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Genetic consequences of natal dispersal in the colonial lesser kestrel

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Abstract

Dispersal is a life-history trait that plays a fundamental role in population dynamics, influencing evolution, species distribution, and the genetics and structure of populations. In spite of the fact that dispersal has been hypothesized to be an efficient behavioural mechanism to avoid inbreeding, the expected relationship between dispersal and mate relatedness still remains controversial. Here, we examine the genetic consequences of natal dispersal, namely the higher chance of obtaining genetically less similar mates as a result of moving from natal to breeding sites, in a lesser kestrel (*Falco naumanni*) population. Relatedness between individuals tended to decrease with distance between their breeding colonies, indicating that the study population follows an 'isolation-by-distance' pattern of spatial genetic structure. Such a fine-scale genetic structure generates a scenario in which individuals can potentially increase the chance of obtaining genetically less similar mates by dispersing over larger distances from their natal colony. Using dispersal information and genotypic data, we showed that mate relatedness decreased with natal dispersal distance, an effect that remained significant both while including and excluding philopatric individuals from the data set. These results, together with the well known detrimental consequences of reduced genetic diversity in the study population, suggest that dispersal may have evolved, at least in part, to avoid the negative fitness consequences of mating with genetically similar individuals.

Keywords: *Falco naumanni*, genetic diversity, genetic structure, isolation by distance, microsatellites, relatedness

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Introduction

Matings between genetically related individuals generally result in progenies with low reproductive success due to the unmasking of deleterious or partly deleterious recessive alleles and increased homozygosity in offspring (Charlesworth & Charlesworth 1987; Falconer & Mackay 1996). The negative consequences of reduced genetic diversity are likely to be a strong selective agent for the evolution of life-history adjustments to avoid the costs associated with such crosses (Blouin & Blouin 1988; Pusey & Wolf 1996). Dispersal – in particular, natal dispersal for its higher frequency and impact on populations – has been hypothesized to be an efficient behavioural mechanism to avoid inbreeding because related individuals tend to be clustered around natal sites (Greenwood 1980; Greenwood & Harvey 1982; Perrin & Goudet 2001). However, in spite of the fact that inbreeding avoidance has been suggested to be a key driver for the evolution of natal dispersal, the expected relationship between dispersal and future mate relatedness still remains controversial (Lambin *et al*. 2001; Perrin & Goudet 2001).

Traditionally, it has been suggested that natal dispersal could have evolved as a mechanism to reduce the chance of encountering and mating with kin either passively (Greenwood 1980; Pusey 1987) or as an active behaviour promoted in the presence of relatives of the opposite sex (Lambin 1994; Pusey & Wolf 1996; Daniels & Walters 2000; Wheelwright *et al*. 2006). Dispersal may have also evolved if dispersers obtain a complementary mate to maximize offspring heterozygosity, and thereby fitness, rather than

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by simply avoiding mating with close relatives. In fact, the negative consequences of mating with genetically similar individuals do not only result from consanguineous unions but also as consequence of nonincestuous crosses involving unrelated individuals that share a higher number of common alleles (Bensch *et al*. 1994; Keller & Waller 2002). Accordingly, several studies have found correlations between individual genetic diversity at neutral markers and different components of fitness in open natural populations that, otherwise, show low rates of incestuous crosses (e.g. Bensch *et al*. 1994; Ortego *et al*. 2007a, b). Thus, given that consanguineous matings are generally rare in the field (Harvey & Ralls 1986; Ralls *et al*. 1986), it is likely that dispersal have evolved to avoid inbreeding in the broad sense of the term (Bensch *et al*. 1994; Keller & Waller 2002).

It is thought that a prerequisite necessary for dispersal to become an efficient mechanism to obtain a genetically less similar partner is the presence of at least a fine-scale spatial genetic structure (Van de Casteele & Matthysen 2006). Such situation may be relatively common as indicated by the fact that several contiguous and continuous populations follow an isolation-by-distance pattern of spatial genetic structure, where the distance between individuals is the overriding factor contributing to genetic differentiation (Foerster *et al*. 2003, 2006; Temple *et al*. 2006; Van de Casteele & Matthysen 2006). Hence, nonrandom genetic patterns are likely to be frequent in natural populations because of different forms of geographically restricted dispersal (Wright 1943; Slatkin 1993). The presence of a fine-scale genetic population structure will increase the chance of encountering genetically similar potential mates around natal sites. At the same time, such structure enables individuals to obtain genetically less similar partners by dispersing far away from natal sites (Foerster *et al*. 2003, 2006; Van de Casteele & Matthysen 2006). Under this scenario, natal dispersal would be an efficient and simple mechanism to obtain genetically less similar mates.

