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Causes of natal dispersal in the lesser kestrel: inbreeding avoidance or resource competition?

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Summary

1. Natal dispersal of seven cohorts (1988–94) of the colonial lesser kestrel (*Falco naumanni*) was studied in southern Spain. We ringed 1852 nestlings and resighted 321 (17·3%) which survived at least the first migration to Africa. Of the returning individuals, 57% settled in their natal colonies and the remaining 43% dispersed to other colonies. Resights fell off markedly with increasing distance from the natal colony; more than 90% of resights were within 30 km of the birthplace.

2. Contrary to most avian studies, dispersal from the natal site was not sex-biased in our population. The proportion of dispersing males (41%, n = 171) did not differ significantly from that of females (45%, n = 150). Excluding philopatric individuals, the median dispersal distance for males (19 km) did not differ from that of females (18.5 km).

3. Siblings (72 twos) dispersed or were philopatric independently of each other. This result provides no support for either a genetic basis of dispersal (which predicts the same strategy for both siblings) or the inbreeding avoidance hypothesis (which predicts greater dispersal in one sex than the other). This latter hypothesis also conflicts with our observation that the presence of the parent of the opposite sex in the natal colony has no effect on whether returning individuals disperse.

4. Generalized linear models (GLMs) showed that the probability of dispersal for an individual increased when the absolute growth of its natal colony decreased and also from beginning to end of the study, coincidental with a general population increase. These results point to a link between colony saturation and dispersal. GLMs also showed that dispersal distances tended to increase with size of the natal colony and higher breeding success. These results are also consistent with intraspecific competition for resources.

5. Some individuals were observed in two different colonies in their year of first return. These observations, and the lack of active inbreeding avoidance, suggest a scenario for the dispersal process: individuals would prefer to settle in their natal colonies. If they cannot secure a nest site or a mate, they will have to decide whether to stay as nonbreeders or to disperse in search of another breeding chance elsewhere. The actual decision to disperse could be triggered by the level of aggression the unmated individuals encounter in their natal colonies.

Key-words: dispersal, *Falco naumanni*, generalized linear models, philopatry, raptors. *Journal of Animal Ecology* (1997) **66**, 640–648

Introduction

Dispersal affects the demography and genetic structure of populations (Arcese 1989; Johnson & Gaines 1990). The potential impact of dispersal on demography is obvious due to emigration and immigration of individuals: some populations (sinks) may only persist because they receive individuals produced in other populations (sources) (Marzluff & Balda 1989). From a genetic perspective, the extent of dispersal determines the potential for gene flow between populations and thus their relative degree of isolation and genetic differentiation (Greenwood 1980; Johnson & Gaines 1990). For these reasons, the investigation of dispersal patterns should be of paramount importance for students of ecology, evolution and conservation biology alike.

In birds, dispersing individuals are typically the

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young and immature (Baker 1978; Greenwood 1980). Adults, on the other hand, usually remain faithful to the site where they have bred previously. In addition, dispersal in bird species is often female-biased (Greenwood 1980). Two main hypotheses have been proposed to explain why juveniles make the bulk of the dispersers and the sex-bias (Greenwood 1980; Johnson & Gaines 1990): (i) intraspecific competition for resources (food, territory, mate); and (ii) inbreeding avoidance. According to the competition hypothesis, juveniles would be less competitive than the adults in acquiring resources. The inbreeding avoidance hypothesis proposes that juveniles disperse to reduce the chance of mating with relatives. Sex-biased dispersal has also been related to a resource defence mating system (Greenwood 1980): in many bird species, the females, contrary to males, do not defend resources during the mating season. Differential dispersal between the sexes would also reduce the chance of inbreeding.

There are relatively few studies of dispersal in natural populations of birds (for a review see Johnson & Gaines 1990), but most of them favour Greenwood's (1980) resource competition hypothesis. Arcese (1989) found compelling support for this hypothesis in the song sparrow *Melospiza melodia*. In his study, Arcese supplemented territories with food and dramatically reduced dispersal. In addition, subordinate birds emigrated from the population more often than dominants. The inbreeding avoidance hypothesis, typically invoked as the cause of dispersal in mammals (Johnson & Gaines 1990), has been suggested in at least two avian studies (Koenig & Pitelka 1979; Redmond & Jenni 1982).

