Natal dispersal in great bustards: the effect of sex, local population size and spatial isolation

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Summary

1. We investigated the causes of natal dispersal in four Spanish areas where 35 breeding groups of the polygynous great bustard *Otis tarda* were monitored intensively. A total of 392 juveniles were radio-tracked between 1991 and 2006 by ground and via aeroplane to avoid potential biases derived from the non-detection of long-distance dispersers.

2. We explored 10 explanatory variables that were related to individual phenotypic features, habitat and conspecific traits in terms of group size and breeding performance, and spatial distribution of available breeding groups. Probability of group change and natal dispersal distances were investigated separately through multifactorial analyses.

3. Natal dispersal occurred in 47·8% of the birds and median natal dispersal distance of dispersers was 18·1 km (range 4·97–178·42 km). Sex largely determined the dispersal probability, with 75·6% of males being dispersers and 80·0% of females being philopatric, in contrast to the general pattern of female-biased dispersal found in most avian species.

4. Both the frequency of natal dispersal and dispersal distances were affected by the spatial distribution of breeding groups. More isolated groups showed a higher proportion of philopatric individuals, the effect being more evident in males than in females. This implies a reduction in gene flow in fragmented populations, as most genetic exchange is achieved through male dispersal. Additionally, dispersers hatched in more isolated groups tended to exhibit longer dispersal distances, which increases the associated energetic costs and mortality risks.

5. The dispersal decision was influenced by the number of conspecifics in the natal group. The individual probability of natal dispersal was related inversely to the size of the natal group, which supports the balanced dispersal model and the conspecific attraction hypothesis.

6. Overall, our results provide a good example of phenotypic plasticity and reinforce the current view that dispersal is an evolutionary complex trait conditioned by the interaction of individual, social and environmental causes that vary between individuals and populations.

Key-words: balanced dispersal, conspecific attraction, fragmented distribution, *Otis tarda*, philopatry, radio-tracking, sex-biased dispersal, Spain, steppe-land bird

Introduction

Dispersal is one of the most important processes affecting population dynamics and species evolution. It has profound consequences on the demography and persistence of populations and plays a primary role in the distribution and abundance of species (Greenwood 1980; Johnson & Gaines 1990; Clobert *et al.* 2001). It drives the gene flow between local populations and therefore influences the speciation process and biological adaptation to local conditions (Shields 1982; Avise 1994; Lenormand 2002). On the other hand, it is essential to metapopulation dynamics and survival (Hansson 1991; Hanski & Gilpin 1997; King & With 2002). In this respect, knowledge of the dispersal patterns of endangered species is crucial in the development of appropriate management plans (Meffe & Carroll 1994; Macdonald & Johnson 2001).

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Because human-induced habitat alteration and fragmentation represents one of the major environmental threats to the persistence of many species, their ability to disperse between patches of suitable habitat is essential to ensure their survival (Clobert *et al.* 2001).

Studies on natal dispersal, i.e. the movement of an individual from its natal site or group to the site or group of first breeding attempt (Greenwood 1980), have focused traditionally on sex-related differences in dispersal patterns in birds and mammals. As a result, two major and potentially complementary hypotheses have emerged: the mating system hypothesis and the avoidance of close inbreeding hypothesis (Greenwood 1980; Johnson & Gaines 1990; Pusey & Wolf 1996; Lambin, Aars & Piertney 2001). The first states that sexual asymmetries in the level of intrasexual competition for resources resulting from the prevailing mating system may lead to differences in the cost and benefits of dispersal among sexes. Thus, in resource-defence mating systems, which are the most widespread in birds, males have to acquire and defend territories and thus may benefit from remaining near their natal area, where they are most familiar with resources and are probably best able to compete for them. In mate-defence mating systems, which are prevalent in mammals, males are the more likely sex to disperse because they benefit from seeking to find accessible females (Greenwood 1980). The second hypothesis proposes that dispersal should contribute to separating kin of different sex to prevent mating with close relatives, which may produce disadvantageous effects on the viability and fecundity of offspring (Koenig & Pitelka 1979; Pusey 1987; Ralls, Ballou & Templeton 1988; Pusey & Wolf 1996; Keller 1998; Saccheri *et al.* 1998; Young *et al.* 1998). The direction of any sex bias will then depend upon the social and ecological conditions of the species and populations under study. However, novel theoretical models suggest that inbreeding avoidance cannot be the only ultimate cause of dispersal, and kin interaction has to be considered together with inbreeding avoidance (Perrin & Goudet 2001).