The assessment of genetic relationships among individuals is necessary to determine the consequences of natal dispersal on mate relatedness. The advent and application of DNA-based methods has allowed inferring genetic similarity between individuals from genotype data without actually knowing pedigrees, boosting the interest to study several aspects of dispersal in natural populations (e.g. Double *et al*. 2005; Temple *et al*. 2006; Van de Casteele & Matthysen 2006). Nevertheless, the expected genetic consequences of natal dispersal, namely the higher chance of obtaining genetically less similar mates as a result of moving from natal to breeding sites, have hitherto been rarely studied (Van de Casteele & Matthysen 2006).

The aim of this study was to analyse whether natal dispersal is a suitable mechanism to obtain genetically less similar mates using as model organism the lesser kestrel (*Falco naumanni*), a migratory and small-size colonial bird of prey. Previous studies have found that reduced genetic diversity has detrimental consequences on different components of fitness in this species, including fertility (Ortego *et al*. 2007a) and risk of parasitism (Ortego *et al*. 2007b; but see Ortego *et al*. 2007c). This would have favoured the evolution of behaviours to avoid mating with genetically similar individuals which may also involve natal dispersal. Using detailed dispersal information and genotypic data, we first analysed the spatial genetic structure in the study population and then examined the genetic consequences of natal dispersal, testing whether individuals are able to reduce future mate relatedness by dispersing over larger distances.

Materials and methods

Study population and field procedures

The study was conducted in La Mancha, central Spain (600–800 m above sea level), in an area covering approximately 1000 km^2 (39°20′N, 3°15′W; see Ortego *et al*. 2007a for a detailed description). In our study area, lesser kestrels form colonies of between 1 and 60 pairs located in abandoned farm houses where they nest under tiled roofs and inside holes in walls. The number of breeding pairs in the study area has increased from 127 pairs in 1993 to 350 pairs in 2005 (Ortego *et al*. 2007d). From 1991 on, we have studied a total of 30 colonies. Monitoring included the capture and banding of breeding adults, recording of breeding parameters, and intensive ringing of nestlings in the colonies (for more details on field methods, see Aparicio 1997). We located nests sites before the onset of egg-laying and each potential nest was regularly examined to determine laying date (Ortego *et al*. 2007a). Adults were trapped with a noose carpet or by hand during incubation, measured and individually marked with metallic and coloured plastic rings for further identification. Young were marked at hatching with a waterproof felt-tip pen, and they were banded 5–7 days later. Blood samples (100 μL) were obtained by venipuncture of the brachial vein and preserved in ~1200 μL ethanol 96% at –20 °C.

In this study, we focus on a 5-year period (2001–2005 breeding seasons) in which we carried out a more intensive monitoring of the population, and blood samples for DNA analyses were extensively collected. During this period, almost all nestlings born in the study area were ringed (~400 chicks/year) and the effectiveness of capture (i.e. the ratio between the number of captured birds and the total number of individuals at a colony) of breeding adults in the studied colonies was on average 70%. We analysed the consequences of natal dispersal on mate relatedness using data from individuals that were ringed as nestlings and recruited in the breeding population during 2003–2005 breeding seasons. These recruits included individuals 1–2 years old, depending on whether first breeding occurred at the first or second year of life (Negro *et al*. 1997; Serrano *et al*. 2003). Natal dispersal was calculated as the straight-line distance between natal and breeding colonies. We considered as philopatrics those individuals that returned to their natal colony to breed (i.e. natal dispersal distance was zero). We are confident that our data set is not substantially biased towards short dispersal distances because the maximum distance between two breeding colonies in the study area (39.3 km) is much longer than the median dispersal distance observed in both our (median dispersal distance, excluding philopatric individuals: males: 2.6 km; females: 4.1 km) and other populations of lesser kestrels (Negro *et al*. 1997; Serrano *et al*. 2003).

Genotyping

We genotyped 381 lesser kestrels across 11 highly polymorphic microsatellite markers: Fp5, Fp13, Fp31, Fp46-1, Fp79-4, Fp86-2, Fp89 (Nesje *et al*. 2000), Fu1, Fu2 (J. H. Wetton, unpublished), Fn1-11, and Fn2-14 (Ortego *et al*. 2007e; see Ortego *et al*. 2007a, b for microsatellite details). All individuals were genotyped at all these 11 microsatellite markers. We used QIAamp DNA Blood Mini Kits (QIAGEN) to extract and purify genomic DNA from the blood samples. Approximately 5 ng of template DNA was amplified in 10-µL reaction volumes containing 1× reaction buffer (67 mM Tris-HCL, pH 8.3, 16 mM $(NH_4)_2SO_4$, 0.01% Tween-20, EcoStart Reaction Buffer, Ecogen), 2 mM $MgCl_2$, 0.2 mM of each dNTP, 0.15 µM of each dye-labelled primer (FAM, HEX or NED) and 0.1 U of *Taq* DNA EcoStart Polymerase (Ecogen). All reactions were carried out on a Mastercycler epGradientS (Eppendorf) thermal cycler. The polymerase chain reaction programme used was 9 min denaturing at 95 °C followed by 30 cycles of 30 s at 94 °C, 45 s at the annealing temperature (Ortego *et al*. 2007a, e) and 45 s at 72 °C, ending with a 5-min final elongation stage at 72 °C. Amplification products were electrophoresed using an ABI 310 Genetic Analyser (Applied Biosystems) and genotypes were scored using GENESCAN 3.7 (Applied Biosystems).

