Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*

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Between 1991 and 1997 we studied the offspring independence and juvenile dispersal in a wild population of great bustards (*Otis tarda*). Young males were independent and began their juvenile dispersal at an earlier age (6–11 months) than young females (8–15 months). The juvenile dispersal period was longer and the distances reached farther in males than in females. Natal dispersal distances were also longer in males, all of which dispersed from their natal areas and established as adults at 5–65 km from their natal nests. In contrast, most females were strongly philopatric, settling at 0.5–5 km from their natal nests. These marked sex differences in offspring independence and dispersal may have evolved originally to maintain genetic diversity and are probably reinforced through male competition for mates. Young males that had fed at higher rates and received more feedings from their mothers during the early maternal dependence period became independent and tended to disperse earlier. They also integrated earlier into adult male flocks and settled earlier at their definitive leks, which were closer to their natal sites, in areas of higher adult male density. None of these correlations was found among young females. These results suggest that enhanced food intake and maternal care of male offspring are vitally important in increasing their competitive ability during the immature period and probably also in their fitness as breeding adults. These results are in accordance with the selective value of large size in males and suggest how this species might have reached such a marked sexual dimorphism in size. *Key words:* dispersal, great bustard, natal dispersal, ontogenetic switch hypothesis, *Otis tarda*, proximal and ultimate causes, sex differences. *[Behav Ecol 9:243–252 (1998)]*

Natal dispersal has important consequences for the genetic structure, demography, and social evolution of animal species (Hamilton, 1972; Lidicker, 1975; Taylor and Taylor, 1977). The evolutionary and proximate causes of dispersal have been the subject of intensive debate during the last two decades (Dobson, 1982; Greenwood, 1980; Johnson and Gaines, 1990; Liberg and von Schantz, 1985; Moore, 1993; Moore and Ali, 1984; Packer, 1985; Shields, 1983, 1993; Waser, 1985; Wolff, 1993, 1994). As a result, three major hypotheses have emerged to explain the ultimate causes of natal dispersal in a wide range of species: reduction of competition for resources, reduction of competition for mates, and avoidance of close inbreeding (Greenwood, 1980; Greenwood and Harvey, 1982; Johnson and Gaines, 1990; Pusey, 1987; Pusey and Wolf, 1996). Among several ontogenetic mechanisms acting as proximate factors, aggression from conspecifics (social subordination hypothesis; Christian, 1970), absence of strong enough social ties to the natal group (social cohesion hypothesis; Bekoff, 1977), and attainment of a threshold body mass before dispersal (ontogenetic-switch hypothesis; Dobson, in Holekamp, 1986), have drawn most of the attention from researchers (for a review see Holekamp, 1986).

To date no consensus on the evolution of natal dispersal among birds and mammals has been reached, probably because proximate and ultimate causes differ between species (Lidicker, 1975; Moore and Ali, 1984; Shields, 1982; Waser and Jones, 1983), and even sometimes between sexes of the same species, often leading to sex-biased dispersal (reviews in Dobson, 1982; Greenwood, 1980; Pusey, 1987; Wolff, 1993). On the other hand, dispersal behavior may depend on several interacting factors rather than on a single cause, and the var-

ious hypotheses proposed may not necessarily be mutually exclusive (Dobson and Jones, 1985). Moreover, some of these hypotheses generate identical predictions, albeit for different reasons. Therefore, testing the alternative hypotheses has remained elusive, and long-term studies are needed to accurately determine the costs and benefits of dispersal versus philopatry (Moore, 1993; Shields, 1993). Greenwood (1980) found, after reviewing the literature, that in most birds dispersal was female biased, whereas in most mammals it was male biased. He related these trends with the prevalence of monogamy and a resource-defense mating system in birds and polygyny and a mate-defense mating system in mammals and hypothesized that the mating system was the main determinant of any sex bias in dispersal and the direction of the bias.

Since publication of Greenwood's paper, the dispersal process has been studied in many mammal but few bird species (review in Johnson and Gaines, 1990). Studies are particularly scarce in polygynous and promiscuous bird species, despite various authors drawing attention to the importance of these species in understanding the evolution of dispersal (Greenwood, 1980; Liberg and von Schantz, 1985; Pusey, 1987). Greenwood (1980) mentioned a single polygynous lekking bird species with female-biased dispersal, the white-bearded manakin (*Manacus manacus*). He proposed, with some reservations, that lek systems should be placed among resource-defense mating systems. Female-biased dispersal has also been found in the sage grouse (*Centrocercus urophasianus*; Dunn and Braun, 1985), the greater prairie chicken (*Tympanuchus cupido*; Hamerström and Hamerström, 1973), and the capercaillie (*Tetrao urogallus*; Koivisto, 1963), all of them true lekking species with territory defense by males, and also in two species with promiscuous, dispersed leks where area defense has been interpreted as securing a resource necessary to attract females: the blue grouse (*Dendragapus obscurus*; Jamieson and Zwickel, 1983) and the ruffed grouse (*Bonasa umbellus*; Gullion and Marshall, cited in Koivisto, 1963). In most

of these and other grouse species the length and frequency of seasonal movements are also female biased (references in Schroeder and Braun, 1993). However, area defense is not a common characteristic of all lek types (Höglund and Alatalo, 1995; Johnsgard, 1994) and does not justify including all of them in the resource-defense group. Male-biased dispersal has been found in birds of the family *Anatidae* (Greenwood, 1980). Many species of this family share several mating system attributes with lekking species, like competitive displays in male groups, mate selection by females, elaborate male displays, and ornamental male plumages, and usually low male investment in breeding. This led Johnsgard (1994) to suggest that their mating system could be regarded as "quasi-arena behavior."