Other individual, social and environmental factors that could potentially affect dispersal patterns have remained less explored, but are the focus of a recently increasing research effort (Negro, Hiraldo & Donázar 1997; Verhulst, Perrins & Riddington 1997; Alonso *et al.* 1998; Spear, Pyle & Nur 1998; Forero, Donázar & Hiraldo 2002; Serrano & Tella 2003; Serrano *et al.* 2003; Winkler *et al.* 2005). For example, intraspecific competition has been proposed recurrently to promote dispersal and high or increasing population densities have been associated frequently with high levels of emigration (Clobert, Ims & Rousset 2004). This effect has been documented empirically in a wide number of species (e.g. Andreassen & Ims 2001; review in Lambin *et al.* 2001; Wauters *et al.* 2004) and also emphasized in some theoretical studies (Travis, Murrell & Dytham 1999; Amarasekare 2004), although a negative relationship between population density and emigration rates has been found in several cases (Kuussaari *et al.* 1998; Meylan, Clobert & Sinervo 2007). It also has been suggested that phenotypic differences in competitive abilities could bias dispersal behaviour towards poor quality or less competitive individuals, i.e. those hatched in later dates or with inferior body condition (social subordination hypothesis; Christian 1970).

The distribution and quality differences between patches of suitable habitat in spatially structured populations could also be moulding dispersal patterns. Such fragmented populations can be visualized as metapopulation or source–sink systems, where dispersal ensures connectivity of the subpopulations and also influences local abundances, patch occupancy and regional population dynamics (Pulliam & Danielson 1991; Hanski & Gilpin 1997). In recent years a huge effort has been dedicated to theoretical modelling of dispersal in spatially structured populations. Many of these studies have concentrated on the role of spatiotemporal heterogeneity in the evolution of dispersal and its consequences (Johnson & Gaines 1990; Holt & Barfield 2001). One of these models, often referred to as the 'balanced dispersal model', predicts the selection of dispersal when spatial heterogeneity occurs even in temporally constant environments (McPeek & Holt 1992). These authors found that when dispersal rates are free to vary between patches of different quality in terms of carrying capacity (i.e. habitat conditional dispersal), at evolutionary equilibrium the propensity of dispersing from a habitat is related inversely to the carrying capacity of that habitat (McPeek & Holt 1992; Lemel *et al.* 1997; Diffendorfer 1998). Thus, the number of individuals dispersing between patches becomes equal or 'balanced' and realized fitness in each patch is equal to 1. Other models have highlighted that dispersal behaviour can be altered through excessive patch isolation (Hanski & Gilpin 1997; Travis & Dytham 1998; Thomas & Kunin 1999; Fleishman *et al.* 2002). However, the amount of empirical information on factors governing movement rates between subpopulations is scarce and distributed irregularly among taxa. While a number of studies have been dedicated to dispersal in subdivided populations of some invertebrate species (e.g. Thomas & Harrison 1992; Hanski, Kuussaari & Nieminen 1994; Hill, Thomas & Lewis 1996; Doak 2000; Caudill 2003; Baguette & Schtickzelle 2006), empirical evidence for vertebrates is clearly deficient (Spendelow *et al.* 1995; Doncaster *et al.* 1997; Lindberg *et al.* 1998; Serrano & Tella 2003). This scarcity is due to both the enormous effort necessary to collect sufficient data about movement rates within a system of several subpopulations and also the difficulties linked to the detection of long-range dispersal events outside a limited study area (Koenig, Vuren & Hooge 1996).

To date, we have incomplete knowledge of the factors controlling the dispersal decisions of individuals of most species and populations. This is particularly true for spatially structured populations of long-lived species, even though the dynamics of such populations are especially interesting in terms of casting light on the evolutionary causes of such behaviour (Hanski & Gilpin 1997). One of these species is the great bustard *Otis tarda* (Linneo), a sexually dimorphic bird that exhibits a lek-like mating system and whose current populations inhabit cereal steppes from the Iberian Peninsula and north-western Morocco to eastern Asia (del Hoyo, Elliot & Sargatal 1996). Most great bustard populations have declined

in past decades, due mainly to hunting and agricultural intensification (Glutz, Bauer & Bezzel 1973; BirdLife-International 2000) and today the species is threatened globally (Collar, Crosby & Stattersfield 1994). Its last stronghold of about 24 500 individuals still survives in the Iberian Peninsula (Alonso, Palacín & Martín 2003b), but even here the species' range is highly fragmented and great bustards now occur in separate patches, many of which hold only a few tens of birds. These local populations are connected into metapopulations through dispersal, but landscape fragmentation due to rapidly expanding human infrastructures is causing habitat deterioration and isolation of reproductive groups and represents a serious threat to their survival (Alonso *et al.* 2004).

