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Migration Patterns in Male Great Bustards (*Otis tarda*)

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The Great Bustard (*Otis tarda*) is distributed from Iberia and Morocco in the west to China in the east and has been considered sedentary in all but the northern and eastern parts of its range (Gewalt 1959, Glutz et al. 1973, Cramp and Simmons 1980). However, some studies have reported seasonal changes in population numbers in different areas in the Iberian Peninsula (Hidalgo and Carranza 1990, Alonso et al. 1995), suggesting that the species is a partial migrant (*sensu* Terrill and Able 1988) in this region.

We describe seasonal movements of marked adult male Great Bustards and discuss observed patterns in relation to the following questions: (1) Do migratory males display interannual fidelity to breeding and postbreeding areas? (2) Do males travel significantly farther than females in their seasonal movements? We also suggest several hypotheses that could explain patterns of partial and differential migration in male Great Bustards.

Methods.—Our study was carried out in the Wildlife Reserve of Villafáfila (41°50'N, 5°35'W; ca. 700 m elevation), which extends over 32,682 ha of dry, treeless and gently undulating farmland in the Province of Zamora, northwestern Spain. The land is almost entirely cultivated with wheat and barley. The remaining surface (ca. 9%) is occupied by natural grassland used for sheep grazing. The Reserve holds the world's densest population of Great Bustards (Alonso et al. 1995), which are ground-dwelling lekking birds that inhabit natural and cultivated grasslands. The Great Bustard is endangered in most of its range except for the Iberian Peninsula, which is the main stronghold for the species (Alonso and Alonso 1996). It exhibits one of the highest amounts of sexual size dimorphism of all vertebrates, and males and females generally occur in separate flocks. Between late winter and early spring, males concentrate at traditional arenas where they fight to establish rank and display in an exploded-lek mating system (see Höglund and Alatalo 1995). Juvenile males usually disperse after independence. From their third year on, they begin to establish territories at

leks 5 to 65 km from their natal sites, but generally they do not succeed in mating until they are at least four years old. Compared with males, females tend to remain closer to their natal site (0.5 to 5 km) and begin breeding earlier (Alonso et al. 1998).

Each summer from 1983 to 1993, we captured young Great Bustards (body mass 1 to 3.5 kg) by chasing them down while they were still being attended by the female parent. We marked a total of 105 juvenile males with patagial tags, and in the last three years of the study we attached backpack-mounted radio transmitters to 58 of these birds. Battery life of the transmitters averaged three to four years, which allowed us to track birds from ground vehicles or aircraft from the time they dispersed until they settled as breeding adults (and sometimes for longer periods). Only 15 males from the original pool survived long enough to settle in the study area and be studied during their adult life. Once established, these males could be located by sight (even when transmitters no longer functioned) during our surveys of the Reserve and its surroundings. In addition, in February and March 1993 and 1994, we captured 11 adult males using a rocket net and provided them with backpack transmitters and dorsal PVC tags for visual identification. During the three years after capture, we obtained locations for each of these males at least once per month. Therefore, the total sample of marked adults was 26, from which we gathered more than 800 locations on different days.

We located all radio-tagged individuals by triangulation and subsequent visual observation. Two of the 15 birds marked as juveniles settled as resident adults in the Reserve and could be located monthly. These two, plus the 11 marked as adults, resulted in 13 adult males for which we obtained data on monthly patterns of movement. The remaining 13 birds in the total sample of 26 were seasonal visitors to the Reserve and could be contacted only at leks during the breeding season, thus yielding information only on their presence or absence in the Reserve. Whenever a marked Great Bustard was found during surveys, we recorded its location to the nearest 100 m on 1:50,000 maps.

