Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues

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Summary

1. The role of individual experience vs. the use of conspecific cues on breeding dispersal decisions have seldom been determined in colonial birds. We studied causes of breeding dispersal in the lesser kestrel (*Falco naumanni*), a species that breeds in colonies of variable size as well as solitarily. During a 6-year study in Spain, we gathered information on 486 subsequent breeding attempts and on 26 explanatory variables which evaluated individual experience, conspecific cues in terms of breeding performance and colony size, and different ecological and populational characteristics.

2. Two decisions were separately analysed: whether or not to disperse, and how far to move. Generalized Linear Mixed Models (GLMMs) allowed us to identify the relative contribution of each explanatory variable while controlling for the non-independence of individual dispersal decisions across years.

3. Females seemed to disperse more often than males (34% vs. 19%), and both sexes apparently dispersed less with age. However, a GLMM showed that experience (i.e. the number of years a bird bred in a particular colony) was the only factor influencing breeding dispersal. Birds showed higher site fidelity the greater their experience in a colony, which could be related to benefits derived of increased local familiarity. A second GLMM showed that, before birds acquired experience in a particular colony, individual nest failure due to predation and proximity to other colonies increased the probability of dispersal, dispersal being also higher in colonies with poor conspecific breeding success. Furthermore, solitary nesting birds were more prone to disperse and dispersal probability decreased the larger the colony of origin, according to fitness expectations associated with colony size.

4. A GLMM explaining dispersal distances retained two variables – birds dispersed farther the lower the breeding density in the surroundings, and the larger the distance to the nearest colony. Dispersing birds tended to settle within their previous foraging areas (median dispersal distance = 1·6 km), being constrained by the availability of nearby colonies.

5. Lesser kestrels mainly cue on their own breeding performance and experience in a particular colony at the time of taking a dispersal decision. However, inexperienced birds also partially cue on the size and breeding success of their own colonies (but not on the size or breeding performance of other colonies), and birds moved larger distances when dispersing from areas of low populational density. These results support some degree of conspecific attraction.

Key-words: breeding dispersal, breeding experience, conspecific cues, facultative coloniality, *Falco naumanni*.

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Introduction

Dispersal is one of the important traits in the life-history of animals, affecting the structure and dynamics of populations (Greenwood & Harvey 1982; Johnson & Gaines 1990; Dieckmann, O'Hara & Weisser 1999). It is common with two different kinds of dispersal processes during an individual's lifetime: natal dispersal (movement between birth place and the first breeding place), and breeding dispersal (movements between successive breeding places) (Greenwood 1980).

Avian breeding dispersal has received much attention in recent decades. Research usually shows female-biased dispersal (Greenwood 1980) which could be related to differences in gender roles in territory acquisition and defence. Another important finding is that individuals tend to be more philopatric with increasing age (Desrochers & Magrath 1993; Bried & Jouventin 1998; Forero *et al.* 1999), which could be understood in terms of increased benefits from breeding-site familiarity (Newton & Marquiss 1982; Pärt 1995; Forero *et al.* 1999). Other factors determining breeding dispersal have been related to the previous reproductive performance of individuals (e.g. Gavin & Bollinger 1988; Beletsky & Orians 1991; Switzer 1997; Forero *et al.* 1999) and other aspects of breeding-site quality (Bollinger & Gavin 1989; Wiklund 1996; Forero *et al.* 1999). Movements after mate loss have also been reported for numerous bird species (Wiklund 1996; Flynn, Nol & Zharikov 1999; Forero *et al.* 1999).

Dispersal patterns may vary among species with different life histories and breeding systems (Paradis *et al.* 1998). In particular, coloniality offers an interesting framework for research on dispersal strategies. It seems likely that dispersal in colonial birds could be influenced by colony-related characteristics, such as the spatial distribution of the colonies (Aebischer 1995; Spendelow *et al.* 1995). Moreover, fitness of individuals is known to vary among colonies and with colony size (Brown, Stutchbury & Walsh 1990; Brown & Brown 1996; Tella 1996). Therefore, individuals of colonial species are expected to make dispersal decisions based on their own experience as well as on conspecific cues, such as breeding performance and size of the colonies (Smith & Peacock 1990; Reed & Dobson 1993; Brown & Rannala 1995; Danchin & Wagner 1997; Tella, Hiraldo & Donázar 1998). Hence, dispersal probability would increase if fitness prospects are higher in other colonies than in the 'home' colony (Spendelow *et al.* 1995).

Although factors influencing breeding dispersal have been examined in colonial birds (e.g. Spendelow *et al.* 1995; Oro, Pradel & Lebreton 1999), few studies have considered conspecific cues (Danchin, Boulinier & Massot 1998; Schørring, Gregersen & Bregnballe 1999; Brown, Brown & Danchin 2000), and the combined effects of several factors driving dispersal (see Forero *et al.* 1999). Furthermore, facultatively colonial species (i.e. those breeding in colonies of varying size as well as solitarily) offer still unexplored research avenues

for the study of breeding dispersal in birds. Within populations of these species, individuals could make dispersal decisions based on their own experience, on conspecific cues, or on both, and even in different degree depending on the breeding strategy chosen (nesting solitarily or in colonies of different size).