Genetic structure

We analysed data on fine-scale genetic structure to explore the potential of individuals to obtain a genetically different pair by dispersing from their natal colony. In the same study population, we previously showed a complete absence of genetic structure in female lesser kestrels using a model-based clustering method (maximum number of clusters modelled = 5; Ortego *et al*. 2007a). Here, we expand this analysis to males and to both sexes combined. As in this previous study, we used a Bayesian model-based clustering method (STRUCTURE 2.1, Pritchard *et al*. 2000) for inferring population structure based on multilocus genotype data. We ran STRUCTURE assuming correlated allele frequencies and admixture, and conducted five independent runs of $K = 1–10$ to estimate the true number of clusters with 10^6 Markov chain Monte Carlo cycles, following a burn-in period of 100 000 iterations (Pritchard *et al*. 2000).

Spatial genetic structure of the study population of lesser kestrels was also tested using multilocus spatial correlation analyses in GENALEX version 6.0 (Peakall & Smouse 2006). This software calculates an autocorrelation coefficient r using two pairwise matrices, one containing geographical distances and the other containing squared genetic distances. The autocorrelation coefficient r is calculated for a specified number of distance classes, and provides a measure of the genetic similarity between pairs of individuals falling within each distance class. Pairwise squared genetic distances were obtained one locus at a time using the methods described in Peakall *et al*. (1995) and Smouse & Peakall (1999). Genetic distances for each locus are summed across all loci to obtain covariance matrices, under the assumption of statistical independence. This assumption is reasonable, since the 11 microsatellites employed showed no evidence of linkage disequilibrium (Ortego *et al*. 2007e). The linear pairwise geographical distance matrix was calculated from the x- and y-coordinates of the centre of each of the 30 colonies studied. All individuals breeding in the same colony were given identical coordinates. Variable distance classes were used because there were distances of up to 39 km between sample pairs, but previous research suggested that spatial autocorrelation was likely to occur only in the first distance classes (Double *et al*. 2005; Temple *et al*. 2006). Distance classes were set at 1 km, 2 km, 3 km, 4 km, 5 km, 10 km, 15 km, 20 km, 25 km, 30 km, 35, and 40 km. The same distance classes were used to analyse the entire population and male and female microsatellite genotypes separately. The calculated autocorrelation coefficients r, were plotted as a function of distance to produce spatial genetic autocorrelograms. Tests for statistical significance were performed using two methods: random permutation and bootstrap estimates of r, with the number of permutations and bootstraps set to 999 (Peakall *et al*. 2003).

Finally, we designed a new analysis to determine whether the study population follows an isolation-by-distance model of spatial genetic structure. In this case, we analysed the correlation between genetic and geographical distance only comparing opposite sex individuals, which may be more informative of the potential of individuals to obtain a genetically less similar mate by dispersing over larger distances in the study population. For this purpose, we first calculated for each individual its relatedness with all opposite-sex individuals captured breeding in the study area in a given year. To calculate relatedness between individuals, we used the similarity index described by Li *et al*. (1993) which has been proved to be an adequate marker-based estimator of relatedness in natural populations (Van de Casteele *et al*. 2001) and a good predictor of offspring heterozygosity in the study population (J. Ortego, unpublished data). On the other hand, we calculated the pairwise geographical distance between the colony of the individual being considered and the colony of all other opposite sex breeding adults. Metric distances were transformed as $\log(x + 1)$ in all analyses, because relatedness is expected to decrease linearly with the logarithm of spatial distance (Rousset 1997; e.g. Van de Casteele & Matthysen 2006). We then performed a linear regression analysis between pairwise relatedness values and distances, and obtained the correlation coefficient (r) of this regression. Negative r values indicate that genetic similarity decreases with distance between breeding sites, suggesting an isolation-by-distance pattern of genetic structure in the study population (Slatkin 1993). We repeated this process for each individual, and then we determined whether the r values obtained for all individuals differed significantly from zero using a Student's t-test. All these calculations were performed in EXCEL (Microsoft) using the macros of this program.