In a previous paper we described the male-biased dispersal in the great bustard (*Otis tarda*), based on the frequency of resightings in a closed study area of birds marked with patagial tags (Alonso and Alonso, 1992). We discussed the agreement of the pattern observed in this promiscuous lekking species with Greenwood's model and argued that the benefits derived from a better knowledge of their natal area would probably determine a higher value of philopatry for females, provided that they take over all breeding duties. In the present study we investigated in greater detail the process of natal dispersal in this species, focusing on the individual differences between radiotagged birds followed continuously throughout their first 4 years of life. Radiotelemetry enabled us to measure real dispersal distances and to know the fate of each individual, in contrast to our previous study (Alonso and Alonso, 1992). Here we describe the timing of juvenile independence and dispersal initiation, the age of establishment as breeder, and the natal dispersal distance of radiotagged individuals and study the relationships between these variables and their possible causal factors. Specifically, we tested the following predictions: (1) the frequency of aggression by parent birds or conspecific adults should increase before or at the time of dispersal (social subordination hypothesis), (2) heavier or better nourished individuals should disperse earlier (ontogenetic-switch hypothesis), but (3) they should show shorter natal dispersal distances than smaller or less well-fed individuals (social subordination hypothesis), (4) birds born in densely occupied areas should disperse more (resource competition hypothesis), (5) more competitive males should settle to breed earlier (social subordination and mate competition hypotheses) and (6) in areas of higher male density than less competitive males (mate competition hypothesis), and (7) a strong sex bias in natal dispersal distance should exist (inbreeding avoidance hypothesis). We also discuss two fitness costs of dispersal: the predicted increased mortality associated with greater dispersal distances and the decrease in reproductive success caused by later settlement as breeders.

METHODS

Study area and species

The study was conducted in Villafáfila Wildlife Reserve (327 km²) and its surroundings in northwest Spain. Cereal cropland is the dominant habitat (>90%), with some other crops and small, natural grassland plots used for sheep grazing. The land is treeless and gently undulating, representing an optimal habitat for the species, which probably reaches the world's highest densities in the reserve, with up to 6.2 birds/km² in early spring (Alonso et al., 1996a). The climate is characterized by dry, hot summers and cold winters with moderate rainfall.

The great bustard is a large, globally endangered bird that has declined in numbers considerably during the present cen-

tury and whose current populations inhabit cereal steppes of Europe and Asia. The species is highly sexually dimorphic, with adult males weighing 10–15 kg, compared with females which weigh only 4–5 kg. Males and females occur generally in separate flocks. Between late winter and early spring males concentrate at traditional arenas, where they fight to keep or gain the highest possible hierarchical status within the flock and later disperse over a wider area (exploded or dispersed lek) to display individually and attract females for copulation. Our preliminary observations on mating behavior of marked males suggest that high-ranking individuals keep their status in the lek for several years. Rather than defending particular display territories, most males change exhibition sites with other individuals, usually within a limited area of several hectares (although some males may wander several kilometers between two displaying sites within the same season). The number of mates males and females have is not known, but males display and try to copulate with virtually all females that approach and accept them as partners. We have seen marked males copulating with several females, but no marked female mating with more than one male. After mating in April, females nest in May close to the lek where they mated, although at variable distances from the mating site, and take over all breeding duties. Most males abandon the lek site and may even disappear from the area surrounding it and the adjacent nesting sites during part or all of the nonmating season (June–October and June–February, respectively). The young (usually one, less frequently two) depend on their mother through most of their first year of life, most becoming independent during the next spring, just before their mothers begin a new breeding attempt. Later they spend a variable amount of time in juvenile dispersal, after which they establish as breeding adults. Low annual adult mortality and the current age of our oldest marked birds (14 years) suggest that longevity may perhaps be around 20 years. The age of first breeding is 2 years in females and 4–5 years in males (Alonso JC et al., personal observation).

Data collection

In early summer of 1991 to 1993 we captured 44, 13, and 51 young great bustards at ages of 4–7 weeks, marked them with patagial wing-tags, and tagged 101 of them with BIOTRACK or TELONICS harness or poncho transmitters. The long life of the transmitters (2–4 years) and the wing-tags enabled us to track most surviving birds until spring 1997. We aged the birds using their weight at capture and published growth curves and sexed them through a biometrical index that discriminated nearly 100% of the cases (see Alonso et al., 1996b), confirming later the sex in the field when dimorphism allowed it. In all cases marked young joined their mothers immediately after release. We located radiotagged birds with hand-held yagi antennas from vantage-points or from aircraft (about 200 flight-h) with a frequency varying between one and several times per month until they died or the transmitter battery depleted, except four individuals that were lost with unknown fate. Although radiotelemetry locations, including aerial ones, were usually accurate enough, we always confirmed locations visually and plotted them on maps 1:50,000 to the nearest 100 m. After transmitter signal termination, we located marked birds during periodic censuses of the reserve by car (between one per week and one every 2–3 months) and made at least monthly searches for those birds that had settled outside the reserve.

The high juvenile mortality during the first 3 months of life of the young, and a small percentage of wing-tag or transmitter loss, reduced our initial sample sizes to 15 males and 20 females. We radio-tracked each individual during whole days

throughout their maternal dependence period to collect behavioral data that could be related to their subsequent dispersal behavior, for a total of 220 days observation of 34 birds, some of which were excluded from the analyses due to early mortality or transmitter failure. Each observation day we recorded with 20–60× telescopes the number of feedings that each young received from its mother, its food intake (number of pecks), and the aggressive encounters between the focal young and other birds during 3-min periods at 30-min intervals and extrapolated the food intake and aggression rate values to the whole day.

Because it was not possible to recapture marked individuals, we could not determine their weight increase. We assumed that weight was correlated with food intake (see, e.g., Pugesek, 1995) and used the daily food intake averaged through the first 4 months of life as a reasonable estimate of the body weight reached by each bird before becoming independent. The first 4 months are the period of highest growth rate, most intensive maternal care, and highest frequency of maternal feedings, young reaching >80% of their weight acquired at independence (Heinroth and Heinroth, 1928; Radu, 1969).

Dispersal variables

Because the exact location of the natal nest was usually unknown, we used the place where young were captured as the natal site, as the distance between them was negligible (<500 m) in those cases when both were known. We used two measures of natal dispersal. The first was the straight line between the natal site and the site selected for the first breeding attempt. However, the site selected for the first breeding attempt is not equivalent in both sexes: in males it is a display area (lek), whereas in females it is a nesting area that may be at variable distances from the lek they attend to mate. To account for these differences, our second measure of natal dispersal was the number of leks that were closer to the natal site than to the site selected for the first breeding attempt. Because the location of the various leks in the reserve did not change during our study and most females went to mate at the lek closest to their breeding sites, this second measure of dispersal gives an estimate of the leks ignored by a dispersing individual (i.e., those that could have been used as mating sites with less dispersal cost than the lek they selected to settle). A male scored 0 if it settled at the lek closest to its natal nest, while a female scored 0 if the lek closest to both its natal nest and breeding nest was the same, regardless of the linear natal dispersal distance. For the purposes of this paper, the site selected for the first breeding attempt was synonymous with settlement site as adult because our marked birds did not make any breeding dispersal movements between years.