In this paper, we study causes of breeding dispersal in the lesser kestrel *Falco naumanni* (Fleischer), a facultatively colonial falcon for which breeding dispersal patterns are almost unknown (Negro 1997). We gathered information from a Spanish population during a 6-year monitoring programme of banded individuals. Contrary to most studies dealing with dispersal as a single process, we have considered two decisions: whether or not to change colony, and how far to disperse (Negro, Hiraldo & Donázar 1997). Since individual and/or environmental factors often co-vary, we employed an extension of traditional Generalized Linear Models (McCullagh & Nelder 1983) in an attempt to separate their effects on dispersal decisions (Forero *et al.* 1999). Our main aims were: (i) to describe dispersal patterns, examining variations related to sex and age of individuals; (ii) to determine whether probability of dispersal and dispersal distances result from the same causes; (iii) to identify individual and conspecific cues affecting dispersal decisions; and (iv) to assess the relative contribution of these different cues in different scenarios of bird aggregation.

Methods

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The lesser kestrel is a small migratory falcon inhabiting open areas of the Western Palearctic where it breeds mainly in buildings, and feeds mostly on invertebrates (Negro 1997). Monogamy is the predominant mating system, while polygyny and extra-pair fertilizations are rare (Negro *et al.* 1996; Tella *et al.* 1996a). Males choose nest sites, display to attract females, and then feed their mates during the prelaying period (Donázar, Negro & Hiraldo 1992). Both sexes incubate (usually 4–5 eggs) and raise the young, but only females incubate and brood young chicks at night (Donázar *et al.* 1992; authors' unpublished data). Birds are sexually dichromatic from the nestling stage onward (Tella *et al.* 1996b). Average life-span for the species is 3–4 years (Negro 1991).

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The study was carried out in the Mid Ebro Valley, North-eastern Spain (*c.* 10 000 km^2; Fig. 1). An isolated population of lesser kestrels breeds there in abandoned farmhouses, using cavities under the tiles of roofs for nesting (Forero *et al.* 1996). Distances between occupied buildings range from 50 to 12 600 m. Lesser kestrels breed as solitary pairs or in colonies ranging from 2 to 43 pairs, with a total of 553 pairs breeding in 108 buildings in 1998. Most buildings were occupied by one
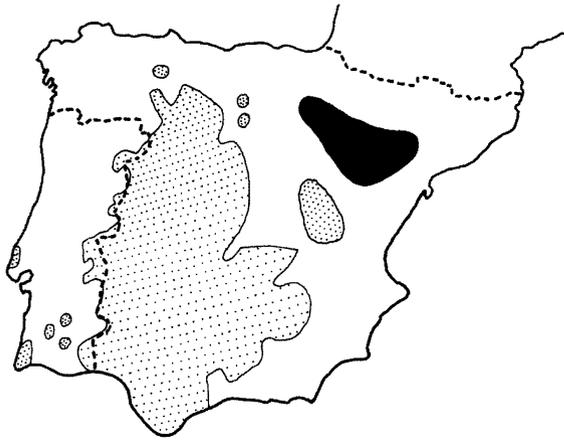
Fig. 1. Breeding distribution of lesser kestrels in Spain (shaded area) and location of the studied population (dark area).

to three pairs, but most birds bred in medium (4–27 pairs) and large (> 27 pairs) colonies (Tella 1996). Nest-hole availability and suitable buildings for breeding did not represent a limiting factor for lesser kestrels' movement in the studied population (Forero *et al.* 1996; Blanco & Tella 1997). The landscape around nest sites was a homogeneous pseudo-steppe, with extensive dry-farmed cereal crops where lesser kestrels foraged. Home ranges of lesser kestrels during the chick-rearing period in the study area averaged $12\cdot36 + 8\cdot28$ km^2 (Tella *et al.* 1998).

Studies on dispersal of vertebrates are often biased because they are based on small study areas; thus, long-distance dispersers could be unnoticed (Koenig, Vuren & Hooge 1996). We tried to reduce this kind of bias by surveying the large area occupied by an isolated population (Fig. 1). The largest distance between two occupied buildings surveyed in any one year (130·5 km) was much larger than the observed median and maximum dispersal distances (1·6 and 65·22 km, respectively, see Results). Moreover, we have not received information about metal band recoveries of breeding individuals outside the limits of our area (897 adults and 5151 fledglings ringed between 1988 and 1997).

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The lesser kestrel population was intensively monitored between 1993 and 1998. During this period, we tried to band as many fledglings and adults as possible in all colonies. We used plastic coloured bands with a two-character code, thus offering an unique code for each bird that could be read using spotting scopes. We estimate that more than 90% of the fledglings were banded annually, and so we knew their exact age as adults. We also knew the age of many adults captured during the study period because they had been banded with metal rings in previous years (1988–92; Tella *et al.* 1996c). Overall, in 1993–97 we colour-banded 4014 birds (3395 fledglings and 619 adults).