On the other hand, some studies (Greenwood, Harvey & Perrins 1979; Keppie 1980; Newton & Marquiss 1983; Alberico, Reed & Oring 1992) have reported similarities of dispersal distances between siblings and/or between parents and offspring. Although these studies are consistent with dispersal having a genetic basis (Howard 1960; Schroeder & Boag 1988), other factors, such as the microdistribution of nests and the size of the study area, could explain those observations (van Noordwijk 1984; Arcese 1989; Alberico *et al.* 1992). So far, there is no unequivocal evidence of heritability of dispersal tendencies in birds (Johnson & Gaines 1990).

We studied dispersal in a ringed population of colonially breeding lesser kestrels (*Falco naumanni*, Fleischer) in southern Spain. Our goal was to examine whether patterns of natal dispersal in the lesser kestrel could be related to inbreeding avoidance or to competitive abilities of the individuals, accepting that these hypotheses are not mutually exclusive. Our specific objectives were to determine: (i) whether there is a sex bias in the proportion of individuals, or (ii) in the distances from the birthplace to the site of first settlement; (iii) whether siblings disperse or are philopatric independently of each other; (iv) whether the presence of close relatives in the colony affects natal dispersal; and (v) the relationship between both probability of dispersal and dispersal distance with a set of variables that may be indicative of resource competition (hatch date, rank in the brood, long-term survival).

Materials and methods

THE STUDY SPECIES

The lesser kestrel is a small colonial falcon that has experienced a dramatic decline in its Western Palearctic breeding range in recent decades (Cramp & Simmons 1980; Biber 1990). Nonetheless, it is still abundant in our study area, where the population breeds at the highest densities recorded in Europe (Biber 1990). Most colonies are located on buildings within urban areas, where the kestrels nest in holes or crevices of roofs and walls (Negro & Hiraldo 1993). Small colonies and solitary breeders are on isolated rural constructions. Monogamy is the preponderant mating system, although a few cases of polygyny have been documented (Hiraldo, Negro & Donázar 1991; Tella et al. 1996). The incidence of both extra-pair copulations and extra-pair fertilizations is low (Negro, Donázar & Hiraldo 1992; Negro et al. 1996).

The duration of the postfledging dependence period of young lesser kestrels is very short (approximately 5 days) compared to that of other raptors, during which the young stay in the vicinity of the nest site within the colony (Bustamante & Negro 1994). Fledglings become independent and disperse from the colonies in June–July, while their parents stay. According to ring recoveries, the young wander widely for about 45 days before undergoing true migration to the south in mid-September (Bustamante & Negro 1994). It is unknown whether the extent of the premigratory movements, or the locations they visit, influence the decision on where to settle the following breeding season.

Lesser kestrels are long-distance migrants (Cramp & Simmons 1980), although a fraction of the adult population stay year-round in the colonies in southern Spain, including our study area (Negro, de la Riva & Bustamante 1991). Some juveniles return in the breeding season following that of their hatch and try to reproduce (Hiraldo *et al.* 1996). Other individuals (around 40% of returning juveniles) are first sighted only two or more years after they were banded as nestlings, presumably because they stay in the wintering grounds during their first potential breeding season and do not attempt breeding (Hiraldo *et al.* 1996).

Lesser kestrels are sexually dichromatic from the nestling stage on (Cramp & Simmons 1980; Negro & Hiraldo 1992), and so individuals can be sexed based on plumage characteristics. Yearling males have a distinctive plumage (Cramp & Simmons 1980).

Upon returning to the colonies, the males choose a

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642 Natal dispersal in lesser kestrels nest site that they defend against other males, and display (sky-diving and inspecting the nest cavity) to attract a female (Negro *et al.* 1996). Pairs seem to form in a matter of hours and from then on both partners defend the nest site.

STUDY AREA

The study was made in the provinces of Sevilla and Huelva, southern Spain, in an area of $\approx 13\,000 \,\text{km}^2$ located in the lower part of the Guadalquivir valley (Fig. 1). This is a predominantly flat area (elevation range 5–200 m), intensively cultivated with cereals, sunflowers and olive trees. In an exhaustive survey conducted in the breeding seasons of 1994 and 1995, we counted 1084 lesser kestrel pairs in 19 urban colonies (mean colony size = 57 pairs, range 2–200 pairs), and 177 pairs in 18 colonies located on human constructions scattered in the countryside (mean colony size = 10 pairs, range 1–40 pairs).