In this paper we study the causes determining the decision whether to disperse from or settle at the natal site, and the factors influencing dispersal distances in Spanish great bustards. Our long-term study (1991–2006) is based on ground and aerial radio-tracking of a large number of individuals between hatching and settlement as breeding adults at ages 2–5 years. This allowed us to gather detailed monitoring of individual movements and fates, avoiding potential biases derived from the non-detection of long-distance dispersers (Koenig *et al.* 1996). We explored the effects of individual, social and environmental features on natal dispersal patterns at four different areas in the Iberian Peninsula. Our main objectives were: (1) to identify individual features influencing both fidelity to the natal site and dispersal distances; (2) to evaluate the potential role of number of conspecifics on dispersal behaviour; and (3) to examine the effects of spatial isolation of natal site and availability of breeding groups on both dispersal rates and distances travelled. Specifically, we tested the following predictions: (a) a strong sex bias in natal dispersal distances should exist and be prevalent over other factors in all populations (inbreeding avoidance hypothesis); (b) the most competitive individuals, i.e. those hatched earlier in the season or with better body condition should show shorter natal dispersal distances than less competitive individuals (social subordination hypothesis); (c) the probability of dispersal should be related to the size of the natal group, either negatively (balanced dispersal) or positively (intraspecific competition); and (d) the propensity of dispersal should be reduced in individuals hatched in more isolated groups and dispersers should exhibit longer dispersal distances (spatial isolation hypothesis).

Methods

STUDY SPECIES AND STUDY AREAS

The great bustard is a large and highly sexually dimorphic bird, with adult males weighing 10–15 kg and females 4–5 kg. Males and females live in separate flocks and meet only for mating. In winter, males gather at traditional arenas where they defend their status or fight for a better one within the male flock. Later they display and attract females for mating. In this study males displaying at a lek site along with females visiting them to mate were defined as a breeding group. After mating, females nest close to the lek where they mated, although at variable distances from the mating site (Alonso, Morales &

Table 1. Numbers of breeding groups found in the four study areas and juvenile great bustards radio-marked and tracked until recruitment as breeding adults between 1991 and 2006

Area	Breeding groups	Radio-marked juvenile birds	Birds tracked until settlement (males, females)
Zamora	11	101	28 (11, 17)
Navarra	2	11	5 (4, 1)
Madrid	16	260	54 (28, 26)
Sevilla	6	20	3 (2, 1)
Total	35	392	90 (45, 45)

Alonso 2000; Magaña 2007), and take over all brood-rearing duties. The chicks (usually one, sometimes two) depend upon their mother during > 6 months. Typically, they leave their natal site later and perform an exploration phase of variable duration, after which they settle as breeding adults. During the non-mating period males and females behave as partial migrants between breeding and non-breeding areas (Alonso *et al.* 2000, 2001; Morales *et al.* 2000).

Our study was conducted between 1991 and 2006 in four Iberian areas where 35 great bustard breeding groups were monitored intensively (Table 1):
• Zamora province, north-western Spain: Important Bird Area 039 'Villafáfila', 41°50′ N 5°35′ W, 327 km², ~2000 birds;
• Navarra region, north-eastern Spain: 42°27′ N 1°57′ W, 180 km², ~30 birds;
• Madrid region, central Spain: IBA 074 'Talamanca-Camarma' (40°40′ N 3°25′ W, Madrid and Guadalajara, 520 km², ~1100 birds) and other smaller areas within Madrid province (~500 birds); and
• Sevilla province, southern Spain: IBA 238 'Llanura cerealista de Écija-Carmona' (37°25′ N 5°10′ W, 622 km², ~100 birds) and other minor areas within this province (~40 birds).

Further information concerning these populations can be found in Alonso *et al.* (1996, 2003a, 2005), Onrubia *et al.* (2000) and Viada (1998). The size and spatial distribution of the breeding groups monitored were markedly stable throughout the study.