Great bustard families lived as isolated units throughout the summer and later joined flocks with other families and nonbreeding females. Young remained dependent on their mothers in these winter flocks, and although most mothers were unmarked, juvenile dependence was clearly apparent through unequivocal signs like occasional mother–offspring feedings, or the tendency of the young to follow their mothers closely within the flock. Because the process of family break-up frequently lasted several days, during which the young was seen alternatively with its mother and separated from her, we estimated two dates for juvenile independence. The first was the latest age when the young was seen as clearly dependent on its mother, and the second was the age when it was seen clearly independent, either alone or in a flock with other independent young. We defined the age of juvenile dispersal initiation as that at which an independent juvenile made its first major dispersal movement, covering a distance of more than twice its distance from the natal site at the start of the move-

ment. This movement was normally followed by a dispersal period characterized by relatively erratic displacements generally far from the usual natal area. With the exception of four females for which we could not identify any marked juvenile dispersal movements, this dispersal period ended when the bird established at a site where it attempted its first breeding. This age was defined as the age of settlement. During the juvenile dispersal period we calculated the mean and maximum distances to the natal site from the sample of all contacts for each individual.

After becoming independent from their mothers and before their definitive settlement as adult birds, immature (2nd and 3rd year) males integrated in flocks, initially of juvenile males and later of adult males. The duration of this social integration process varied between individuals, and we used the ages at which each bird was first seen as a member of a flock of juvenile and adult males and the frequency of sightings in male flocks compared to total sightings as estimates of its social integration ability.

To test if dispersal behavior was related to the density of birds at the natal area, we divided the reserve into 9 zones varying between 19 and 49 km² and separated from each other by major roads and towns. For each marked bird we correlated the variables defining its dispersal behavior with the densities of males, females, and total numbers of birds censused in its natal zone when the young was 3, 7 and 10 months old (in September, January, and April respectively, after hatching).

Statistical analyses

We used two-tailed nonparametric tests unless otherwise specified. When we used a parametric test, we log-transformed the data. Because there were no interannual differences in any of the dispersal variables studied (all $p > .05$, two-way ANOVA including year and sex), we pooled data from the 3 years for analysis.

RESULTS

Age of independence and juvenile dispersal initiation

Young males were independent and began their juvenile dispersal earlier than females (Figure 1, Table 1). Although all males abandoned their natal areas after independence, four females (20%) did not make any appreciable dispersal movements. In both sexes the highest frequency of family breakup events occurred when the young was 10 months old, coinciding with the initiation of its mother's next breeding attempt (April), but the frequency distribution differed between sexes: only two female offspring became independent before late April, but most male offspring became independent earlier (Figure 1a).

The median time spent in the natal area once independent was only 8 days in males and 46 days in females, although the sex difference was not significant. This time was not correlated to the age of independence ($p = .80$ in males; $p = .24$ in females). One male delayed its dispersal exceptionally until it was 22 months old, 10 months after being independent.

Age of independence, bird density, and aggression from adult females

When the young was more than 4 months old, families began to assemble with other females in flocks, where offspring received occasional attacks from adult females. The age when young suffered peak aggressive behavior was correlated with their age of independence (Figure 2), although our low sam-
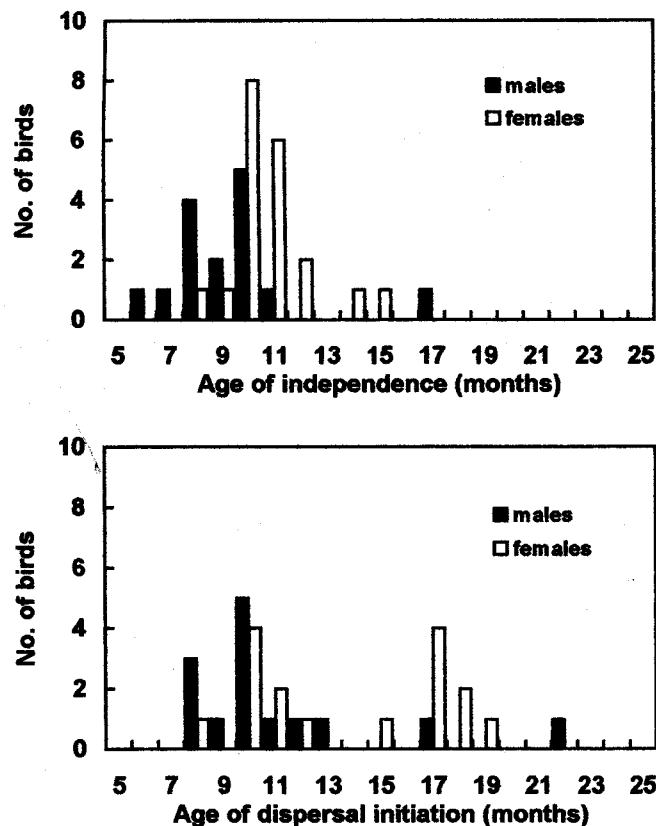
Figure 1

Frequency distributions of the ages when young great bustards became independent from their mothers and began their juvenile dispersal. The graphs include a male that died at an age of 17 months (511 days), when it was still dependent on its mother, so if it had survived it should have become independent and dispersed at an older age than that represented. All other males became independent at ages of 206–345 days; females became independent at ages of 269–464 days.

Table 1

Sex differences in age of offspring independence and dispersal behavior in the great bustard (mean ± SD) (age in days, distance in km)

Variable (n)	Males	Females	Test of difference[a]	
			Z	p
Age when last time clearly dependent from mother (15 males, 20 females)	270 ± 78	309 ± 47	2.90	.004
Age when first day clearly independent (15 males, 20 females)	296 ± 71	336 ± 46	2.78	.005
Age after first major juvenile dispersal movement (15 males, 16 females)	349 ± 116	424 ± 106	1.85	.064[b]
Mean distance to natal area during the juvenile dispersal period (15 males, 20 females)	14.1 ± 10.8	4.3 ± 2.2	4.66	<.001
Maximum distance to natal area during the dispersal period (15 males, 20 females)	29.6 ± 17.4	12.5 ± 6.1	3.40	<.001
Natal dispersal distance (13 males, 18 females)	18.6 ± 16.0	3.5 ± 3.9	4.02	<.001
Natal dispersal distance in number of leks[c] (13 males, 18 females)	6.6 ± 3.5	0.4 ± 1.4	4.72	<.001
Age of settlement at first breeding site (10 males, 17 females)	916 ± 325	568 ± 213	1.90	.057
Difference between ages of settlement and dispersal initiation (10 males, 14 females)	561 ± 253	191 ± 185	3.48	<.001

[a] Mann-Whitney test.