We conducted 50 censuses of Great Bustards in the Reserve between January 1987 and March 1998 with

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a frequency that varied from once per fortnight to one every four months. All parts of the Reserve were covered with equal effort to avoid biases in the probability of contact with individual birds. Some adjacent areas were also surveyed, although less intensively. Each survey was carried out by four people in two cars during two consecutive days. Surveys followed predetermined transects to cover the entire Reserve and always used the same starting location. Transects covered nearly 400 km in length and required 20 h per team to complete. Surveying was interrupted during midday hours (between 1000 to 1100 and 1500 to 1600 GMT, depending on the season), when birds usually were inactive and thus less detectable. Given the large size of Great Bustards, the generally flat terrain, and the fact that the maximum distance between roads in the Reserve was about 1 km, we assumed that we sighted nearly all of the birds in the study area (see Alonso and Alonso 1990). The census results that we present refer to males that were older than one year. Monthly variation in the number of male Great Bustards observed was analyzed by one-way ANOVA, and monthly differences were assessed with the LSD test using values based on more than three censuses. To account for interannual effects on the monthly variation in male numbers, we performed a two-factor ANOVA, adding the variable year to the original model.

To determine the central location of each male's lek, we plotted all sightings of a given male on 1:50,000 maps that contained the boundaries of all leks in the Reserve (Morales et al. 1996, Morales 1999). Sightings were plotted during the period when copulation rate is highest, which in our study area is between 25 March and 15 April (Carranza et al. 1989, Morales et al. 1996). For this analysis, data were pooled over the duration of the study, which yielded 17 to 45 locations for each male. The arithmetic mean of these coordinates was used as the coordinate of the lek that each male visited each year (this mean was calculated for every marked bird). All statistical analyses were conducted using STATISTICA 5.0 (Statsoft 1995).

For each of the 13 males for which we obtained the monthly pattern of movements (see above), we calculated the linear distance from its lek coordinates to every other sighting of that bird and obtained a monthly mean distance to the lek using all sightings of that bird over the study period. We analyzed the monthly variation of the mean distance to the lek for each of these males with a one-way ANOVA after log-transformation of the data.

We used the total sample of 26 males to measure interannual fidelity to leks and postbreeding areas by calculating the percentage of males that was seen displaying at the same lek or using the same postbreeding area, respectively. Any relocation of a male within 3 km of its average postbreeding coordinate was considered to be within that bird's postbreeding

area. To account for the total percentage of sedentary and dispersing males, we counted birds in this global sample that were sighted in the Reserve during the mating season only and birds that were detected in the vicinity of their leks throughout the year. We further used this sample to analyze the influence of age as a factor in the migratory behavior of the birds after dividing the sample into two age groups, <5 years and ≥ 5 years. Although the exact age was known only for birds that we caught as chicks ($n = 15$), males captured as adults ($n = 11$) were easily assigned to one or the other age category based on plumage characteristics (Glutz et al. 1973).

The degree of development of secondary sex traits such as male body mass or ornamental feathers can be used as an indirect measure of social status among males (Andersson 1994). Body mass and the degree of development of "moustache" feathers (see Gewalt 1959, Hidalgo and Carranza 1990) have been shown to play a role in determining social rank in male Great Bustards (Delgado et al. 1991, Carranza and Hidalgo 1993). We used these two traits to investigate the relationship between social dominance and migratory behavior among male bustards. Because adult body mass was not known for all birds in our global sample, we used only those marked as adults ($n = 11$). We divided this subsample into males that weighed less than 10 kg (median value) and males that weighed 10 kg or more to test the association between body mass and migratory status. With respect to moustache feathers, during three consecutive springs we classified birds visually in the field into three discrete categories of development: (1) poorly developed, (2) developed, and (3) highly developed (see Gewalt 1959, Morales 1999). It was possible to make such classification for 15 males in our global sample. We obtained a mean value for each of these males based on the value assigned to them each spring over the duration of the study. We then assigned each of these males into one of two groups based on the mean development of moustache feathers: (1) ≥ 2.5 , and (2) < 2.5 (2.5 was the median value for this sample of males).

To investigate the extent to which migration mirrors juvenile dispersal, we used a subsample of seven males for which enough data existed to determine the percentage of birds that revisited as migrant adults any of the areas where they had been located during their period of juvenile dispersal. We compared this value with the percentage of birds that did not visit such areas using a test of the difference between two percentages (Statsoft 1995). To test for sexual differences in migration distance, we compared data from marked females that were migratory ($n = 10$; Morales 1999) with data from our sample of nonsedentary males ($n = 6$).