Every breeding season, from February to April, we searched for banded birds by visiting all buildings suitable

for lesser kestrels (i.e. with available cavities under the roofs; Forero *et al.* 1996). Plastic colour bands were read from hides at a distance (up to 100 m) without disturbing the birds. During these surveys, we counted and mapped all nests to obtain colony size and to plot each identified bird in its nest. Additionally, the monitoring of nests (see below) allowed us to capture some banded adults which were unnoticed during the band-reading surveys. As a result, we identified 2133 adults between 1993 and 1998. For this study, we used only those adults observed during: (i) the 2 weeks preceding laying (the period of female fertility, maximum copulation rates, and strong pair-bonding; Negro, Donázar & Hiraldo 1992); (ii) incubation; and (iii) chick-rearing. We therefore avoid any mistake about the actual breeding performance of individuals due to potential mate or nest changes which could occur early in the season.

Breeding performance of focal pairs was monitored by visiting their nests about four times during the season. Focal pairs were randomly selected to represent the whole colony (i.e. pairs with different phenologies and distributed throughout the colony), their number varying from all pairs in small colonies to 33–60% of the pairs in the largest ones. In doing so, we reduced the time required for nest monitoring (usually 5–20 min per colony) and thus potential investigator effects on breeding performance. At some colonies there was a risk of nestlings switching nests (Tella *et al.* 1997), so we banded the chicks with a metal ring at 7–15 days old to detect cases of nest switching and then correctly recorded the actual number of fledglings produced by each focal nest in a later visit. In addition to focal fledglings, we tried to band with both metal and plastic bands all nestlings of the population some days before flying. All banded fledglings were weighed and the length of the 8th primary measured to estimate nestling age and laying date (Negro *et al.* 1997). Most nest failures were due to predation, mainly by red foxes [*Vulpes vulpes* (L.)] and rats [*Rattus rattus* (L.)] (Blanco & Tella 1997), as determined through examination of remains of eggs or chicks and predator's tracks. Losses of young birds without evidence of predation, and chicks found freshly dead that were underweight for their age, were attributed to starvation (Negro 1991). We considered as fledged those kestrels which were older than 21 days at the last visit to the nest, and whose remains were not found in further visits to the colonies when we searched for dead fledglings.

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Breeding dispersal measurements

We determined U.T.M. co-ordinates of all buildings occupied by lesser kestrels during the study period. Each building occupied by at least one pair was defined as a 'colony'. In our study area, pairs breeding in a certain colony share common features, such as risk of predation and number of neighbours (Tella 1996).

Table 1. Explanatory variables used to assess the factors affecting the probability of colony change and dispersal distances in lesser kestrels through GLMM modelling. All variables were measured in year t, i.e. before a individual dispersed or had the opportunity to disperse

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Characteristics of individuals
INDIVIDUAL IDENTITY
SEX
AGE: in years
EXPERIENCE: number of years breeding in the same colony until year t
AGE OF THE MATE
MATE CHANGE: change mate or not

Breeding performance of individuals
LAYING DATE: in Julian calendar
PREDATION: total nest failure due to predation or not
BREEDING SUCCESS: at least one chick fledged or not
PRODUCTIVITY: number of chicks fledged

Characteristics of colony
COLONY IDENTITY
COLONY SIZE: number of breeding pairs
PREDATION IN NEIGHBOURS: proportion of neighbouring nests with total breeding failure due to predation
MEAN PRODUCTIVITY OF NEIGHBOURS
MEAN PRODUCTIVITY OF NEIGHBOURS EXCLUDING PREDATED NESTS

Differences between colony of origin and colony of destination
DIFFERENCE IN MEAN PRODUCTIVITY BETWEEN NEIGHBOURS OF COLONY OF ORIGIN AND COLONY OF DESTINATION
DIFFERENCE IN MEAN PRODUCTIVITY BETWEEN THE NEIGHBOURS OF THE COLONY AND THE REST OF THE POPULATION
DIFFERENCE IN PREDATION RATES BETWEEN THE COLONY OF ORIGIN AND COLONY OF DESTINATION
DIFFERENCE IN COLONY SIZE BETWEEN THE COLONY OF ORIGIN AND COLONY OF DESTINATION

Characteristics of the population
BREEDING DENSITY: number of breeding pairs within a 1600-m radius (median dispersal distance) excluding those of the own colony
NUMBER OF SURROUNDING COLONIES, within a 1600-m radius
NUMBER OF SURROUNDING LARGE COLONIES: number of colonies with more than 10 pairs within a 1600-m radius
DISTANCE TO THE NEAREST COLONY
MEAN PRODUCTIVITY OF THE WHOLE POPULATION
MEAN PRODUCTIVITY OF THE WHOLE POPULATION EXCLUDING PREDATED NESTS
YEAR