[b] Sex differences were significant after excluding an outlier male (see Figure 1): males: 325 ± 69 (n = 14); Z = 2.30, p = .021.

[c] Number of leks closer to the natal nest than to the site selected to settle on as an adult (a lek in males, a nesting site in females).

ple sizes did not show a clear correlation with age of dispersal initiation (r_s = .60, n = 4, p = .30 for males, r_s = .47, n = 11, p = .18 for females). Three of another four males that did not receive any aggression became independent later than average males, at ages of 9.9, 10.5, and 11.5 months (mean male independence age = 9.8 months). In spite of the positive correlation, juvenile independence occurred usually several weeks after peak aggressive behavior from adult females.

There was a negative correlation between the age of independence of young males and the density of great bustards at the natal area averaged through the first 8 months of life (r_s = −.72, n = 14, p = .01 with summer density, r_s = −.47, n = 14, p = .08 with winter density, r_s = −.56, n = 14, p = .04 with average of both). Age of dispersal initiation was only marginally correlated with summer density (r_s = −.54, n = 14, p = .06). In female offspring, age of independence and age of dispersal initiation were independent of bird density (p > .25 in all correlations).

Duration of the juvenile dispersal period and distance traveled

Age of independence and age of dispersal initiation were positively correlated (p = .01 in both sexes). After beginning dispersal, independent offspring spent a variable time moving far from their natal areas, initially alone or in small flocks of

other same-sex and same-cohort birds, later in adult flocks of the same sex. A few male offspring exceptionally joined female flocks for a short time. These excursions were composed of erratic and irregular movements troughout their juvenile-immature dispersal period, which usually began with a first major movement outside the natal area. Male offspring began their dispersal period earlier, finished it later, and reached greater mean and maximum distances during dispersal than female offspring (Table 1). The farthest distance reached by a male was 65 km, whereas some females did not travel more than a few kilometers from their natal nests. The dispersal period ended when birds settled as adults in an area that would be their usual display (males) or nesting area (females) in subsequent years. In females but not in males, the average distance to the natal area throughout the dispersal period was negatively correlated with the age of independence (r_s = −.56, n = 20, p = .01).

Natal dispersal, philopatry, and age of settlement

Natal dispersal was longer in males than in females (Table 1). All males clearly dispersed from their natal areas to breeding
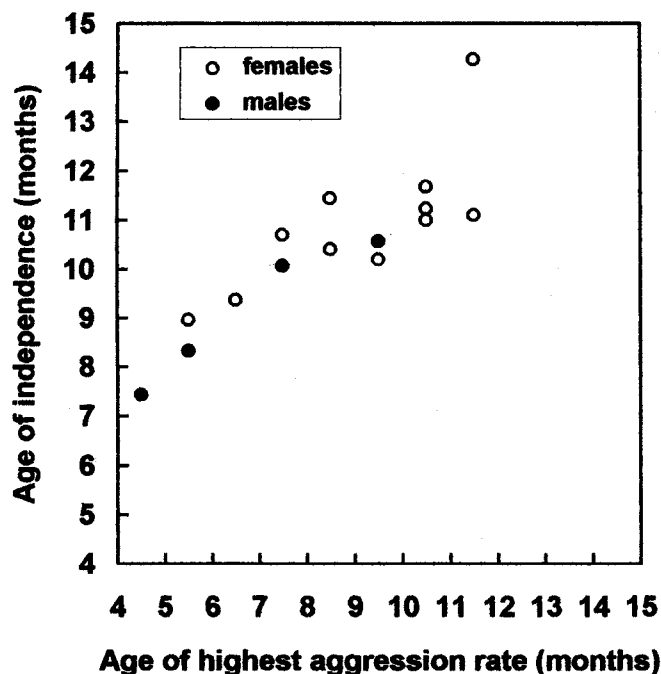
Figure 2

Relationship between the age when young great bustards received the highest aggression rate from adult females and their age of independence. The correlation was significant for males ($r_s = 1.00$, $p = 0$) and females ($r_s = .75$, $p = .017$).

sites located 4.7–65 km away (Figure 3a) and settled as breeding adults on leks different from those closest to their natal sites, most frequently at more than 10-lek distances (Figure 3b). In contrast, 15 (83%) of 18 females settled as breeding adults <5 km from their natal nests, 9 of them (50%) within 2 km of their natal nests. With the exception of two birds (11%), all other females were extremely philopatric, attending as a rule the lek closest to their natal nests (Figure 3b).

Natal dispersal distance was positively correlated with the mean and maximum distances reached during the juvenile dispersal period only in males (Table 2). In females the relationship between mean juvenile dispersal and natal dispersal measured in kilometers disappeared when it was transformed to number of leks. Thus, although males dispersing farther during their immature period settled farther from their natal sites, most females were markedly philopatric, independently of how far they had dispersed as immatures.

Males settled to attempt breeding later than females (Table 1). During their dispersal period males usually visited more than one lek in spring and joined temporarily one or more male groups during other seasons, settling definitively in the spring of their 2nd (five birds), 3rd (three birds), or 4th year of life (two birds). Females tended to settle earlier, when they were 1 (seven birds) or 2 years old (9 birds), or rarely 3 (one bird).