DATA COLLECTION

We captured 392 young great bustards in early summer, 1991–2003 (Table 1), when they were 3–10 weeks old and still dependent on their mothers. All birds were marked with Biotrack radio-transmitters (< 3–5% of the bird's weight at capture) and located at least once per month throughout their lives using Telonics TR2-TS1 telemetry receivers. When a radio-tagged bird dispersed outside the range usually covered by ground tracking we performed aerial searches of its radio-signal using E-24 Beechcraft aeroplanes from the Spanish Air Force. After locating the signal from the aircraft we confirmed the sighting on the ground. With the aid of aerial radio-tracking we were able to locate all our marked birds, and in this manner we resolved the main problem commonly affecting dispersal studies, i.e. the emigration of individuals outside the study area (Koenig *et al.* 1996). The total flight time during this study exceeded 1000 h. As a result of high juvenile mortality (Martín *et al.* 2007), many radio-tagged birds died before settling and our initial sample size was reduced to 90 individuals that completed juvenile dispersal (Table 1). Sample sizes could not always be fixed by us because regional nature conservation authorities limited capture and marking permits: great bustards are classified as vulnerable in most Spanish autonomous communities and endangered in some of them.

NATAL DISPERSAL MEASUREMENTS

We defined two natal dispersal distances: the first was the straight-line distance between the place of hatching and the place of the first breeding attempt; the second was the number of breeding groups left behind by dispersing birds between their natal and breeding sites. Because the exact location of hatching was generally unknown, we used the place of capture as a proxy because families usually remain within a radius of *c.* 500 m of the nest during the first weeks of life of the chick.

Due to the lekking behaviour of this species the place selected for the first breeding attempt was different between sexes. In males we defined it as the centre of the display area or lek site where they settled as breeding adults, while in females we defined it as the location of the first nest. When juveniles were recruited as adults in a breeding group different from the natal group we defined them as 'dispersers', and when they showed natal group fidelity they were considered 'philopatrics'. In both sexes the site selected for the first breeding attempt is synonymous with settlement site because breeding dispersal movements between consecutive years are unusual (< 10%) in great bustards (Alonso *et al.* 2000, 2001; Morales *et al.* 2000; Magaña 2007), and thus natal dispersal accounts for most of the dispersal occurring during the life of great bustards.

VARIABLES ANALYSED

For each juvenile we recorded sex, body mass, length of wing arch, hatching date, as estimated from the growth curves based on body mass published by Heinroth & Heinroth (1928) and Radu (1969), and hatching year. For those birds that completed juvenile dispersal we also recorded body condition, calculated as the residuals from the analysis of covariance (ANCOVA) of log body mass as the dependent variable, sex as a factor and length of wing arch as a covariate ($F_{1,87} = 259 \cdot 02$, $P < 0 \cdot 001$), and age of settlement, which takes place during the second, third or fourth year of the bird's life.

We analysed several sets of explanatory variables that could influence dispersal patterns. Five variables represented individual features that could determine dispersal asymmetries among individuals: sex, Julian hatching date, hatching year, body condition at capture and age of settlement. Two variables described the characteristics of the natal group on the year of hatching and were used as possible indicators of their relative quality: group size after hatching (range: four to 361 individuals) and reproductive success (juveniles/females; range: 0·04–1·08). The third set of variables reflected local population characteristics around the natal location, which would indicate the availability of breeding groups where to settle, and the distance to reach them: distance to the nearest breeding group beyond the natal group (range: 2·3–23·5 km), number of breeding groups within 20 km radius (i.e. approximately the median dispersal distance of dispersers; range: 1–21) and number of breeding groups at 20–50 km (range 0–33). The spatial distribution of the breeding groups outside our four study areas was obtained from Estudios Territoriales Integrados (1994, 1998) and own unpublished data. Our sample of groups is representative of the range of group sizes and spatial isolation degrees of great bustards in Spain.

STATISTICAL ANALYSES

We used multifactorial approaches to identify the factors influencing the probability of group change and the magnitude of the natal dispersal distance. The probability of dispersal from the natal group was modelled using a logistic regression with a binomial response

variable (1, dispersers; 0, philopatric) and a logit link function. Natal dispersal distances were previously log-transformed and then used as dependent variables to model distances between hatching and first breeding attempt through multiple regression. Philopatric individuals were excluded from the second analysis. All variables and the interactions between factors were fitted to the observed data following a backward stepwise procedure with $P = 0 \cdot 05$ to enter and remove variables. The result is the most adequate model for explaining the variability in the response variable, where only the significant variables are retained. STATISTICA version 6·0 (StatSoft 2001) software was used for the analyses.