This, together with the fact that distances covered between nests were much larger among than within colonies, moved us to define as 'philopatric' those birds that returned to the same building where they bred the year before independently of the nest-hole occupied. On the other hand, 'dispersers' were individuals that changed buildings between two consecutive breeding attempts. For dispersers, we measured dispersal distance as the straight-line distance between the two breeding sites. Birds that were prevented from nesting in the same building 1 year later, due to building demolition or restoration, were removed from the analyses in order to avoid biases derived from forced site change. After that, we examined dispersal processes in 28 colonies-year where kestrels bred solitarily, 29 colonies-year gathering 2–3 breeding pairs, 40 comprising 4–9 pairs, 33 with 10–27 pairs, and 10 colonies with more than 27 pairs. This data set accurately reflects the whole range of colony sizes and the percentage of individuals that bred in colonies of different size in the whole population (Tella 1996).

Factors affecting dispersal

To determine causes of breeding dispersal we chose a series of variables evaluating individual and environmental conditions, colony characteristics, and breeding performance for each individual and its conspecifics (Table 1). First, a set of six variables deals with characteristics of the individuals and their mates in year t (i.e. before it abandoned the colony or had the opportunity to abandon). It includes individual identity, which allows us to detect if breeding dispersal decisions are more variable among than within individuals. Secondly, four variables evaluate breeding performance of the bird in year t as cues based on individual breeding experience. Since the risk of predation and breeding success in our population largely varies between colonies and with colony size (Tella 1996), birds could also base their decisions on cues from conspecifics. Thus, five variables describe the colony performance where the individual settled in year t. We expected that birds inhabiting larger and/or more successful colonies would

have lower dispersal probabilities since performance-based (Danchin *et al*. 1998) or simple conspecific attraction would be in operation (Tella *et al*. 1998). Colony identity helps to detect whether or not dispersal decisions varied more among than within colonies. Another four variables evaluate differences between the colony of origin and the colony of destination in year *t*. If individuals base decisions on cues from conspecifics, one can predict that they would more likely disperse to colonies with higher breeding success (performance-based attraction; Danchin *et al*. 1998) and/or higher number of breeding pairs (conspecific attraction; Smith & Peacock 1990; Danchin & Wagner 1997) than their own colony. On the other hand, six variables measure the number of conspecifics and colonies surrounding the colony of origin (which would indicate both the availability of breeding opportunities and the number of potential competitors), and the breeding performance of the study population in the year *t* which would mainly indicate the quality of the year (e.g. in terms of food availability). Finally, we included the year as a categorical variable because many ecological conditions (climate, food availability, habitat composition) can vary from year to year without clear trends (Spendelow *et al*. 1995). It should be noted that we estimated the mean productivity (number of fledglings per nest) of colonies and years in two ways: (i) actual productivity, including predation, and (ii) productivity without predation, which more accurately evaluates food availability (Tella 1996).

Statistical analyses

We used Generalized Linear Mixed Models (GLMMs; Littell *et al*. 1996) to identify the factors influencing the probability of breeding dispersal and the distances moved by dispersers between consecutive years. GLMMs represent an useful extension of traditional GLMs (see McCullagh & Nelder 1983), allowing us to incorporate independent variables as random effects in the models. In our case, since some individuals shared the same colonies, and some individuals and colonies were monitored across years, we fitted individual, colony and year as random terms in GLMMs using SAS Macro program GLIMMIX (Littell *et al*. 1996). GLIMMIX macro automatically adjusts extradispersion. We used scaled deviance in extradispersed models to quantify the contribution of each variable to the change in the original deviance. Probability of change of colony was modelled as a binomial response variable (1 = change, 0 = no change) using a logistic link function. Log-transformed dispersal distances were employed as the response variable in the second group of analyses, using normal distribution of errors and identity link function. Each explanatory variable (Table 1) and its interactions were fitted to the observed data by following a forward stepwise procedure (e.g. Bustamante 1997), beginning with the random terms and testing each variable separately. The variable best

explaining variance in the dependent variable was incorporated to the model and the significance of the remaining variables tested again, until no additional variables significantly increased the fitting of the model. Finally, Kappa statistics (Titus, Mosher & Williams 1984) were applied to evaluate if model discrimination between groups improved significantly chance classifications. All P-values refer to two-tailed tests.

Results

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Information on dispersal performance was available for 486 subsequent breeding attempts (173 males and 313 females). Most kestrels remained faithful to the colony where they bred the year before (71·6%). Dispersal frequency was sex-biased: males changed colony less frequently than females (19·1% vs. 33·6%; $\chi^2_1 = 11·48$, $P = 0·0007$). For both sexes, dispersing birds tended to be younger than philopatric ones (Mann Whitney *U*-test, males: $Z = -2·42$, $P = 0·0154$, $n = 106$, females: $Z = -2·12$, $P = 0·0339$, $n = 175$).