Relationship between food intake during the maternal dependence period, age of independence, and dispersal

Young great bustards obtained most of their food by pecking at food items (on average, 11,236 ± 1164 SE pecks/day in males, 8,521 ± 752 SE in females), but received complementary feedings from their mother, at a rate decreasing throughout the dependence period (average rates through the first 4 months of age: 64.4 ± 22.1 SE feedings/day in males and 52.5 ± 10.0 SE in females). We recorded the last maternal feedings in March, when young were 10 months old. To study the influence of body
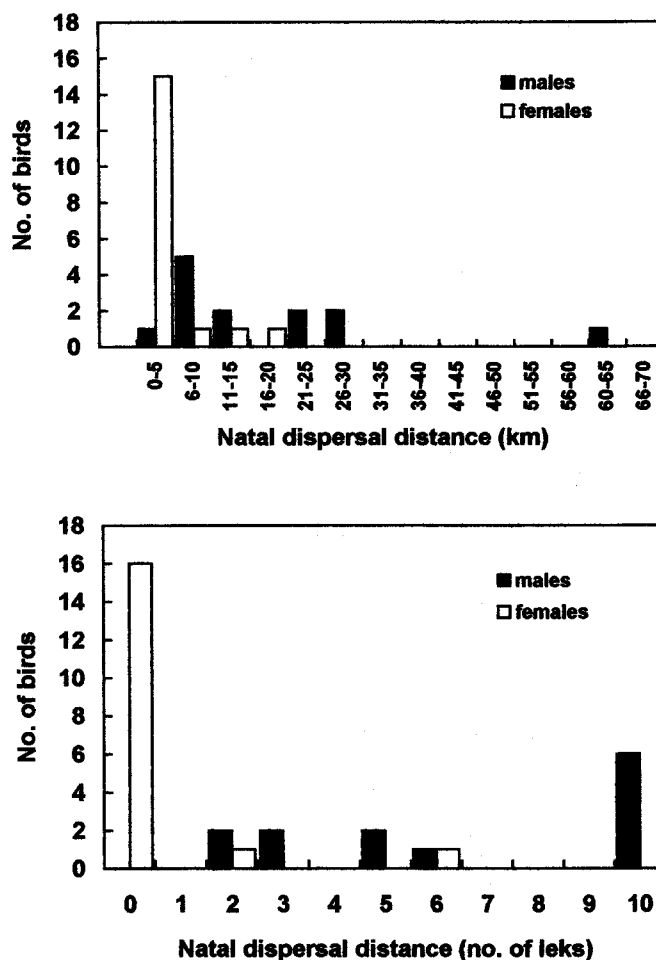
Figure 3

Frequency distribution of two measures of natal dispersal distance: linear distance between natal and breeding site (upper graph), and number of leks closer to the natal nest than to the site selected to settle on as an adult (a lek in males, a nesting site in females) (lower graph).

condition on dispersal behavior, we correlated all dispersal variables with both food intake components of the young, its own intake rate, and the maternal feeding rate. Male offspring that had fed at a higher rate became independent earlier (Figure 4) and tended to begin their juvenile dispersal earlier ($r_s = -.67$, $n = 8$, $p = .07$). They also settled to breed earlier (Figure 5) and closer to their natal sites (Figure 6). The distance at which males settled was positively correlated with their age of settlement ($r_s = .70$, $n = 10$, $p = .037$ in kilometers, $r_s = .74$, $p = .026$ in number of leks). The three males that had fed at highest

Table 2

Spearman correlation coefficients between natal dispersal distance and distance to natal area during juvenile dispersal ($n = 13$ males, 18 females)

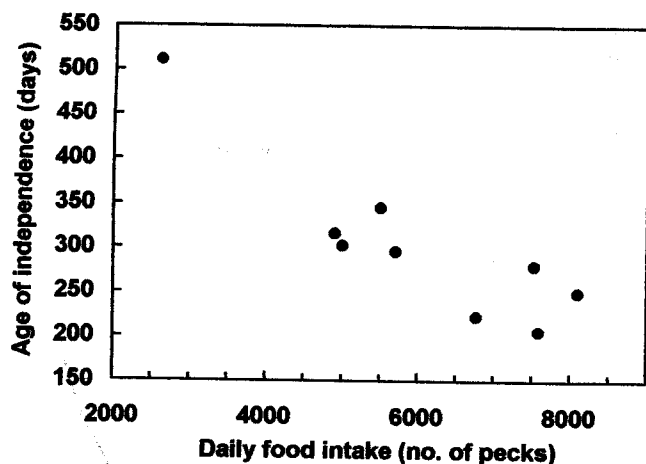| Measurement of natal dispersal		Mean		Maximum	
		r_s	p	r_s	p
Kilometers	Male	.746	.010	.644	.026
	Female	.562	.020	−.104	.667
Number of leks	Male	.674	.019	.595	.039
	Female	.418	.085	.042	.834

Figure 4
Relationship between mean daily food intake of male great bustards during their first 4 months of life and their age of independence ($r_s = -.88$, $p = .019$).

Figure 5
Relationship between mean daily food intake of male offspring during their first four months of life and the age when they settled definitively as adults ($r_s = -.83$, $p = .06$).

rates settled in areas of higher male density than the other four males ($p < .05$, one-tailed Fisher Exact probability test; as a mean value for comparison we took the mean male density in our study area in April).

In female offspring food intake during the first months of life was not correlated with any dispersal variables ($r_s = .15$, $n = 11$, $p = .62$ for age of independence, $r_s = .13$, $n = 10$, $p = .71$ for dispersal initiation, $r_s = -.24$, $n = 10$, $p = .47$ for age of settlement, and $r_s = .26$, $n = 10$, $p = .43$ for natal dispersal distance). Food intake was not correlated with mean and maximum distances reached during the dispersal period ($p > .05$ in both sexes).

Maternal food provisioning rate was not correlated with dispersal parameters in either sex. The offspring's own food intake rate was correlated with feeding rate received from the mother in males ($r = .61$, $p = .03$, $n = 12$ birds), but not in females ($r = .10$, $p = .76$, $n = 11$ birds). In both sexes, the offspring's intake rate was positively correlated with that of the mother ($r = .89$, $p < .01$, 10 males; $r = .85$, $p < .01$, 15 females).

Finally, the more feedings a young received during its first 4 months of life, the steeper the feeding rate was decreased (estimated as the slope of the linear regression between feeding rate and offspring age) throughout the dependence period ($r_s = .93$, $n = 8$, $p = .013$ for males, $r_s = .67$, $n = 14$, $p = .016$ for females, $r_s = .81$, $n = 22$, $p < .001$ both sexes pooled). Because there were no sex differences in the mean values of feeding rate decrease, we pooled sexes and found that steep decreases of maternal feeding rate tended to correlate with earlier independence ($r_s = -.40$, $n = 23$, $p = .06$).