Correlates of mate relatedness

We analysed correlates of mate relatedness (estimated using the similarity index; Li *et al*. 1993; see above) using generalized linear mixed models (GLMMs) implemented with the GLIMIX macro of SAS (SAS Institute 2004). GLMMs allow analyses of data where the response variable is determined by both random and fixed effects. To avoid pair members contributing data in the same analysis, we randomly selected a single data from those individuals included in the relatedness database both as a natal disperser and as a mate of another disperser ($n = 10$ cases). To avoid pseudoreplication, we included into the analyses a single data per individual, only considering relatedness with the mate obtained in the year of recruitment (i.e. just after natal dispersal; e.g. Van de Casteele & Matthysen 2006). We constructed three separated GLMMs, fitting natal dispersal distance including philopatric individuals (covariate), dispersal distance excluding philopatric individuals (covariate), and philopatric/disperser status (fixed factor) together with the size of the breeding colony (covariate). Further, we also included year of recruitment as an additional covariate because it has been found that relatedness between mates has decreased in the study lesser kestrel population over the last six years (2000–05; Ortego *et al*. 2007d). No pair of these independent variables was significantly correlated; thus, we initially included all of them in our analyses. Natal dispersal distances were transformed as $\log(x + 1)$. The identities of natal and breeding colonies and cohort were included as random effects to control for the potential nonindependence of mate relatedness within colonies and cohorts, in the manner of a randomized complete block design to avoid pseudoreplication (Krackow & Tkadlec 2001).

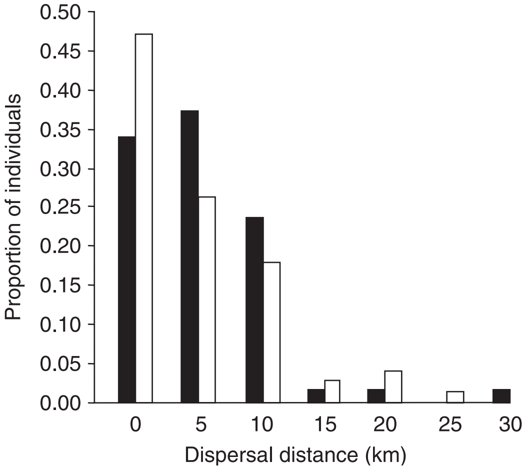

Fig. 1 Frequency distribution of dispersal distances for male (black bars: $n = 59$, mean ± SE = 3.1 ± 5.1 km) and female (white bars: $n = 72$, mean ± SE = 3.1 ± 4.9 km) lesser kestrels between natal and breeding colony; data from years 1991–2005.

Initially, each GLMM was constructed with all explanatory terms fitted, including first-order interactions and quadratic effects to account for potential nonlinear relationships. Final models were selected following a backward procedure, by progressively eliminating nonsignificant variables. The significance of the remaining variables was tested again until no additional variable reached significance. The result is the minimal most adequate model for explaining the variability in the response variable, where only the significant explanatory variables are retained. All tests were performed using the residual degrees of freedom (SAS Institute 2004). All P values refer to two-tailed tests.

Results

Considering all data obtained over the entire study period (i.e. from years 1991–2005), we found that a higher proportion of individuals (58.8%) dispersed from their natal colony. Only considering data from the period in which we analysed the genetic consequences of natal dispersal (i.e. 2003–2005 breeding seasons) when we carried out a more intensive monitoring of the population, we found that 68.1% of individuals dispersed from their natal colony. Dispersal distances ranged from 179 to 29 506 m (data from years 1991–2005: median = 3121, $n = 131$; Fig. 1; data from years 2003–2005: median = 2360, $n = 72$). After controlling for random effects (natal colony, cohort), we did not find any difference between sexes in natal dispersal distances during the entire study period (including philopatric individuals: $F_{(1,129)} = 0.44$; $P = 0.509$; excluding philopatric individuals: $F_{(1,76)} = 0.73$; $P = 0.396$) or when only data from birds that

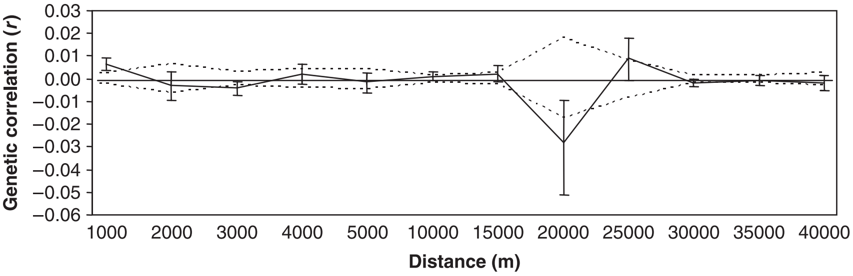

Fig. 2 Correlogram plot of the genetic correlation coefficient (*r*) as a function of distance. The permuted 95% confidence interval (dashed lines) and the bootstrapped 95% confidence error bars are also shown.

recruited in 2003–2005 breeding seasons were considered (including philopatric individuals: $F_{(1,70)} = 0.26$; $P = 0.613$; excluding philopatric individuals: $F_{(1,47)} = 0.03$; $P = 0.859$). However, females tended to be more philopatric than males (data from years 1991–2005: $F_{(1,129)} = 2.89$; $P = 0.092$; data from years 2003–2005: $F_{(1,70)} = 2.93$; $P = 0.092$).