Results.—Monthly variation in the number of male Great Bustards seen in the study area was significant ($F = 7.10$, $P < 0.05$), whereas the interannual effect

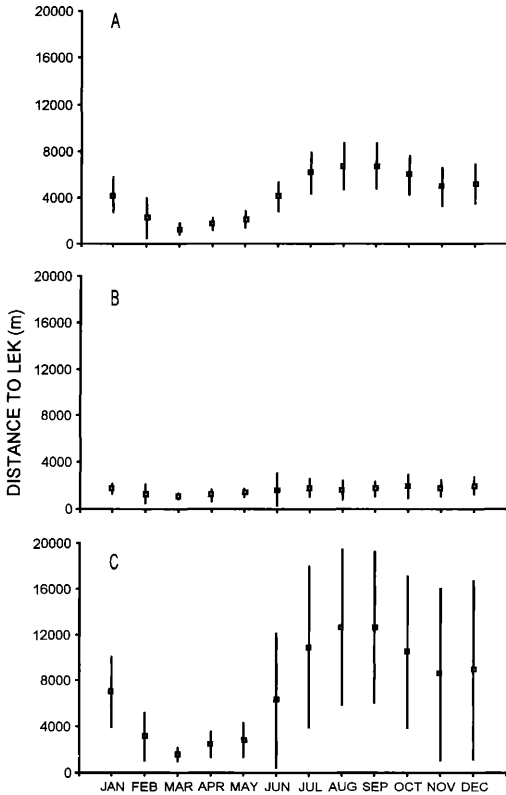


FIG. 1. Mean distance to lek (\pm SD) for male Great Bustards for which we had contacts in all months of the year. (A) Global pattern, all males ($F = 2.86$, $df = 11$ and 143 , $P = 0.002$); (B) sedentary males ($F = 1.22$, $df = 11$ and 70 , $n = 6$, $P = 0.29$); and (C) migratory males ($F = 3.87$, $df = 11$ and 60 , $n = 7$, $P < 0.001$).

was negligible ($F = 1.64$, $P > 0.05$). The highest average number of males occurred in March, and differences between March and all other months were significant ($P < 0.05$). Numbers decreased to a minimum during summer, representing 39% of the March population on average. The difference be-

tween the summer months combined versus all the other months was significant ($P < 0.05$).

A seasonal pattern of postbreeding dispersal from the lek was clearly distinguishable when we considered all 13 males that we radio tracked continuously (Fig. 1A). Moreover, by studying each individual separately, two distinct patterns emerged: (1) a sedentary pattern, corresponding to males that stayed close to their leks year-round and performed no significant monthly movements (< 3 km from their mating center; Fig. 1B); and (2) a migratory pattern. Males in the migratory group made significant seasonal movements between their breeding areas, which they attended from late January to early March through May (four males), or from October to May through June (two males), and their postbreeding areas, which they used during the rest of the year (Fig. 1C). Migrating individuals tended to abandon and return to the lekking areas at around the same dates each year (Table 1).

We observed no significant change of wintering area during the postbreeding period, but one male visited two leks that were more than 10 km apart and regularly repeated this pattern each year. The distances between lek and postbreeding areas varied from nearly 7 km to more than 20 km. Some birds with wing tags but no radio transmitter may have traveled longer distances.

Of the total sample of 26 birds (including males with wing tags but no transmitter), 8 (31%) behaved as sedentary individuals, and the remaining 18 (69%) performed migratory movements, spending either the summer or the summer and winter away from their breeding ranges (generally outside the Reserve). We found no significant difference in the proportion of each migratory pattern between males younger than 5 years versus older than 5 years (Fisher's exact test, $P = 1.00$, $n = 26$), males weighing < 10 kg versus ≥ 10 kg ($P = 1.00$, $n = 11$), or males with poorly developed moustache feathers versus highly developed moustache feathers ($P = 1.00$, $n = 15$).

We observed all 26 males in our global sample on the same lek every year during the main copulation period. Even the "lek-shifting" male, referred to above, visited the same leks each year. All males that

TABLE 1. Months of return to and departure from leks for six migratory male Great Bustards that were equipped with radio transmitters.