All lesser kestrel nests in a given town, even if located in separate buildings, were considered as belonging to the same colony because the area occupied by the average town was relatively small ($\approx 2 \text{ km}^2$) and buildings with nests were generally in the even smaller, old downtown area. This criterion, plus the fact that urban kestrels usually nest in large buildings with numerous potential nest sites, such as churches or castles, may explain why urban colonies are usually larger than rural ones.

DATA COLLECTION

Dispersal data were derived from capture and resighting data from 1852 colour-ringed individuals in the period 1988–95 (seven cohorts of young, 1988–94). Nestling lesser kestrels were individually marked with coloured rings, displaying a two-character code that could be read using spotting scopes. Ringing of nestlings was undertaken in 13 different colonies. Three urban colonies, located in the towns of Arahal, Morón and Mairena del Alcor, respectively, were ringed each year throughout the entire study period. In those three colonies, which were located approximately in the centre of the study area (Fig. 1) in the province of Sevilla, we ringed 1395 nestlings (75% of the total). In three other, smaller colonies (Clavinque, Sendilla, and Caracol) ringing and monitoring of marked birds was also annual from 1990. In seven other colonies, ringing was carried out in occasional years.

Although ringing was confined to selected colonies and years, considerable effort was put into reading rings or retrapping birds in the other colonies located in the study area. The authors and two full-time assistants monitored the colonies with spotting scopes, from the arrival of the first kestrels in February until the end of the breeding season in August. The observers searched for perched kestrels in ledges or at nest entrances in the colonies during 2-3 h sessions from a distance of 20-70 m (lesser kestrels are generally not wary of human presence around the colonies). Colony surveys were undertaken following a rotating schedule, and large colonies were visited more often than small ones. Many birds were trapped in their nests or in roosting sites within the colonies, enabling their identity to be confirmed in the hand. Few recoveries (< 1%) were reported by the public. In relation to other studies of dispersal in territorial bird species, we have the advantage that lesser kestrel



Fig. 1. Study area. \bullet represent breeding colonies of lesser kestrels. \bigcirc denote the three colonies where ringing has been conducted annually during the period of study (1988–95).

colonies were easily detectable and accessible. Thus, it was possible to survey vast areas containing most individuals in the population.

In many cases we were unable to determine whether returning individuals bred where they settled. Nonetheless, all resightings of individuals occurred in breeding colonies during the nesting period, between March and July each year. Given this situation, we adopted Howard's (1960) definition of dispersal in our study: 'dispersal is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate.' This type of dispersal was termed 'natal dispersal' by Greenwood (1980).

Dispersal was measured as the straight-line distance between the natal colony of an individual and the colony of first settlement. For those individuals first sighted when 2 or more years old, we assumed that the observation corresponded to first settlement, and dispersal distance was estimated accordingly. Dispersal distance for individuals returning to their natal colonies was considered to be zero and these individuals were called philopatric; the remaining birds were called dispersers.

During the nest visits for colour-banding we recorded gender, mass and eighth primary length of each nestling. Hatching date of the individuals was estimated from the equation Y = 10.44 + 0.14 X (r = 0.94, n = 43 nestlings, P < 0.001), where Y was the age of the nestlings in days, and X the length of the eighth primary feather in mm. The rank in the brood for each nestling was assigned according to feather length, and, if there was a tie, mass as well.

ANALYTICAL PROCEDURE

Univariate analyses of data were made using nonparametric statistics (Siegel & Castellan 1988). In addition, we made a mathematical description of both the probability of dispersal (as opposed to an individual being philopatric), and the variation of the dispersal distance, using generalized linear models (GLMs) (Nelder and Wedderburn 1972; Dobson 1983; McCullagh and Nelder 1983). In order to minimize potential biases due to variation in the observation effort in the different colonies, calculations were made using data from the six colonies that had been more intensively monitored during the study period. Individuals both ringed and resighted in any of the six colonies were characterized using the 12 variables summarized in Table 1. For each individual we determined the colony and the year in which it hatched, the mean breeding success of the population in the year of birth, the size of the natal colony in the period 1994-95, and the growth rate of the colony in the same period. We chose data from the period 1994-95 because an intensive colony survey was carried out in the whole of Andalusia and population data were considered to be the most reliable then.