Results

Natal dispersal occurred in 43 birds (47·8%) and dispersal distances ranged from 0·14 to 178·42 km (median = 4·6 km, mean = 15·0 km, $n = 90$) showing a skewed and leptokurtic distribution (Fig. 1). Dispersal distances in number of groups ranged from 0 to 42 (median = 0 groups, mean = 4·6 groups, $n = 90$). When we excluded philopatric individuals from the analyses, dispersal distances ranged from 4·97 to 178·42 km (median = 18·1 km, mean = 29·3 km, $n = 43$) and dispersal distances in number of groups from 1 to 42 (median = 8 groups, mean = 9·7 groups, $n = 43$).

Dispersing birds settled between their second and fourth year of life. Females performed their first nesting attempt during the second year of life in 24% of the cases, third year in 64% and fourth year in 11%. Regarding males, 24% integrated in adult male flocks in their settlement site during their second year of life, 53% during their third year and 22% during their fourth year. Nevertheless, males began having access to copulations at an older age (Magaña 2007).

FACTORS AFFECTING GROUP CHANGE

Following a backward stepwise procedure we obtained a highly significant model for probability of dispersal ($\chi^2 = 42 \cdot 730$, d.f. = 3, $P < 0 \cdot 001$) that explained 34·3% of the observed variation and included three variables (Table 2). Sex largely determined dispersal frequency, with males showing a
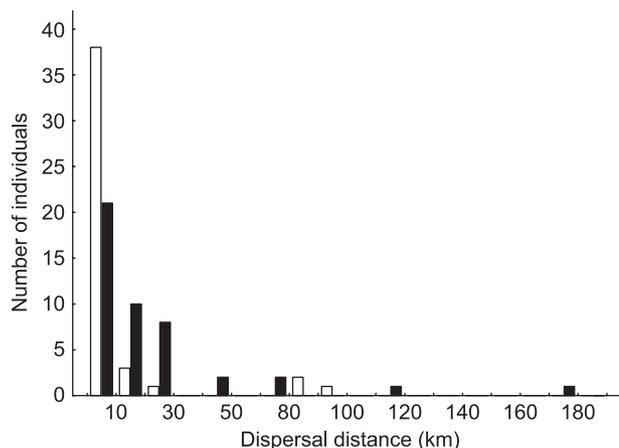

Fig. 1. Natal dispersal distances in male (black bars; $n = 45$) and female (white bars; $n = 45$) great bustards in Spain.
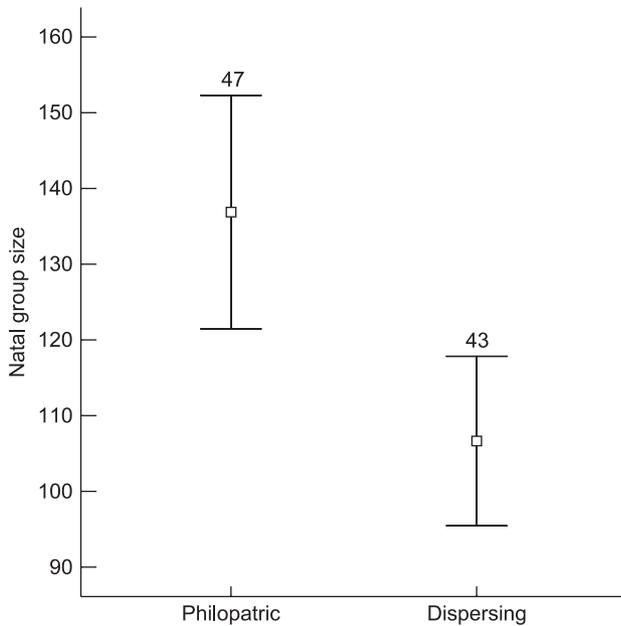
Fig. 2. Natal dispersal behaviour in relation to natal group size in great bustards. Means, standard errors and sample sizes are represented.