The best significant GLMM obtained for the probability of dispersal accounted for 70·4% of the original deviance (Table 2). Individual identity entered significantly as random term in this model (Table 2), showing that dispersal decisions performed by the same individual across years cannot be considered as independent events. After controlling for the effect of individual variation in this dispersal decision, the only variable retained significantly into the model was experience. This model showed that the probability of dispersal from any colony decreased as the breeding experience of the individual in that colony (i.e. the number of years breeding there) increased (Fig. 2). No other variables or interactions entered significantly into the model. It classified correctly 96% of philopatric kestrels and 83·7% of dispersers. A Kappa analysis showed that this classification was 75·4% better than chance (Kappa test, $Z = 7·76$, $P < 0·0001$).

Since breeding experience in a colony results from previous individual decisions on whether to disperse or not in successive years, we built a second GLMM for birds with only 1 year of experience in a particular colony (year *t*). This GLMM accounted for 35·8% of the original deviance (Table 3). Significance test associated

Table 2. GLMM model for probability of colony change, using binomial error and logistic link function

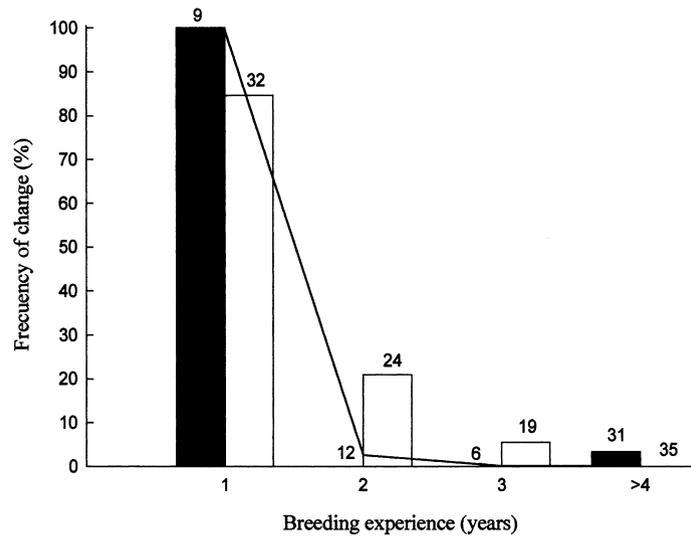|	Parameter estimate	SE	Test	*P*
Intercept	5·2217	0·9793		
INDIVIDUAL	34·5137	7·4139	$Z = 4·66$	0·0001
EXPERIENCE	−8·9014	0·7832	$F = 129·18$	0·0001
Scaled Deviance	171·32			

Fig. 2. Frequency of colony change in relation to the years of breeding experience of individuals in a particular colony. Bars indicate the observed frequencies in the population of males (□) and females (O). The line indicates the frequency of change predicted by the GLMM. Sample sizes are indicated above the bars.

Table 3. GLMM model for probability of colony change for individuals without more than 1 year of breeding experience in a particular colony, using binomial error and logistic link function

	Parameter estimate	SE	Test	P
Intercept	5·5056	0·9154		
INDIVIDUAL	5·8847	0·8364	$Z = 7·04$	0·0001
NO PREDATION	−4·4332	0·8336	$F = 28·28$	0·0001
COLONY SIZE	−0·0594	0·0143	$F = 17·15$	0·0001
DISTANCE TO THE NEAREST COLONY	−0·0005	0·0001	$F = 11·47$	0·0010
MEAN PRODUCTIVITY OF THE NEIGHBOURS	−0·6045	0·1690	$F = 12·79$	0·0005
Scaled deviance	371·55			

with individual identity showed again that breeding dispersal events performed by the same individual were not independent (Table 3). Tests for fixed effects showed that nest failure due to predation, low values of productivity in the neighbours, and proximity to other colonies increased the probability of dispersal. Furthermore, solitary nesting birds were more prone to disperse, and dispersal probability decreased the larger the colony of origin (Fig. 3). No other variables or interactions entered significantly into the model. This second GLMM classified correctly 97·8% of philopatric birds and 30·1% of dispersers, the classification being 34·9% better than chance (Kappa test, $Z = 4·84$, $P < 0·0001$).

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For those birds that changed colony, the distances covered between successive breeding sites did not differ significantly between sexes (males: median = 1320 m, $n = 33$; females: median = 1630 m, $n = 105$; Mann–Whitney U-test, $Z = −1·49$, $P = 0·13$). Dispersal distances ranged from 100 to 65 220 m (median = 1600 m, $n = 138$). Long-distance movements (> 10 000 m) only involved 6·1%

of the dispersing males and 6·4% of the females (Fig. 4). There were no age-related trends in dispersal distances in males (Spearman Correlation, $r_s = −0·146$, $P = 0·51$, $n = 23$) nor in females ($r_s = 0·161$, $P = 0·20$, $n = 64$).