Relationship between food intake during the maternal dependence period and social integration of juvenile males in adult male flocks

A juvenile male arriving at a lek from a different natal area has to be accepted as a new member of the male flock in order to have opportunities to mate at that lek. During this social integration phase, aggressive encounters among lower-ranking males are frequent (see also Cramp and Simmons, 1980; Gewalt, 1959). Individuals that had ingested more food and received more maternal feedings tended to integrate earlier in flocks (Table 3). Similarly, male offspring becoming independent at an earlier age integrated earlier in flocks of males (Table 4). Those individuals integrating earlier in flocks of juvenile males settled earlier and closer to their natal areas
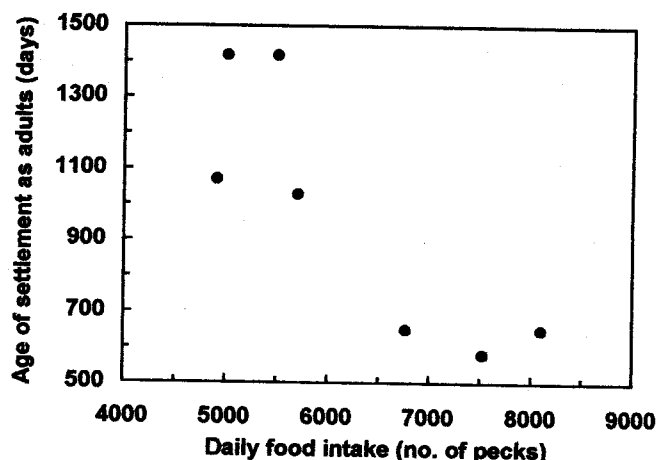
as breeding adults. Because the age when first seen in a flock of juvenile males was correlated with the age when first seen in a flock of adult males ($p = .02$), the timing of definitive integration in an adult flock ($p = .05$), and the frequency of presence in male flocks ($p = .02$), overall the results suggest that all estimators of social integration behaved in a similar way with respect to dispersal variables.

Relationship between density of birds at the natal area, food intake during the maternal dependence period, and dispersal

The mean food intake of young during their first 4 months of life was not correlated with the density of adult birds at the natal areas ($r = .28$, $p = .33$, $n = 13$ males, $r = -.04$, $p = .89$, $n = 14$ females). Natal dispersal distance was not positively correlated with density of birds at the natal area, either when measured at any given month during the maternal dependence period or when averaged throughout it. In fact, the trend found in our study between dispersal distance and bird density at the natal area was opposite to that predicted by the
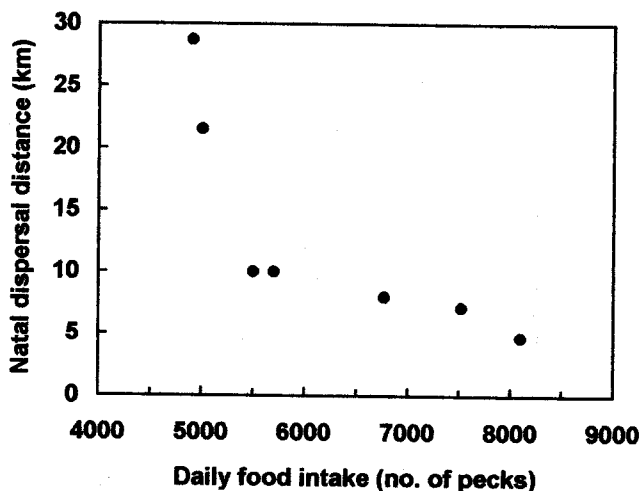

Figure 6
Relationship between mean daily food intake of male offspring during their first 4 months of life and their natal dispersal distance ($r_s = -1.00$, $p = 0$).

Table 3

Spearman rank correlations between food intake during the first 4 months of life of male offspring and their social integration in male flocks ($n = 8$ birds)

	Food intake of young		Feeding rate from mother	
	r_s	p	r_s	p
Age when family unit was first seen in flocks of females in autumn	−.19	.611	−.86	.02
Age when bird first seen in flocks of juvenile males	−.79	.04	−.67	.08
Age when bird first seen in flocks of adult males	−.57	.13	−.79	.04
Age of definitive integration in adult male flock[a]	−.48	.21	−.74	.05
Frequency of presence in male flocks during the immature period (2nd–3rd year)	.71	.05	.93	.01

All social integration variables were significantly correlated with at least one food intake variable.

[a] Later never seen again as immature with adult females or other immature birds.

Table 4

Spearman rank correlations between variables defining the dispersal process and those defining the social integration of juvenile male great bustards in male flocks

		FJM	FAM	DFAM	FPFM
Age of independence ($n = 9$ birds)	r_s	.97	.84	.61	−.89
	p	.01	.01	.06[a]	.01
Age of settlement ($n = 7$ birds)	r_s	.82	.69	.76	−.75
	p	.04	.09	.06	.07
Natal dispersal distance (km) ($n = 8$ birds)	r_s	.72	.54	.47	−.54
	p	.05	.15	.22[a]	.15
Natal dispersal distance (leks) ($n = 8$ birds)	r_s	.72	.58	.53	−.54
	p	.05	.13	.16[a]	.15

FJM, age when bird first seen in flocks of juvenile males; FAM, age when bird first seen in flocks of adult males; DFAM, age of definitive integration in an adult male flock; FPFM, frequency of presence in male flocks during the juvenile-immature dispersal period (2nd–3rd year).

[a] Using a Fisher Exact probability test, these relationships were significant at $p < .05$: the four males that integrated later in male flocks had become independent later and dispersed farther.

resource competition hypothesis. In male offspring the correlation was negative and marginally significant only with the density of adult females ($r_s = -.56$, $p = .06$, $n = 13$ birds), but not with the density of adult males ($r_s = -.44$, $p = .15$, $n = 13$ birds), whereas in female offspring it was also negative and significant only with the density of adult males ($r_s = -.51$, $p = .04$, $n = 18$ birds), but not with that of adult females ($r_s = -.33$, $p = .17$, $n = 18$ birds). Males that had spent their first year in areas with a higher density of females tended to show lower natal dispersal values, and females that had spent their first year in areas with a higher density of males had lower natal dispersal values. When dispersal was measured in number of leks, the negative marginally significant correlation held for males ($r_s = -.52$, $p = .08$), while it disappeared for females ($r_s = .18$, $p = .46$).