Table 2. Logistic regression model for probability of dispersal from the natal group in great bustards (only significant terms after backward selection procedure are included); SE: standard error

	Parameter estimate	SE	Wald Statistic	*P*
Intercept	−2·509	0·782	10·294	0·001
Sex (male)	3·264	0·680	23·040	0·000
Number of breeding groups within 20 km radius	0·185	0·060	9·433	0·002
Natal group size	−0·008	0·003	4·735	0·029
Explained deviance (%)	34·30			
Residual deviance	81·859			

far greater tendency to disperse from the natal group than females (75·6% vs. 20·0%, see Fig. 1). Controlling for sex differences, dispersal probability increased with the number of breeding groups in the vicinity of the natal location, and decreased with size of the natal group (Table 2, Fig. 2). When we looked at the interactions between the variables retained in the model, we also found a significant interaction between sex and number of breeding groups within 20 km around the natal location (Wald = 3·870, *P* = 0·049), which indicated that this effect was stronger in males than in females (Fig. 3). The remaining interactions were not significant (*P* > 0·10).

FACTORS AFFECTING DISPERSAL DISTANCE

Natal dispersal distances were larger in males than in females both in geographical distance (males, mean = 21·2 km, *n* = 45; females, mean = 8·8 km, *n* = 45; *t* = 2·169, d.f. = 88, *P* = 0·033) and in number of groups left behind (males, mean = 7·0 groups; females, mean = 2·2 groups; *t* = 2·862,
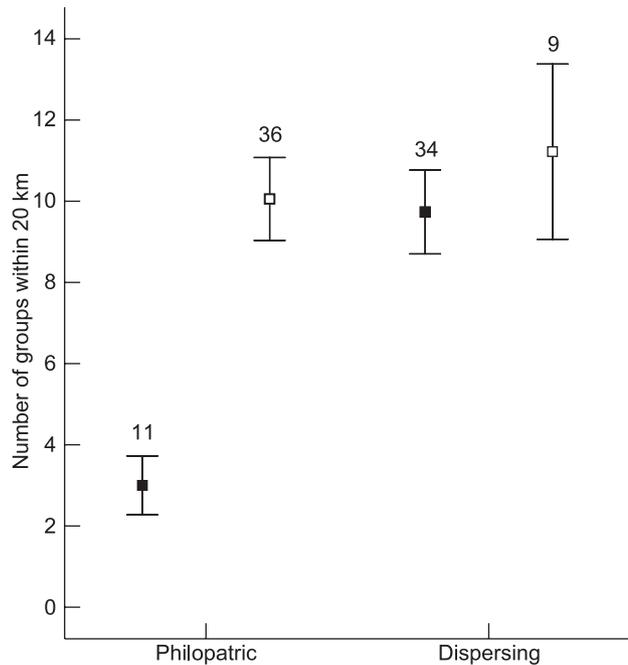

Fig. 3. Variation in natal dispersal of great bustards in relation to sex and number of breeding groups in the vicinity of the natal location. Means, standard errors and sample sizes are represented for males (solid squares) and females (open squares).

Table 3. Regression model for dispersal distance from the natal group in nonphilopatric great bustards (only significant terms after backward selection procedure are included); SE: standard error

	Parameter estimate	SE	*t*	*P*
Intercept	1·494	0·110	13·550	0·000
Number of breeding groups within 20 km radius	−0·022	0·009	−2·370	0·023
Explained variance (%)	12·05			
Residual variance	5·637			

d.f. = 88, *P* = 0·005). However, when we excluded philopatric individuals from the analyses we did not find such differences between sexes (geographical distance: males, mean = 27·3 km, *n* = 34; females, mean = 36·9 km, *n* = 9; *t* = −0·731, d.f. = 41, *P* = 0·469. Distance in number of groups: males, mean = 9·3 groups; females, mean = 11·2 groups; *t* = −0·528, d.f. = 41, *P* = 0·600).

The regression model for the geographical dispersal distances of dispersers was significant (*R²* = 0·120, *F* = 5·615, *P* = 0·022). This model retained one variable and showed that geographical dispersal distance was correlated inversely to the isolation of the natal group measured as the number of breeding groups within a radius of 20 km (Table 3). The interaction between sex and number of breeding groups within 20 km was not significant (*t* = 0·464, *P* = 0·645). The regression model for the dispersal distances in number of breeding groups did not retain any explanatory variable.

Discussion

Our results show that dispersal behaviour of great bustards is influenced mainly by sex, the presence of breeding groups in the surroundings of the natal location and the number of conspecifics in the natal group. Although the extreme male-biased natal dispersal pattern of this species has been described in previous papers (Alonso & Alonso 1992; Alonso *et al.* 1998; Martín *et al.* 2002), the present study confirms this sex-biased pattern in other areas of the species' distribution range in Iberia. The other important contribution of the current study was to show that the dispersal tendency was reduced when the natal group was large or relatively isolated from other groups.