Dispersal distances covered by the same individual in different years were not independent. In fact, repeatability (Lessells & Boag 1987) of dispersal distance for the 16 birds which dispersed more than once was high ($r = 0·64$, $F_{15,33} = 4·83$, $P = 0·001$). This high repeatability arises from the fact that 12 out of the 16 dispersing birds moved to the nearest colony and 1 year later come back to the original one, thus repeating the same dispersal distances. Therefore, individual identity entered significantly as a random term in the GLMM. The resulting model accounted for 73·5% of the original deviance (Table 4), showing that the distance covered by a dispersing bird between subsequent breeding attempts, after controlling for individual identity, was positively correlated with the distance to the nearest colony and inversely with the number of breeding pairs within a 1600-m radius. No other variables or interactions entered significantly into the model.
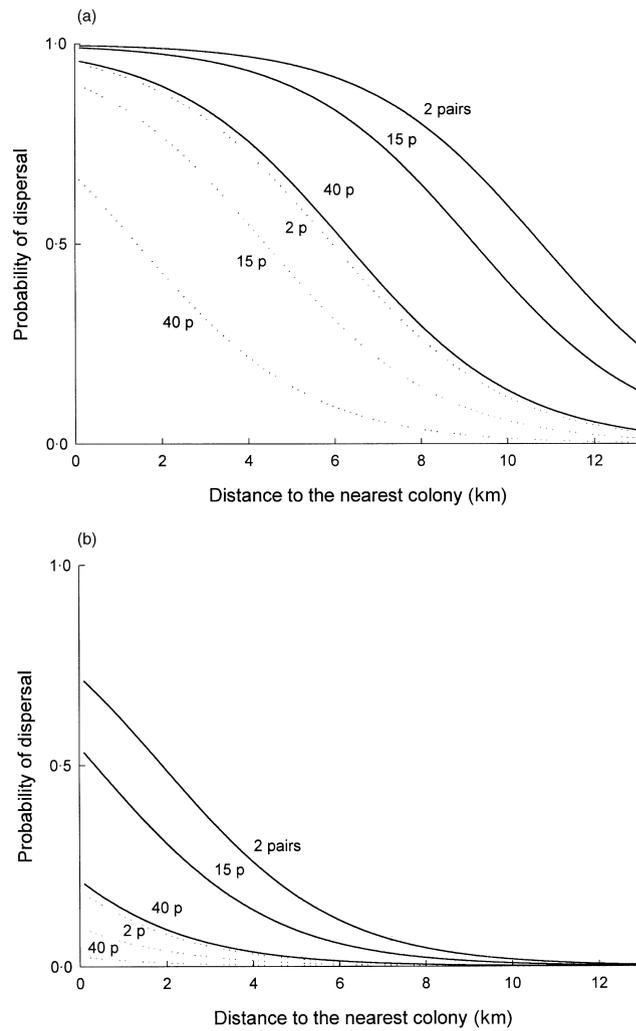
Fig. 3. Probability of colony change as predicted by the GLMM for inexperienced birds: (a) individuals whose nests were predated; (b) individuals whose nests were not predated. Continuous lines correspond to breeding failure of colony neighbours and discontinuous lines to colony neighbours raising an average of four fledglings. Number of pairs show probabilities for three different colony sizes.
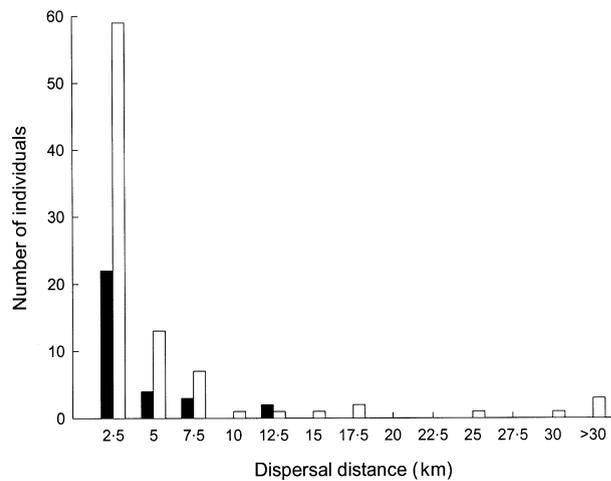

Fig. 4. Observed dispersal distances for male (□) and female (O) lesser kestrels.

Table 4. GLMM model for dispersal distance (log-transformed), using normal error and identity link function

	Parameter estimate	SE	Test	P
Intercept	7·4436	0·1741		
INDIVIDUAL	1·2683	0·2199	$Z = 5·77$	0·0001
DISTANCE TO THE NEAREST COLONY	0·0002	0·0001	$F = 6·22$	0·0239
BREEDING DENSITY	−0·0158	0·0068	$F = 5·37$	0·0341
Scaled Deviance	36·29			

Discussion

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This study confirms the recently suggested need for analysing breeding-site changes and dispersal distances as two potentially different processes (Negro *et al*. 1997; Forero *et al*. 1999). Our multivariate analyses suggested that decisions on whether to disperse and how far to disperse have been mostly based on different factors. Only the distance to the nearest colony appeared to partially influence both the probability of colony change for inexperienced birds in a particular colony and breeding dispersal distances. These different effects would therefore have been hard to detect with a single analysis for the two decisions combined.