Male	Month of return	Years	Month of departure	Years
A	January	1995, 1996	July	1994, 1995, 1996
B	February	1994, 1995, 1996	July	1994, 1995
C	March	1994, 1995, 1996, 1997	June	1994, 1995, 1996
D	March	1996, 1997	July	1996, 1997
E	October	1994, 1995, 1996, 1997	May	1994, 1995, 1996, 1997
F	October	1994, 1995	June	1994, 1995

made significant seasonal movements and could be radio tracked regularly or sighted during surveys visited the same areas during their postbreeding dispersal ($n = 6$). Moreover, no male changed its status from sedentary to migratory or vice versa during the study.

For seven males, we had enough data to compare the areas they visited as dispersing juveniles with those they regularly moved to as migrant adults. Both areas coincided in six cases (86%), and in only one case (14%) they did not ($P = 0.01$). Postbreeding dispersal distance from the lek was higher in males (median = 12,483 m, range 5,946 to 20,062 m, $n = 6$) than in females (median = 3,981 m, range 2,405 to 10,892 m, $n = 10$; Mann-Whitney U -test, $Z = 3.04$, $P = 0.002$).

Discussion.—We identified two well-differentiated patterns of seasonal movement with respect to leks in our sample of marked Great Bustard males: (1) sedentary males, which stayed within 2 to 3 km of their lek all year and did not exhibit a defined pattern of movement, and (2) migratory males, which moved yearly from leks to postbreeding areas 7 to 20 km away. This range of distances may underestimate the true distance moved by males, because birds without radio transmitters might have moved longer distances. The distinction between these two patterns was not arbitrarily based on a linear distance boundary but rather on the presence or absence of each bird during the postbreeding season in the area occupied by the exploded lek to which it belonged in spring. The two movement patterns agree with the seasonal variation in numbers of males censused in the Reserve of Villafáfila, which peaked in March, reflecting the arrival of individuals from outside the study area to concentrate at leks within the Reserve.

Although no other study based on marked individuals has been published, the few data available for other western populations of Great Bustards suggest that the pattern of seasonal movements described here is typical for the species, with average dispersal distances perhaps being dependent on local habitat characteristics (Alonso and Alonso 1990, Hidalgo and Carranza 1990). For example, in a study that is being conducted in central Spain, some radio-tagged males have traveled much greater distances from their leks to postbreeding areas (M. Morales et al. unpubl. data). Most reports of Great Bustard movements in other parts of Europe refer to observations of irruptive migrations into milder areas during harsh winters (Cramp and Simmons 1980). Whereas some populations from central and eastern Asia undertake long-distance movements from north to south, it is unclear whether these are total or partial migrations (Dementiev et al. 1969, Cramp and Simmons 1980).

All males showed year-to-year fidelity to leks and postbreeding areas, and none changed its status between years from migratory to sedentary or vice ver-

sa. Moreover, each male apparently showed constancy in departure and return dates, suggesting that seasonal movements are quite independent of the environmental conditions of particular years. The coexistence of sedentary and migratory individuals in the same population corresponds to a partial migration pattern as defined by Terrill and Able (1988). Partial migration has been reported in other lekking or polygynous birds, many of which were previously considered sedentary, such as several species of grouse (Schroeder 1985, Rolstad 1989, Cade and Hoffmann 1993, Schroeder and Braun 1993).

Partial migration may be regarded as a strategy with two condition-dependent states (migratory or sedentary) that are determined, for instance, by age, body condition, social status, or sex (Lundberg 1988). Two lines of evidence seem to reject age as a factor of the migratory status in our study: (1) we did not record any status change from migratory to sedentary or vice versa, and (2) the proportion of males that was migratory or sedentary did not change between age classes.

In polygynous, size-dimorphic species, male reproductive success is tied to social status, which often is determined through agonistic behavior in which body mass and other secondary sexual traits play an important role (Clutton-Brock et al. 1988, Andersson 1994). In partially migrant species, dominant individuals are expected to stay close to their breeding territories, whereas subordinate individuals should leave as a consequence of intraspecific competition (Gauthreaux 1982, Smith and Nilsson 1987). However, the lack of a significant association between migratory status and either male body mass or the development of moustache feathers does not seem to support this hypothesis.