Dispersal and mortality

Mortality was high during the first 2–3 months of life of young birds, generally due to predation, and decreased later to values similar to those of adults (Martín, 1997). Only one female died during the juvenile dispersal period, due to a collision with a powerline. This was also the cause of death of a male at an age of 17 months, when it was still dependent on its mother (see Figure 1). These scant data did not enable us to conclude that dispersal was associated with an increased mortality. However, even if mortality had been found to be higher among dispersing males (something that at the population level has been found to be true through sex-ratio analysis, Martín, 1997), this would not enable us to conclude that the cost of dispersal is high, as it is impossible to separate cost of dispersal from cost of fighting for dominance in the group of males.

DISCUSSION

Ultimate causes of dispersal: inbreeding avoidance and mate competition

The results of the present study confirm the extreme male-biased natal dispersal in the great bustard described in a previous paper (Alonso and Alonso, 1992) and show marked sex

differences in other features of the species' dispersal behavior. Young males had shorter maternal dependence periods than young females, began juvenile dispersal earlier, dispersed farther as juveniles, and settled as breeding adults later and further from their natal sites. The great bustard indeed represents one of the most extreme sex-biased dispersal patterns among birds and mammals (reviews in Johnson and Gaines, 1990; Pusey, 1987). Females returned to their natal sites no matter how far they traveled during their juvenile dispersal period, whereas males settled as breeding adults farther from their natal sites the farther they had dispersed. Although no male attempted breeding at the lek closest to his natal site, almost all females settled very close to their natal nests and later attended the closest leks. These leks were probably the same as those attended by their mothers, as adult females usually mate at the lek closest to their breeding territory (Alonso et al., 1996a). This marked female philopatry suggests that some matrilineal relationships probably exist among females living in a given area.

Sex-biased dispersal is a central prediction of the inbreeding avoidance hypothesis, but it can also be explained as a consequence of sex differences in intrasexual competition for mates (Dobson, 1982; Greenwood, 1980; Moore and Ali, 1984; see reviews in Pusey, 1987; Pusey and Wolf, 1996). A direct test of the inbreeding avoidance hypothesis would have required comparing the reproductive consequences of various degrees of inbreeding or parent removal experiments, something that was not possible in our case and is rather infrequent in studies with wild populations (Pusey and Wolf, 1996; Shields, 1993). However, three lines of evidence suggest that maintenance of genetic diversity has been of prime importance in the evolution of sex-biased dispersal in the great bustard. First, the combination of extreme male dispersal and extreme female philopatry has been generally accepted to be a mechanism to avoid close inbreeding. When only mate competition is involved, Waser (1985) and Buechner (1987) suggested that the distribution of natal dispersal distances should approximate a geometric distribution. Although our sample size was small, apparently more females and fewer males settled close to their natal sites than predicted by a geometric distribution. Second, as predicted by the inbreeding avoidance hypothesis, the probabilities of mother–son and brother–sister matings are very low in the great bustard, and father–

daughter matings remain the only possible inbreeding combination, which can only be avoided by some kin-recognition mechanism. Avoidance of nuclear family incest has been shown in other species with similar extreme sex biases in dispersal and has been proposed as the main, ultimate cause of dispersal in primates and other species living in permanent social groups (reviews in Pusey, 1987; Pusey and Packer, 1987b; Pusey and Wolf, 1996). Third, the negative correlation found between density of adult females and male, but not female, natal dispersal distance could also be interpreted as a consequence of the inbreeding avoidance mechanism. In areas of lower female density, there is an increased risk of close inbreeding, and thus it is more important for males to disperse farther. Without marked sex bias in dispersal, great bustards could incur the negative effects of decreasing genetic diversity, given their longevity, site fidelity, highly skewed male mating success, and absence of any significant breeding dispersal.

As for the mate competition hypothesis, two predictions were supported by our results in males. First, more competitive males settled earlier to breed than less competitive males. Second, more competitive males settled at closer distances from their natal sites and on areas of higher male density. We could not test more specific predictions of the mate competition hypothesis (e.g., comparing intrasexual aggression rates experienced or rank gained by males dispersing versus males remaining in their natal group) because in our study all young males dispersed. However, all dispersing males ranked usually lowest in the hierarchy of the male groups in which they settled, regardless of the natal dispersal distance. We therefore conclude that dispersal contributed to inbreeding avoidance but did not seem to lead per se to the attainment of higher ranks, as predicted by the mate competititon hypothesis, although settlement on lower male density areas could facilitate their access to females.

Because we could not recapture marked birds to measure their weight increases before dispersal initiation, we used their feeding rate during their first months of life as an estimator of their body condition. It is reasonable to assume that young males that had fed at higher rates gained weight faster (e.g., Pugesek, 1995). Several authors have argued that food intake during the early developmental stages of an individual are vitally important in determining its weight and reproductive success at adult age, as individuals with slow growth rates during their first months of life cannot compensate for them later in subsequent years (Clutton-Brock et al., 1982; Festa-Bianchet et al., 1994; Green and Rothstein, 1991). Our results indeed show that male offspring that had fed at higher rates had shorter maternal dependence periods, began their juvenile dispersal period earlier, integrated earlier in male flocks during their immature dispersal period, and established on leks to attempt their first breeding at an earlier age, and in areas of higher male density. The food intake rate of male offspring was correlated with the number of feedings received from their mothers and with their mothers' own food intake rate, suggesting that the ability of some mothers to lead their male offspring to good feeding areas and to encourage them to feed at faster rates might be of fundamental importance in determining the later competitive ability of their young.

The correlations described above show that growth rate, and by implication early maternal care, are important factors determining the age of first breeding in males and thus may affect their fitness. Males establishing earlier at a lek tend to exhibit higher display rates and a better physical appearance, as judged qualitatively through their sexual characters such as amount and length of moustachial feathers, and width and color of neck base (Alonso JC et al., unpublished data). Although males do not try to copulate until they are 4–5 years old (Alonso JC et al., personal observation), establishing at a lek as early as possible obviously represents an advantage, given the intense male intrasexual competition and the marked fidelity shown in later seasons to the lek first selected (Alonso et al., 1996a). Individuals settling early on a social group benefit from later advantages related to rank and breeding success in a wide range of species (e.g., Arnold, 1990; Gauthreaux, 1978; Nilsson and Smith, 1988; Pusey and Packer, 1987b; Russell and Rowley, 1993). Females did not show any of the relationships described for males between feeding rate as offspring and either age of settlement or dispersal distance. However, daughters may benefit more than sons from non-nutritional maternal care, such as information about nesting sites or help to achieve a high social status.