Genetic structure of the study population

Results of our STRUCTURE analysis showed a maximum $\Pr(X \mid K)$ for $K = 1$, indicating no genetic subdivision within the study area. This result was consistent over different runs for the same *K* and when males and females were pooled together in the same analysis or when both sexes were analysed separately. In contrast, autocorrelation analyses found significantly positive *r* values within the 1-km distance class when both sexes were combined into the analyses (Fig. 2). This within-colony (< 1 km) positive autocorrelation is likely to be generated by some related individuals sharing the same colony as a consequence of the high philopatric behaviour reported in this species. However, analyses using only male or female genotypes were positive but not significant at any distance class, probably due to reduced sample size after separating sexes (data not shown). Similarly, when we analysed an isolation-by-distance model of spatial genetic structure only comparing opposite sex individuals, we found that relatedness decreased with distance between breeding colonies. When combining data over all the study years, with average *r* values for individuals captured in more than 1 year to avoid pseudoreplication, we obtained that correlation coefficients were significantly different from zero when both sexes were combined ($t = -2.148$, $P = 0.032$, $n = 381$; Fig. 3) and close to significance when males ($t = -1.771$, $P = 0.078$, $n = 170$; Fig. 3) and females ($t = -1.384$, $P = 0.168$, $n = 211$; Fig. 3) were analysed separately.

Natal dispersal and correlates of mate relatedness

Philopatric/disperser status and breeding colony size had no effect on mate relatedness (Table 1), probably because several individuals only dispersed over a short distance (Fig. 1). However, mate relatedness decreased with natal dispersal distance both while including and excluding philopatric individuals from the data set (Table 1; Fig. 4a). We tested whether the slope of the association between mate relatedness and natal dispersal distance differed between sexes and age classes (i.e. birds that recruited in their first or second year of life). For this purpose, we reanalysed our data including as predictor the interaction between sex/age class (fixed factors) and natal dispersal distance (covariate). The interaction with sex was not significant ($F_{(1,34)} = 0.97$; $P = 0.332$), indicating that the slope of the association between mate relatedness and natal dispersal distance did not differ between sexes. The age of recruitment had no effect on mate relatedness ($F_{(1,35)} = 0.74$; $P = 0.394$), and the slope of the association between mate relatedness and natal dispersal distance did not differ between individuals that recruited in their first and second year of life ($F_{(1,34)} = 0.82$; $P = 0.372$). As found in a previous study, mate relatedness decreased over the study period probably due to the demographic expansion observed in recent years together with the arrival of immigrants regularly introducing novel alleles into the

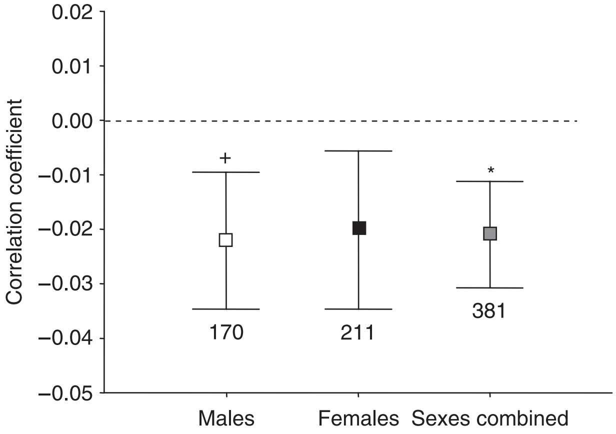

Fig. 3 Correlation coefficients (mean ± 1 SE) obtained from correlation analyses between relatedness (similarity index) and distance between breeding colonies (log-transformed) for all pairwise combinations including all opposite-sex individuals breeding in the study area in years 2003–2005. Males, open squares; females, filled squares; both sexes combined, grey squares. Figures under bars indicate number of individuals analysed. Signs mark observations that departed from zero (*$P < 0.05$; + = $P < 0.1$).

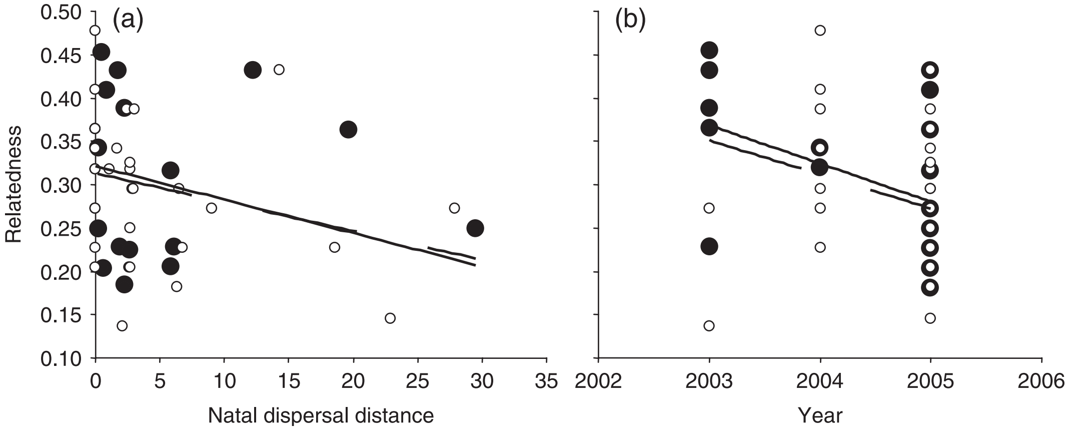

Fig. 4 Relationship of mate relatedness with natal dispersal distance (a), and year of recruitment (b) including (solid line regression) and excluding (dashed line regression) philopatric individuals from the GLMM analysis. Males, solid and bigger circles; females, open and smaller circles.