SEX BIAS IN DISPERSAL

Within the set of potential explanatory variables describing phenotypic traits, we found only a significant effect of sex. Juvenile male great bustards showed a far larger rate of natal dispersal than females, which is in contrast to the general pattern of female-biased dispersal found in most avian species (Greenwood 1980; Clarke, Saether & Roskaft 1997). After juvenile dispersal, most males (75·6%) settled to breed in groups that were different from their natal group, while most females (80·0%) returned to their natal area after a short juvenile dispersal. This extreme sex bias favours the spatial segregation of kin of opposite sex, which reduces the chances of mating with close relatives and provides support to the inbreeding avoidance hypothesis (Pusey 1987; Pusey & Wolf 1996). As discussed in previous papers (Alonso & Alonso 1992; Alonso *et al.* 1998), the lek-like mating system exhibited by great bustards, which is exceptional regarding the widespread monogamy of birds, may have played an important role in the evolution of this male-biased dispersal pattern (Greenwood 1980; Clarke *et al.* 1997). As male great bustards display at traditional arenas without an apparent territory or resource defence behaviour, nor do they take part in the rearing of the young, philopatry does not seem to offer them clear evolutionary advantages regarding reproductive success. However, females take over all breeding duties and their reproductive success depends largely on food availability and individual experience (Quaisser *et al.* 1998; Morales, Alonso & Alonso 2002). By returning to the natal area they might obtain benefits from a previous familiarity with the breeding site, a reason why natural selection may have selected for fidelity to the natal site. In addition to inbreeding avoidance, father–son competition for mating access could also have favoured the observed male-biased dispersal (Alonso *et al.* 1998; Perrin & Goudet 2001).

EFFECT OF BREEDING GROUP ISOLATION

As for the relationship between dispersal patterns and the fragmentation in the distribution of species, a number of studies have pointed out that an increase in patch isolation might cause a decline in the exchange rates among local populations that build a metapopulation, as well as an increase in juvenile and natal dispersal distances (Opdam 1991; Saunders, Hobbs & Margules 1991; Tonkyn & Plissner 1991; Matthysen, Adriaensen & Dhondt 1995; Desrochers & Hannon 1997). Our results support this hypothesis. As predicted, isolated groups, i.e. those with fewer breeding groups in their vicinity, showed a higher proportion of philopatric individuals. Although it seems obvious that isolation of occupied patches could restrict exchange of individuals between them, empirical evidence from fragmented populations using individually marked birds is scarce (see Macdonald & Johnson 2001; Serrano & Tella 2003). It is interesting to note that the effect of spatial isolation on the probability of dispersal was more evident in males than in females. As a rule, and after a juvenile dispersal period visiting different patches, males tend to settle near their natal group but in a lek different from the natal one (Alonso *et al.* 1998). If this condition is not satisfied because the number of leks in the surroundings is limited and, also importantly, nearby sites are of low quality when compared to the natal patch, males are forced to choose between dispersing far away or remaining within their natal group. On the contrary, dispersal behaviour of females did not seem to be influenced by spatial isolation, at least in the range covered in this study, which agrees with their strong philopatric behaviour and may contribute to the gene exchange among subpopulations.

Our study showed that although dispersers from isolated groups were forced to travel long distances to settle, the number of breeding groups they left between natal and settlement group was not affected by the degree of isolation of the natal group. Dispersers left behind a fixed number of groups, independently of the geographical distance travelled. In this way dispersers probably ensure that they do not mate with genetically related individuals throughout the natal-site isolation gradient, in agreement with the inbreeding avoidance hypothesis (Pusey 1987; Pusey & Wolf 1996), and they minimize simultaneously the potential costs associated with dispersal behaviour. Dispersal decisions thus appeared to be influenced by environmental features such as the availability of neighbour groups, rather than being determined by a rigid endogenous control.