© 1997 British Ecological Society Journal of Animal Ecology, **66**, 640–648 **Table 1.** Variables used to characterize individual lesser kestrels that were both hatched and resighted in a restricted study area formed by the six more intensively surveyed colonies

COLONY	Natal colony of the individual
YEAR	Hatch year
BREEDING SUCCESS	Productivity (young/pair) in the year of hatch
COLONY SIZE	Number of breeding pairs in 1995
ABSOLUTE	Increment in the number of
GROWTH	pairs from 1994 to 1995
RELATIVE GROWTH	Absolute growth divided by colony size
SEX	
LAYING DATE	Expressed as Julian date
RESIDUALS	Hatch date of the individual minus the mean hatch date of the population in the same year
RANK	It was assigned according to the relative size of the brood mates
BROOD SIZE	In the brood of the returning individual
AGE FIRST	Age of the individual when
OBSERVATION	detected for the first time in the study area

GLMs permit a very wide range of relationships between the response and the explanatory variables, as well as the use of different error formulations in relation to the nature of the data. For both analyses we used a similar set of variables (Table 1). For the analysis of probability of dispersal, we assumed a binomial distribution of errors and a logistic link function. The response variable reached two values: (i) 0 (the individual does not disperse from the natal colony); and (ii) 1 (the individual disperses). For the dispersal distance analysis we made a log transformation of the response variable (dispersal distance), assumed a normal error, and used an identity function as a link. The significance of all variables and their interactions was assessed by the decrease of the deviance of the model, following a stepwise branching procedure. The most significant variable was included in the model and the process repeated. When a new variable was included, we also examined whether factors previously in the model remained significant, and if not, they were excluded. Following the principle of parsimony, we finally selected the most minimal adequate model able to describe the set of data.

Results

PATTERNS OF NATAL DISPERSAL.

We resighted 321 (17 \cdot 3%) birds of the 1852 that we had ringed as nestlings. Of the returning individuals, 57% settled in their natal colonies, and were thus philopatric. The proportion of dispersers varied

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644 Natal dispersal in lesser kestrels among cohorts from 26% to 61% of the returning individuals (Table 2). Regardless of dispersal distance, the proportion of birds that dispersed did not differ between males (41·5%, n = 171) and females (45·3%, n = 150)($\chi^2 = 0.49$, d.f. = 1, P = 0.491). Considering only dispersers, the median of dispersal distances for males (19·0 km, SD = 17·4, n = 71) and females (18·5 km, SD = 55·1, n = 66) were not significantly different (Mann–Whitney U test, P = 0.498). Given these results, we can safely assume that dispersal was not sex-biased in the population that we studied.

Resights tended to fall off rapidly with increasing distance from the natal colony (Fig. 2). More than 90% of resights were within 30 km of the natal colony. Among dispersers, resights occurred in all directions from the colony of origin, although there was a significantly higher number of directions with a northern component than expected by chance (southern directions = 41, northern directions = 90, expected ratio: 50/50, $\chi^2 = 18.32$, d.f. = 1, P < 0.00001). However, the three colonies where the bulk of ringing took place had more colonies towards the north than to the south within the study area (see Fig. 1), and this fact alone may explain the observed northerly bias.

 Table 2. Frequency of philopatric and dispersing individuals in seven cohorts of lesser kestrels

Cohort	Philopatric	Dispersing	Dispersing (%)
1988	36	17	32
1989	14	5	26
1990	23	13	36
1991	43	32	42
1992	28	31	52
1993	31	30	49
1994	7	11	61
Total	182	139	43

ANALYSIS OF INBREEDING AVOIDANCE

There were 72 instances in which two siblings from the same brood were resighted. Three mutually exclusive possibilities could occur regarding dispersal (the observed frequency and proportion of sibling pairs in each category is given in parentheses): (i) both siblings returned to their natal colony and were thus philopatric (29, 0.40); (ii) both dispersed (5, 0.07); and (iii) one dispersed and the other was philopatric (38, 0.53).