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Our results pointed to the necessity of multivariate approaches in an attempt to avoid effects of covariation in the factors driving dispersal. As in other studies (e.g. Newton & Marquiss 1982; Montalvo & Potti 1992; Bried & Jouventin 1998), we observed a higher probability of breeding dispersal in younger birds, but this age effect disappeared when all variables were included in the GLMM models. Likewise, the female-biased dispersal trend detected through univariate analyses was not maintained in multivariate analyses (Tables 2 and 3), suggesting that the pattern observed univariately was an effect of underlying, more important factors determining the apparent gender-biased dispersal in lesser kestrels. In fact, our sampled females had lower experience (Mann–Whitney *U*-test; $Z = -2·48$, $P = 0·0132$) and bred in smaller colonies (Mann–Whitney *U*-test; $Z = -2·22$, $P = 0·0261$) than the sampled males. Female-biased breeding dispersal has been reported for many bird species (Greenwood 1980), including raptors (Newton & Marquiss 1982; Korpimäki 1988; Wiklund 1996). According to the resource competition hypothesis (Greenwood 1980), species with resource-based mating systems should exhibit such a gender bias in dispersal patterns. In the lesser kestrel, males compete for nest cavities at the beginning of the breeding period while females are not so constrained by such a pressure (Negro 1997), but both members of the pair defend the nest-site vigorously and feed the chicks at a later stage. Therefore, inexperienced males and females could benefit

equally by dispersing or not to a new colony based on their previous breeding performance or colony-related features.

Nest failure due to predation influenced dispersal in kestrels without previous breeding experience in the colony of origin (Table 3). A frequent finding from a wide range of vertebrate species, including both territorial and colonial birds, is that individuals may change breeding sites after a poor breeding performance (e.g. Beletsky & Orians 1991; Nager *et al*. 1996; Forero *et al*. 1999), or under predation pressures (e.g. Greig-Smith 1982; Sonerud 1985; Gavin & Bollinger 1988; Wiklund 1996). Previous studies, including some on raptors, have also shown an association between mate loss and change of breeding site (Wiklund 1996; Forero *et al*. 1999). Mate-fidelity in lesser kestrels is much weaker than in long-lived raptors such as black kites (Forero *et al*. 1999; authors' unpublished data), and probably for this reason mate loss does not affect kestrels' decision whether or not to disperse.

In addition to nest failure, there were three colony-related factors that affected colony change: the size of colony of origin, the availability of colonies in the surrounding area, and the mean productivity of the colony neighbours. Birds breeding solitarily were more prone to disperse than colonial ones, and the probability of colony change diminished the larger the colony of origin (Fig. 3); therefore, colony size seemed to influence individual decisions in this facultatively colonial species. This relationship between breeding sociality and probability of dispersal agrees with measurements of lifetime reproductive success in this population. Previous results indicated that colony size was related to individual variations in lifetime productivity; the larger the colony where an individual settled, the higher the number of offspring recruited to the breeding population throughout the life span of the individual (Tella 1996). Our results, showing an inverse relationship between rates of movement and the size of colony of origin, suggest a density-dependent influence on dispersal (McPeek & Holt 1992), as had been reported for breeding dispersal in a territorial falcon species (Wiklund 1996). However, our results did not support the suggestion that high local breeding densities could promote dispersal due to local habitat saturation (Spendelow *et al*. 1995; Nager *et al*. 1996; Lindberg *et al*. 1998). On the other hand, individuals breeding in colonies close to others were more prone to disperse, in agreement with other studies of colonial birds

(Spendelow *et al*. 1995). If kestrels are reluctant to move to unfamiliar areas, a decision to disperse could be favoured by the close proximity of other colonies, which to some extent may guarantee the availability of nests and mates in already familiar foraging areas. Finally, mean productivity of the colony neighbours in year *t* was inversely related to dispersal probability. Assessment of breeding performance of close neighbours could be a realistic measurement of current local environmental quality, thus providing additional information specially useful if patch quality is predictable in time (Danchin *et al*. 1998). Nonetheless, this variable does not necessarily indicate that kestrels made dispersal decisions based on the assessment of reproductive success of close neighbours, but simply could reflect the individual perception of local environmental quality (e.g. prey availability and risk of predation) around the colony in a given breeding season.

The factors discussed above determined decisions of birds without experience in a particular colony. However, for birds that have bred in a colony previously to year *t*, the number of years of breeding experience in that colony was a major factor influencing colony change (Fig. 2). This finding agrees with other research that has highlighted breeding-site experience and familiarity as the relevant force in determining site tenacity in territorial species (e.g. Bollinger & Gavin 1989; Beletsky & Orians 1991; Pärt 1995). Knowledge and familiarity of local conditions would increase steeply as breeding experience in a particular site is accumulated (Pärt & Gustafsson 1989; Korpimäki 1988; Newton 1993), suggesting some degree of individual memory about successive breeding events (Bollinger & Gavin 1989). Thus, a bad breeding event seems to be outweighed, in experienced birds, by knowledge of the local ecological conditions and neighbours acquired during previous years of settlement (Southern *et al*. 1985). Accordingly, inexperienced breeders dispersed more than experienced ones from a colony of Audouin's gull (*Larus audouinii*) after a predator event (Oro *et al*. 1999).

