their behavior, which adds another variance component to the migratory tendency that is described here for the first time in this species. Among possible causes influencing the decision whether to migrate or not, we found a significant relationship with breeding success. Our results suggest that migrant females tended to remain sedentary in years when they had dependent young. The decision of a female to suppress migration may be related with a reduction of the risks associated to migratory displacements, which might affect offspring survival. The lower distance covered by migratory females with male offspring compared to those with female offspring supports this conclusion. The evolution of an extreme sexual size dimorphism in great bustards has prompted a fast development of juvenile males, and flying ability is less developed in males than in females of the same age (Alonso et al. 2009a). It thus seems reasonable to assume that the lower flying ability of young males may limit the migration capacity of families with male offspring. Supporting our interpretation of a female migratory tendency conditioned by their breeding success, we found that ca 8% of adult females changed from migratory to sedentary in consecutive years, with exactly the same amount doing the reverse change (Fig. 2). Since a female rarely breeds successfully on consecutive years (Alonso et al. 2000, Magaña 2007), these proportions could suggest that females doing the reverse change were those that had remained resident on the previous winter when they had dependent young. These findings provide evidence that the female migratory tendency, like that of males, is also a behaviorally plastic, condition-dependent trait in great bustards.

Our study showed that in all cases where we could unmistakably identify all members of migrant families, they migrate as a unit to the wintering area. We may therefore reasonably conclude that in great bustards, like in other species with extended parental care periods, the winter migratory route, and most likely the winter migratory tendency as well, is most probably learned from the mother, rather than purely inherited. Although previous results on the prolonged maternal care period in great bustards (Alonso et al. 1998, Martín 2001) indicated this would be the case, the evidence provided here is the first suggesting that some traits of the migratory behavior like route and timing may be culturally transmitted from mother to offspring. We cannot completely rule out the influence of a genetic component, since we were not able to analyze the heritability of the migratory tendency in the way done in other studies (Ogonowski and Conway 2009). This was due to our limited sample of families with all members tagged, as well as to the fact that in our strongly polygynous, lekking species the identities of fathers of our marked offspring were unknown.

Our results show that several intrinsic factors may shape the diversity of migration patterns within a species, which is in concordance with other recent studies using individually marked birds (Bêty et al. 2004, Boyle 2008, Ogonowski and Conway 2009, Jahn et al. 2010). Specifically concerning the influence of breeding success, previous radio-tracking studies with grouse species had shown that successful females of blue grouse *Dendragapus obscurus* left the breeding areas later than unsuccessful or nonbreeding females (Cade and Hoffman 1993). Similarly, much of the variability in timing of migration from breeding areas for females of greater prairie chicken *Tympanuchus cupido* was related to brood status (Schroeder and Braun 1993). Reed et al. (2003) obtained similar results to ours in greater snow geese *Anser caerulescens atlanticus*: most successfully breeding females suppressed the post-nesting moult migration.

Additional evidence that the migratory behavior is flexible in great bustards comes from the reintroduction project of this species into United Kingdom (Great Bustard Group 2010). The first successful release of Russian chicks translocated to Britain in 2005 showed that at least three birds migrated in winter to south (450–920 km), following the normal pattern of their original population (ca 1000 km between Saratov and Ucraine, Watzke 2007). However, birds released in the following years (2006–2009) did not apparently migrate, most staying with the few individuals that had returned or remained resident at the release site in previous years. This experiment would support that in spite of the prevalence of an inherited migratory tendency in young great bustards from a migratory population – even if they are separated from their mothers – social transmission from resident conspecifics may inhibit this migratory tendency. Another reintroduction trial with a related species, the little bustard *Tetrax tetrax*, also suggests a genetic component of the migratory behavior. Little bustards hatched in France from eggs collected in Spain remained sedentary in their first winter, in spite of the local population being migratory (Villers et al. 2010). However, the behavior of these birds in their second winter is still unknown. These two experiments suggest that migrant and sedentary phenotypes have a genetic basis in bustards, as has been shown for other birds and is assumed to be widespread across taxa (Berthold et al. 1992, Berthold and Pulido 1994). Since the tendency to migrate or remain sedentary can evolve over a relatively short period (Berthold et al. 1992, Berthold 2001), it has been suggested that genetic variations in the propensity to migrate should exist, even within sedentary populations (Pulido 2007).

In sum, immature females acquired their migratory behavior in two ways: a) by learning from the mother in their first winter migration, and b) by social transmission, when females migrated in their second winter for the first time, accompanying other migrant females. The summer migratory behavior of males was not associated to mother-offspring transmission, as it was developed after termination of the maternal dependence period. Migration was stimulated in immature males by adult male conspecifics. We conclude that: 1) the decision of great bustards to migrate is condition- and sex-dependent and 2) individual life-history strategies play a central role in understanding their migration patterns. Our results show that within the partial migration system of great bustards, family and cultural transmission mechanisms, and individual condition, may contribute to shape the migratory tendency resulting from the genetic polymorphism between migrants and residents. Overall, our study provides evidence of phenotypic plasticity and reinforces the view that migratory behavior is an evolutionary complex trait conditioned by the interaction of individual, social and environmental factors that vary between individuals and populations. Particularly in long-lived species with extended parental care the inherited migration program may be shaped by mother–offspring and social transmission of migratory patterns.

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