Table 1 GLMMs for mate relatedness (normal error and identity link function) in relation to natal dispersal distance [including (a) and excluding (b) philopatric individuals], philopatric/disperser status (c), year of recruitment, and size of the breeding colony. Natal dispersal distance was transformed as $\log(x + 1)$

	Estimate ± SE	Test	P
(a) Including philopatric individuals			
Explanatory terms			
Natal dispersal distance	–0.072 ± 0.024	$F_{1,36} = 8.89$	0.005
Year of recruitment	–0.045 ± 0.014	$F_{1,36} = 9.40$	0.004
Rejected terms			
Size of the breeding colony		$F_{1,35} = 0.06$	0.814
Covariance parameter estimates			
Natal colony	0	—	—
Breeding colony	0.001 ± 0.001	$Z = 0.73$	0.233
Cohort	0	—	—
(b) Excluding philopatric individuals			
Explanatory terms			
Natal dispersal distance	–0.089 ± 0.033	$F_{1,26} = 7.25$	0.012
Year of recruitment	–0.039 ± 0.016	$F_{1,26} = 5.68$	0.025
Rejected terms			
Size of the breeding colony		$F_{1,25} = 0.00$	0.953
Covariance parameter estimates			
Natal colony	0	—	—
Breeding colony	0	—	—
Cohort	0	—	—
(c) Philopatric/disperser status			
Explanatory terms			
Year of recruitment	–0.049 ± 0.016	$F_{1,37} = 9.50$	0.004
Rejected terms			
Philopatric/disperser status		$F_{1,37} = 1.54$	0.222
Size of the breeding colony		$F_{1,37} = 0.27$	0.608
Covariance parameter estimates			
Natal colony	0	—	—
Breeding colony	0.002 ± 0.002	$Z = 0.90$	0.185
Cohort	0	—	—

study population (Table 1; Fig. 4b; Ortego *et al.* 2007d). Quadratic terms and other interactions between independent variables were not significant in any analysis ($P > 0.1$ in all cases).

Discussion

Our results suggest the presence of a fine-scale spatial genetic structure in the study population of lesser kestrels.

Relatedness between individuals tended to decrease with distance between their breeding colonies but we found no significant segregation of individuals in discrete clusters, indicating that the study population follows an isolation-by-distance model rather than an 'island' model of spatial genetic structure (Rousset 1997; e.g. Foerster *et al*. 2003; Van de Casteele & Matthysen 2006). This pattern suggests that the exchange of individuals among colonies may be relatively common but somewhat geographically restricted (Wright 1943; Slatkin 1993). Available information on both natal and breeding dispersal in lesser kestrels based on recovery data of marked individuals indicates that fledglings generally recruit in their local colony or close to it whereas experienced breeders mostly remain faithful to breeding colonies thorough their entire life (Fig. 1; Negro *et al*. 1997; Serrano *et al*. 2001, 2003; G. Calabuig, unpublished data). Thus, the exchange of individuals seems to be restricted enough as to result in the nonrandom genetic pattern observed. The presence of a fine-scale genetic structure in our study population generates a scenario in which individuals can potentially increase the chance of obtaining genetically less similar mates by dispersing from their natal colony (Foerster *et al*. 2003; Van de Casteele & Matthysen 2006).

Lesser kestrels obtained genetically less-related partners after dispersing over larger distances and this association remained significant when philopatric individuals were excluded from the analysis. However, philopatrics and dispersers did not differ on future mate relatedness, indicating that dispersal distance matters but not dispersal status per se. As discussed above, the study population follows an isolation-by-distance pattern of spatial genetic structure and colonies do not form discrete clusters of genetically differentiated individuals, which can explain why lesser kestrels are only able in obtaining genetically less similar mates by dispersing over larger distances rather than merely by leaving the natal colony (Ronce *et al*. 2001). These results, together with the absence of differences between sexes in natal dispersal observed in our and other populations of lesser kestrels, suggest that sex-biased movements are not strictly required to obtain a genetically less similar mate after dispersal. However, the absence of such pattern probably increases the probability of accidental crosses between genetically similar individuals (Greenwood 1980). In this respect, we have found some cases of opposite-sex individuals that were born in the same or closely located colonies and subsequently mated together after dispersal (J. M. Aparicio, unpublished data). In any case, the distance between the natal colony of a focal individual and the colony of origin of the mate it obtains is highly correlated with dispersal distance ($F_{(1,76)} = 154.47$; $P < 0.001$; $r = 0.844$; data from years 1991–2005), suggesting that encounters of individuals from the same colony after dispersal are rare enough as to have a strong impact on the effectiveness of natal dispersal to reduce future mate relatedness.