The differences in dispersal among individual males could probably be determined by the differences in the level of intrasexual competition and thus in the selective value of weight for each sex. The importance of intrasexual competition among male great bustards is supported by their marked sex dimorphism in weight, which is the highest within the family *Otididae* (Johnsgard, 1991) and one of the highest among all vertebrates. Large body size confers male great bustards obvious advantages during social rank fightings, probably increasing their breeding success. These patterns are similar to those found in several mammal species, in which male rank is positively correlated with reproductive success and strongly influenced by body size and growth during the first months of life (Clutton-Brock and Albon, 1982; Festa-Bianchet et al., 1994; Gese et al., 1996; Holekamp, 1984; Mech et al., 1991; White and Harris, 1994; Wigget and Boag, 1993).

Competition for resources

The main prediction of the resource-competition hypothesis, that young born in densely occupied areas should disperse farther, was not supported by our results. In fact, birds raised in areas with a high density of individuals of the opposite sex tended to reduce natal dispersal, which agrees with either the mate competition or the inbreeding avoidance hypothesis. In accordance with the former, birds tended to be more philopatric if around their natal areas they could expect to have more opportunities to find a mate. As for the latter, they tended to disperse farther when there was an increased risk of mating with close relatives in their natal areas due to the lower density of opposite-sex birds there. In a review of literature on mammals, Wolff (1993) found that juvenile dispersal was generally associated with the presence of opposite-sex but not same-sex parents within the natal home range, which he interpreted as supporting the inbreeding avoidance hypothesis.

Early-dispersing male offspring had a higher feeding rate before they dispersed than late dispering male offspring had at the same time, a result contrary to that predicted in a scenario of emigration due to lack of food, suggesting that competition for food resources was not a proximate cause of young male dispersal. The fact that mean food intake of young did not decrease with increasing bird densities further supports this conclusion. Finally, the marked sex bias in dispersal found in our study contradicts the prediction of a similar dispersal in both sexes derived from the resource-competition hypothesis.

Proximate factors

Our results support predictions from two ontogenetic processes that have been proximally related to the initiation of juvenile dispersal: the ontogenetic-switch hypothesis and the social subordination hypothesis. In accordance with the former, the earlier dispersal initiation by male offspring that had

fed at higher rates agrees with the prediction that heavier birds should disperse earlier (Dobson, in Holekamp, 1986). The relationship between early dispersal initiation in male great bustards and their presumed better physical condition due to higher food intake has already been discussed (see "Mate competition hypothesis"). The attainment of a threshold body weight has been shown to be necessary to initiate dispersal in various bird (Ferrer, 1992; Frumkin, 1994; Nilsson and Smith, 1985) and mammal species (Downhower and Armitage, 1984; Holekamp, 1984, 1986; Holekamp and Sherman, 1989; Wahlström and Liberg, 1995; Wauters et al., 1993). Because late dispersers are usually forced to occupy suboptimal habitat due to the rapid establishment of dominance asymmetries in relation to prior residency (Gauthreaux, 1978; Nilsson and Smith, 1988), selection for early dispersal initiation and rapid settlement after indepedence should be expected to be a general rule. Finally, the marginally significant correlation between age of independence and the rate of decrease of maternal feedings suggests that mothers could have some control of their offspring-independence dates by distributing the food delivery rates to them.

Some of our results also provide partial support to the social subordination hypothesis (Christian, 1970). First, the longer natal dispersal in less well-nourished (i.e., less competitive), young males agrees with the assumption that smaller and socially subordinate individuals are forced to disperse farther than dominant individuals. Second, the correlation between offspring independence dates and peak aggressive behavior from adult females in the flock suggests that family break-up might be triggered by intolerance from adult females. However, the long delay between highest aggression rate and date of offspring independence was surprising. Adult agonism has been causally related to yearling emigration only when both coincide in time (e.g., Wigget and Boag, 1992). However, adult aggression might act in great bustards in a similar way to that described by Pusey and Packer (1987a), who showed that adults in multifemale groups behave aggressively toward nonrelated juveniles during a prolonged period, ultimately leading to their dispersal. The role of adult agonism as a proximate cause of juvenile dispersal, as predicted by the social subordination hypothesis, nevertheless remains controversial. In a recent literature review, Wolff (1993) found that only in 4 of 49 mammal species did juvenile dispersal result from adult aggression. The increase in female agonism is often associated with the birth of new offspring. However, most young male great bustards left their mothers long before initiation of a new breeding cycle, in contrast to most young females. Male offspring did not seem to disperse as a direct response to aggression from adult males either, which usually ignored them.

Finally, we also found that male, but not female, offspring became independent and tended to disperse earlier from natal areas with a higher density of adult birds. If adult bird density was acting as a trigger of juvenile independence and dispersal as a consequence of food shortage in the natal area, we should probably have found such correlations in both sexes. A more plausible alternative explanation to early dispersal of young males, but not of young females, from densely occupied areas might be that those areas had higher adult bird densities due to a higher food abundance, which in turn enabled faster growth of young males. The absence of a similar correlation in young females is explained because for them the food intake, and thus the weight reached, is not an important proximate factor determining independence and dispersal initiation.

Conclusions

In conclusion, our results suggest that natal dispersal in the great bustard is a complex behavior determined by the interaction of multiple proximal and ultimate causes. At least some of them differ for males and females, as in several other species. Maintenance of genetic diversity and strong competition for mates are probably the most important ultimate causes of the marked natal dispersal of males, and may act synergistically. In a similar way as that suggested for some mammals, male-biased dispersal may have evolved in the great bustard to avoid close inbreeding and reinforced to improve male access to females through the strong intrasexual selection determined by its promiscuous breeding system, whereas females would have originally developed a mate-choice behavior enabling incest avoidance. Individual differences in male dispersal behavior may be explained by differences in their competitive ability, related mainly to the weight attained during their first months of life, which in turn may be ultimately determined by the quality of their mothers. Females show less variability in their dispersal, returning as a rule to their natal areas. Their reproductive success is more dependent on local food resources and can benefit from association with female kin; therefore, they are selected to be philopatric and accept their daughters on their natal areas. Another view is that male-biased dispersal is a consequence of female philopatry, and female philopatry is a consequence of male polygyny and short residence time in natal areas. The evolution of dispersal behavior in the great bustard is an exception in birds, where the usual pattern is female biased, even among lekking species, and represents an interesting case of evolutionary convergence with polygynous mammals.

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