DENSITY-DEPENDENT EFFECTS ON DISPERSAL

The probability of dispersal was related inversely to the size of the natal group, which gives no support to the intraspecific competition hypothesis. Because group size could reflect habitat quality in terms of site-related characteristics such as food abundance, absence of predators, parasites or disturbances, our finding can be explained in the context of environmental heterogeneity as a key factor promoting dispersal (McPeek & Holt 1992). Indeed, dispersal models assuming patches of different quality, temporal stability and no constraints on dispersal predict an inverse relationship between local population size and local dispersal probability (balanced dispersal model: McPeek & Holt 1992; Lemel *et al.* 1997). This is based on dispersal being an ideal free distribution process that tends to equalize long-term reproductive success across patches (Clobert

et al. 2004). Another explanation to the reduced dispersal propensity in large-sized groups may be found in habitat selection theory and the possible use of presence and abundance of conspecifics as cues of habitat quality (conspecific attraction: Stamps 1988, 2001). Juveniles could use the size of the natal group as an indicator of habitat quality, and comparing that size with those of groups visited during the exploration phase they might be able to evaluate the potential benefits of being philopatric vs. dispersing. Both explanations are not incompatible, and our results provide support to both balanced dispersal and conspecific attraction. Finally, it could also be argued that in a promiscuous species such as the great bustard the probability of mating with close relatives is lower in large-sized groups and therefore birds hatched in large groups are not as constrained by the negative consequences of possible inbreeding and are less prone to disperse (see Frankham 1996).

Our current study did not identify a significant effect of the reproductive success at the natal group on the year of hatching upon the dispersal decision, probably because breeding success is subject to a high interannual variability (Martín 2001; Morales *et al.* 2002). Contrary to young productivity, the number of individuals in the breeding group showed a marked temporal autocorrelation, and it therefore seems to be a more reliable cue for juvenile great bustards to assess the quality of different patches. Within this line, some authors have proposed that public information (i.e. information on the performance of conspecifics, such as breeding success) is likely to produce valuable information for breeding patch selection only when it shows some degree of temporal autocorrelation between information gathering and the subsequent decision (Brown, Brown & Danchin 2000; Valone & Templeton 2002; Doligez *et al.* 2003; Danchin *et al.* 2004).

Conclusions and conservation implications

In conclusion, natal dispersal in the great bustard can be synthesized as follows: (1) the dispersal decision is determined strongly by sex, males typically being dispersers and females philopatric, but (2) social and environmental characteristics at the natal site influence the dispersal pattern by decreasing the proportion of dispersers in larger groups and increasing both the proportion of philopatrics and the natal dispersal distances of dispersers in spatially isolated groups. Our results provide a good example of phenotypic plasticity and strengthen the current view that dispersal is an evolutionary complex behaviour determined by the interaction of individual, social and environmental causes that may change between individuals and populations (Weatherhead & Forbes 1994; Clobert *et al.* 2001; Forero *et al.* 2002; Serrano *et al.* 2003).

Finally, and from a conservation-orientated perspective, the recent extinction of great bustard groups in some areas of the Iberian Peninsula has been explained by fragmentation and destruction of the traditional cereal-steppe habitat (Alonso *et al.* 2003b). This process entails not only a decline in number and size of occupied habitat patches (Saunders *et al.* 1991); it also reduces dispersal and thus connectivity

and genetic flow among populations, probably causing detrimental effects associated with excessive inbreeding (Koenig & Pitelka 1979; Ralls *et al.* 1988; Mills & Smouse 1994; Lynch, Conery & Bürguer 1995; Saccheri *et al.* 1998; Andersen, Fog & Damgaard 2004). It has been shown that dispersal regulates local and regional population dynamics by stabilizing growth rates and reducing the risk of extinction (Johnst & Brandl 1997; Bowne & Bowers 2004). Thus, a reduction in juvenile movements among subpopulations could lead to a decline in metapopulation viability (Stacey & Taper 1992; Lande 1993). In addition, the increasing distances between breeding groups force dispersing individuals to travel longer distances, probably causing an increase in dispersal-related mortality (Waser, Creel & Lucas 1994; Doherty & Grubb 2002; Schiegg, Walters & Priddy 2002), particularly that associated with collisions with power lines, which at present constitutes the main non-natural mortality cause of this species (Palacín *et al.* 2004; Martín *et al.* 2007). Dispersal towards small and isolated groups then happens less frequently than could be expected under a random pattern of dispersal and, thus, recruitment probabilities are reduced in such groups. Without the reinforcement process of immigration from other groups, isolated and particularly small groups might be more vulnerable to demographic reductions and higher extinction probabilities (see Ray, Gilpin & Smith 1991). Along with these constraints imposed by spatial isolation, the particularly complex breeding system of the great bustard predicts that after a local extinction, recolonization of an isolated patch appears highly unlikely (see Hanski *et al.* 1994). Therefore, conservation efforts should be directed at both preventing the extinction of any of extant breeding groups by protecting currently occupied sites and maintaining their size large enough to avoid the negative effects of demographic and environmental stochasticity.

Acknowledgements

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