An absence of association between dispersal and the presence of relatives of the opposite sex in natal sites have led several studies on birds including lesser kestrels (Negro *et al*. 1997; Serrano *et al*. 2003) to conclude that natal dispersal is not likely to have evolved to avoid inbreeding (Moore & Ali 1984). However, most studies have generally disregarded that philopatric behaviours can also increase the chance of mating with genetically similar individuals nongenealogically related. Further, a simple analysis of presence/absence of close kin in natal sites seems to be a poor approach to test the inbreeding avoidance hypothesis for several reasons. First, in colonial species such as the lesser kestrel, dispersal may not be strictly necessary to avoid mating with close kin because, with the exception of small-size colonies, a number of genealogically unrelated individuals will be available as potential mates in natal sites. Second, the positive age-assortative mating generally observed in lesser kestrels (J. M. Aparicio, unpublished data) and several other bird species (Ferrer & Penteriani 2003) may also contribute to reduce the chance that individuals mate with opposite- sex parents and half/full siblings from different cohorts. Third, the ability to recognize kin does not seem to be widespread in birds, and thus, the presence/absence of relatives may be simply useless to decide whether or not to disperse (Komdeur & Hatchwell 1999; Hansson *et al*. 2007). Therefore, how far individuals disperse may depend on the benefits associated with obtaining genetically less similar mates regardless of the presence of close kin in natal sites.

Separating the causes of natal dispersal as a mechanism to avoid inbreeding as opposed to reducing competition with kin is difficult, and the correlative nature of this study prevents us from determining whether inbreeding avoidance is the ultimate cause of natal dispersal in the study population (Perrin & Goudet 2001). In spite of natal dispersal can be influenced in part by the costs of inbreeding, may be also the case that the main force driving the evolution of natal dispersal is avoiding competition with kin and obtaining unrelated mates is only a by-product of that life-history trait characteristic that may have evolved decoupled to the deleterious consequences of mating between close relatives (Moore & Ali 1984; Lambin *et al*. 2001). Thus, regardless of the predominant evolutionary force, dispersal is likely to result in a reduction in both pressures. Unfortunately, experimental approaches to test whether individuals disperse to obtain genetic benefits are unfeasible and more studies are necessary to determine the general prevalence of our observed pattern in other species with contrasting breeding systems and patterns of population genetic structure (Van de Casteele & Matthysen 2006).

In conclusion, we have found that dispersal enables lesser kestrels to obtain genetically less-related partners.

The detrimental consequences of reduced genetic diversity in the study population suggest that dispersal may have evolved, at least in part, to avoid the deleterious consequences of mating with genetically similar individuals. Overall, these results evoke that patterns of dispersal are of major importance in determining the distribution of genetic variation in the study population and may have profound effects on the dynamics and persistence of small and isolated populations.

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References

Aparicio JM (1997) Costs and benefits of surplus offspring in the lesser kestrel (*Falco naumanni*). *Behavioral Ecology and Sociobiology*, **41**, 129–137.

Bensch S, Hasselquist D, VonSchantz T (1994) Genetic similarity between parents predicts hatching failure — non-incestuous inbreeding in the great reed warbler. *Evolution*, **48**, 317–326.

Blouin SF, Blouin M (1988) Inbreeding avoidance behaviors. *Trends in Ecology & Evolution*, **3**, 230–233.

Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics*, **18**, 237–268.

Daniels SJ, Walters JR (2000) Inbreeding depression and its effects on natal dispersal in red-cockaded woodpeckers. *Condor*, **102**, 482–491.

Double MC, Peakall R, Beck NR, Cockburn A (2005) Dispersal, philopatry, and infidelity: dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). *Evolution*, **59**, 625–635.

Falconer DS, Mackay TFC (1996) *Introduction to Quantitative Genetics*, 3rd edn. Longman, Harlow, UK.

Ferrer M, Penteriani V (2003) A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. *Animal Behaviour*, **66**, 137–143.

Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B (2003) Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature*, **425**, 714–717.

Foerster K, Valcu M, Johnsen A, Kempenaers B (2006) A spatial genetic structure and effects of relatedness on mate choice in a wild bird population. *Molecular Ecology*, **15**, 4555–4567.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.

Hansson B, Jack L, Christians JK *et al*. (2007) No evidence for inbreeding avoidance in a great reed warbler population. *Behavioral Ecology*, **18**, 157–164.

Harvey PH, Ralls K (1986) Do animals avoid incest? *Nature*, **320**, 575–576.

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, **17**, 230–241.