ñM̄ⴖⱥŏĕ̆ⱥ M̄ñ̄ⴖⴖⴖŏⴖ́N ⴖⴖ̄ⱥŏⴖ̆ĕ̆ⱥM̄N̄ ⴖⴖⱥⱥM̄ŏⴖⴖⱥ

Contrary to Greenwood's (1980) hypothesis, no sex differences in breeding dispersal distances were found in our population. However, gender-biased dispersal distances could arise in some studies by analysing site fidelity (dispersal distance equal to zero) together with true dispersal distances (but see Newton & Marquiss 1982; Negro *et al*. 1997; Forero *et al*. 1999), since males tend to be more faithful to breeding sites than females. In fact, by including null dispersal distances in the analyses, our data set would indicate that dispersal distances are female-biased (Mann–Whitney *U*-test, $Z = -2.84$, $P = 0.0044$). Furthermore, by pooling this kind of data we would obtain a median dispersal distance of zero, both for males and females, in contrast with the true median of 1600 m (see Results).

Most kestrels in our population dispersed to colonies within their foraging home ranges (males: 1850 m, females: 2000 m; Tella *et al*. 1998) (see Fig. 4), and distances moved were smaller the greater the local population density. In our study area, nearby colonies may differ greatly in size, productivity, and predation pressure (Tella 1996). So, birds that dispersed, e.g. because they bred in a small colony and/or suffered nest predation (Fig. 3), could improve their chance by moving to a nearby colony of different characteristics. By doing so, birds do not lose familiarity with the surroundings and neighbours (Newton & Marquiss 1982; Beletsky & Orians 1987; Bried & Jouventin 1998), and avoid potential costs associated with long-distance movements (Greenwood 1980; Johnson & Gaines 1990). Both males and females could benefit from these potential advantages, thus explaining why dispersal distances are unrelated to the sex of individuals in lesser kestrels, contrary to the gender-biased dispersal distances stated in many bird species. On the other hand, the trend to move short distances seems to be constrained by the availability of nearby colonies, showing that most kestrels are reluctant to move to an unoccupied building.

ⴖ́ⴖñ̄ŏŏ̄ⴖⴖⱥM̄N̄ ŏⴖⴖⴖĕ̆ⱥⱥⱥ ⴖ̆ŏ́ⱥⱥŏ̆ⴖⴖⴖⴖ̄ⴖ ⴖⱥⴖⱥ

Several studies have stated that animals may assess breeding habitat quality indirectly by cueing on the presence of conspecifics (Stamps 1991; Muller *et al*. 1997), specially in colonial species (Reed & Dobson 1993; Forbes & Kaiser 1994; Oro & Pradel 2000). Birds could be more prone to aggregate in large colonies by conspecific attraction, thus departing from an ideal free distribution (Brown & Rannala 1995). A more recent hypothesis suggests that colonial birds cue on conspecific reproductive success to assess breeding habitat quality for the future (Danchin & Wagner 1997), which has been tested using the kittiwake [*Rissa tridactyla* (L.)]. Kittiwakes gather information on local breeding success by prospecting nesting cliffs when the best information is available (Boulinier *et al*. 1996); birds then tend to recruit to the previous year's most productive cliffs and to emigrate from the least productive ones (Danchin *et al*. 1998). There is also evidence for colony quality assessment by prospecting in the great cormorant [*Phalacrocorax carbo* (L.)] (Schørring *et al*. 1999), and the cliff swallow [*Hirundo pyrrhonota* (Vieillot)] (Brown *et al*. 2000).

According to the above hypotheses, one would expect higher dispersal probabilities for lesser kestrels breeding in colonies of small size and/or with low reproductive success with respect to other colonies. However, lesser kestrels seem to base dispersal decisions primarily on their own breeding performance and experience, constrained by the spatial distribution of colonies. Only the fact that inexperienced birds breeding in bigger colonies are less prone to disperse, and that local population density negatively correlates with dispersal distance, suggest that conspecific attraction

by direct assessment of local population size is acting at some degree. However, these kestrels seem unable to compare the size of their own colony with others, since differences in size between the colonies of origin and destination did not enter in the GLMMs. Our results neither provided evidence for supporting the performance-based conspecific attraction hypothesis as one of the most important factors determining dispersal patterns. This is also supported by observations of banded kestrels, showing that few breeders prospected other colonies during the breeding season (authors' unpublished data). The role of their own individual performance vs. the use of conspecific cues seems to vary between species (Oro & Pradel 2000), so more studies on species with different life histories are required before general patterns on the relative contribution of individual and conspecific cues for breeding dispersal can be obtained for colonial birds.

Acknowledgements

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