Great Bustards exhibit partial migration among males (some males migrate, and some do not), and differential migration between sexes (females migrate shorter distances), which has also been described in other species such as Spruce Grouse (*Falci-pennis canadensis*; Schroeder 1985) and Blue Grouse (*Dendragapus obscurus*; Cade and Hoffmann 1993). These sexual differences could give support to the arrival-time hypothesis for the evolution of differential migration between the sexes (Gauthreaux 1982, Ketterson and Nolan 1983, Smith and Nilsson 1987), because females seem to experience higher intrasexual competition for breeding territories and thus higher pressure for early arrival than do males (Morales et al. 1996, Morales 1999).

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What Happens to Old Nests in Natural Cavities?

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It is well known that old nest material accumulates in nest boxes and should be removed to keep the boxes usable. Perrins (1979) and Møller (1989) proposed that the removal of old material, via reduction of ectoparasites, could improve conditions in the boxes. This in turn could have profound effects on nest-site choice, mating success, and reproductive efficiency of the individuals that use the boxes.

Natural cavities are not cleaned by humans. Thus, by implication, conditions in them should deteriorate owing to the accumulation of old nest material. Indeed, Perrins (1979) stated that “. . . the nest material would slowly decompose within the chamber and presumably over a series of years the site might become filled with old nests.” I have tried to find support for this statement in the literature, but so far I have failed to find any information on this issue. Therefore, it seems that the information presented below, which indicates that old nest material disappears rapidly from natural cavities, constitutes the first data on this subject.

Study Area and Methods.—Data were gathered from 1992 to 1998 in the Białowieża National Park in eastern Poland, within which the last surviving fragments of European primeval lowland temperate forest are preserved. The tree stands of the park have never been cut, and the entire area has been strictly protected as a reserve since 1921. Hence, one can still observe cavities and cavity nesters in conditions free of direct anthropogenic disturbance. The forest consists of several types of old-growth stands (see Tomiałojć and Wesołowski 1990, Tomiałojć 1991, Wesołowski and Tomiałojć 1995), but most of the data were gathered in two types of chiefly deciduous stands. One was a stand of riparian trees composed mostly of alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and Norway spruce (*Picea excelsa*); the other was a stand of upland deciduous forest composed of more than 12 species of trees, mainly hornbeam (*Carpinus betulus*), small-leaved linden (*Tilia cordata*), con-

tinental maple (*Acer platanoides*), pedunculate oak (*Quercus robur*), and spruce.

Since 1992, all cavities used by breeding birds within four large study plots (33 to 55 ha each; see Wesołowski 1998) and accessible from a ladder (up to 5 m above ground, in living trees) were marked and checked the following year (in the second half of April) to see whether old nest material was still present. For checking cavity contents, I used a small light bulb on a flexible wire and a small mirror.

The April inspections showed that cavities from previous years could be impossible for birds to use for several reasons (e.g. flooding, or being filled with rotten wood up to the cavity entrance). I have omitted these instances from the present analysis because they are irrelevant to the question at hand. If the cavity contained remnants of old material (e.g. moss and hair), it was classified as an “old nest.” If the cavity contained new material (e.g. fresh pieces of moss), it was classified as a “new nest” (the timing of the cavity inspections coincided with the nest-building phase of earliest breeding species in the study area; Wesołowski and Stawarczyk 1991, Wesołowski 1998). When a cavity contained no nest material and the bottom was covered with decayed material and rotten wood, or occasionally with a single fragment of leaf or piece of moss, it was classified as containing “no nest.”

Because the type of nest material could have influenced the rate of nest disappearance, I divided nests into two categories: (1) “tit” nests, which were constructed mostly of moss, wool, hair, or feathers and were made by *Parus major*, *P. caeruleus*, *P. palustris*, *P. ater*, and *Certhia familiaris*; and (2) “flycatcher” nests, which were composed mostly of dry leaves and other plant material and were made by *Ficedula albicollis*, *E. hypoleuca*, and *Erithacus rubecula*.

Results and Discussion.—No trace of the previous year's nest was visible in two-thirds of the cavities (Table 1), nor did cavities with new nests (ca. 20%) contain remains from the previous year's nest. As a rule, new nests were in the initial stages of construction, so any remains of old material would have been apparent. I found remnants of old nest material in

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