Komdeur J, Hatchwell BJ (1999) Kin recognition: function and mechanism in avian societies. *Trends in Ecology & Evolution*, **14**, 237–241.

Krackow S, Tkadlec E (2001) Analysis of brood sex ratios: implications of offspring clustering. *Behavioral Ecology and Sociobiology*, **50**, 293–301.

Lambin X (1994) Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (*Microtus townsendii*). *Ecology*, **75**, 224–235.

Lambin X, Aars J, Piertney SB (2001) Dispersal, intraspecific competition, kin competition and kin facilitation: a review of empirical evidence. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt AA, Nichols JD), pp. 123–142. Oxford University Press, Oxford, UK.

Li CC, Weeks DE, Chakravarti A (1993) Similarity of DNA fingerprints due to chance and relatedness. *Human Heredity*, **43**, 45–52.

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? *Animal Behaviour*, **32**, 94–112.

Negro JJ, Hiraldo F, Donazar JA (1997) Causes of natal dispersal in the lesser kestrel: inbreeding avoidance or resource competition? *Journal of Animal Ecology*, **66**, 640–648.

Nesje M, Roed KH, Lifjeld JT, Lindberg P, Steen OF (2000) Genetic relationships in the peregrine falcon (*Falco peregrinus*) analysed by microsatellite DNA markers. *Molecular Ecology*, **9**, 53–60.

Ortego J, Calabuig G, Cordero PJ, Aparicio JM (2007a) Egg production and individual genetic diversity in lesser kestrels. *Molecular Ecology*, **16**, 2383–2392.

Ortego J, Aparicio JM, Calabuig G, Cordero PJ (2007b) Risk of ectoparasitism and genetic diversity in a wild lesser kestrel population. *Molecular Ecology*, **16**, 3712–3720.

Ortego J, Cordero PJ, Aparicio JM, Calabuig G (2007c) No relationship between individual genetic diversity and prevalence of avian malaria in a migratory kestrel. *Molecular Ecology*, **16**, 4858–4866.

Ortego J, Aparicio JM, Calabuig G, Cordero PJ (2007d) Increase of heterozygosity in a growing population of lesser kestrels. *Biology Letters*, **3**, 585–588.

Ortego J, Gonzalez EG, Sánchez-Barbudo I, Aparicio JM, Cordero PJ (2007e) Novel highly polymorphic loci and cross-amplified microsatellites for the lesser kestrel *Falco naumanni*. *Ardeola*, **54**, 101–108.

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, **6**, 288–295.

Peakall R, Smouse PE, Huff DR (1995) Evolutionary implications of allozyme and RAPD variation in diploid populations of dioecious buffalograss *Buchloe dactyloides*. *Molecular Ecology*, **4**, 135–147.

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, 57, 1182–1195.

Perrin N, Goudet J (2001) Inbreeding, kinship and the evolution of natal dispersal. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt AA, Nichols JD), pp. 123–142. Oxford University Press, Oxford, UK.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, **2**, 295–299.

Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends in Ecology & Evolution*, **11**, 201–206.

Ralls K, Harvey PH, Lyles AM (1986) Inbreeding in natural populations of birds and mammals. In: *Conservation Biology* (ed. Soulé ME), pp. 35–56. Sinauer Associates, Sunderland, Massachusetts.

Ronce O, Olivieri I, Clobert J, Danchin E (2001) Perspectives on the study of dispersal evolution. In: *Dispersal* (eds Clobert J, Danchin E, Dhondt AA, Nichols JD), pp. 123–142. Oxford University Press, Oxford, UK.

Rousset F (1997) Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

SAS Institute (2004) *SAS/STAT 9.1 User's Guide*. SAS Institute, Cary, North Carolina.

Serrano D, Tella JL, Forero MG, Donazar JA (2001) Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology*, **70**, 568–578.

Serrano D, Tella JL, Donazar JA, Pomarol M (2003) Social and individual features affecting natal dispersal in the colonial lesser kestrel. *Ecology*, **84**, 3044–3054.

Slatkin M (1993) Isolation by distance in equilibrium and nonequilibrium populations. *Evolution*, **47**, 264–279.

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity*, **82**, 561–573.

Temple HJ, Hoffman JI, Amos W (2006) Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the white-breasted thrasher, *Ramphocinclus brachyurus*. *Molecular Ecology*, **15**, 3449–3458.

Van de Casteele T, Galbusera P, Matthysen E (2001) A comparison of microsatellite-based pairwise relatedness estimators. *Molecular Ecology*, **10**, 1539–1549.

Van de Casteele T, Matthysen E (2006) Natal dispersal and parental escorting predict relatedness between mates in a passerine bird. *Molecular Ecology*, **15**, 2557–2565.

Wheelwright NT, Freeman-Gallant CR, Mauck RA (2006) Asymmetrical incest avoidance in the choice of social and genetic mates. *Animal Behaviour*, **71**, 631–639.

Wright S (1943) Isolation by distance. *Genetics*, **28**, 139–156.

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