We calculated the proportion of philopatric (0·67) or dispersing (0·33) individuals in the 72 pairs of siblings. Then, according to those proportions, we used the binomial expansion to calculate the expected values for the three possible situations: both individuals being philopatric ($p^2 = 0.45$), both being dispersers ($q^2 = 0.11$), and one dispersing and the other philopatric (2pq = 0.44), where p = philopatric and q = disperser. Observed proportions (see above) did not differ significantly from expected ones ($\chi^2 = 2.69$, d.f. = 2, P > 0.26).

For the five cases in which both siblings dispersed, we found no significant correlations (Spearman rank) between their dispersal distances ($r_s = -0.40$, P = 0.50, n = 5), nor in the direction (degrees) of dispersal ($r_s = -0.6$, P = 0.28, n = 5). Despite the small samples, these results suggest once again that there is no resemblance among dispersing siblings.

The inbreeding avoidance hypothesis predicts that returning juveniles will disperse more often if the parent of the opposite sex is in the natal colony. There were 74 instances in which a returning bird and one of its parents, irrespective of sex, were alive in the same breeding season. All parents, except one, were philopatric. Among returning young, 46 ($62 \cdot 1\%$) were philopatric, while 28 ($37 \cdot 9\%$) dispersed. These frequencies did not differ significantly from those of returning young whose parents were not known to be



-648 Fig. 2. Dispersal distances from birthplace to first settlement of lesser kestrels in southern Spain, 1988–95.

alive (137, 55.4%, philopatric vs. 110, 44.6%, dispersers, $\chi^2 = 1.04$, d.f. = 1, P = 0.30). Taking into consideration the sex of both the offspring and the parent, there were no significant differences in the frequency of returning young that either dispersed or were philopatric (Table 3). These results do not support the hypothesis that the presence of the parents in the natal colony influences dispersal of their offspring.

ANALYSIS OF RESOURCE COMPETITION

For lesser kestrels which returned to the restricted study area of six colonies, observations of philopatric birds (0) and dispersers (1) were fitted to GLMs, assuming a binomial distribution of errors and a logistic link. The best significant model obtained-the one with smaller residual deviance-included two variables: year (which was entered as a factor), and absolute growth of the natal colony (Table 4). The model showed (Fig. 3) that the probability of dispersal increased when the absolute growth of the natal colony decreased, and also from the beginning to the end of the study. Therefore, maximum probability of dispersal corresponded to lesser kestrels from large colonies during the last study years. None of the other variables nor their interactions significantly improved the model.

The fitting of GLMs to the response variable 'dispersal distance' produced a significant model (Table 4). It included an interaction between two variables: size (number of pairs) of the natal colony and breeding success of the population in the natal year. Moreover, these two variables entered as singles in the model. These results indicate (Fig. 4) that the dispersal distance increased with colony size and with breeding success. In consequence, young born in large colonies and in years with above-average breeding success were more likely to disperse farther away. None of the remaining variables nor their interactions significantly improved the model.

CONSEQUENCES OF DISPERSAL: SURVIVAL OF RETURNING BIRDS ACCORDING TO DISPERSAL STATUS

Lifetime duration of philopatric individuals and dispersers could not yet be compared, as many birds,

Table 3. Numbers of philopatric and dispersing males and females in relation to sex of the parent present in the natal colony

		Parent present		
		Father	Mother	
	Philopatric male	13	14	
	Dispersing male	6	7	
	Yates' corrected $\chi^2 = 0.0$	5, d.f. = 1, $P = 0$	0.82	
© 1997 British	Philopatric female	10	9	
Ecological Society	Dispersing female	10	5	
Journal of Animal	Yates' corrected $\chi^2 = 0.2$	2, d.f. = 1, $P = 0$	0.63	
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Table 4. GLMs for dispersal probability (binomial error and logistic link), and distance of dispersal (log-transformed) (normal error and identity link)

(a) Dispersal probability

	Parameter	
	estimate	S.E.
Constant	-1.628	1.105
YEAR (1989)	0.0	Aliased
YEAR (1990)	0.971	1.460
YEAR (1991)	2.047	1.107
YEAR (1992)	2.141	1.066
YEAR (1993)	2.220	1.090
YEAR (1994)	2.004	1.123
YEAR (1995)	2.878	1.262
Absolute colony growth	-0.199	0.068
Scaled deviance	169.61	
d.f.	173	
r^2	12.43	
Р	< 0.001	

(b) Dispersal distance

	Parameter estimate	S.E.
Constant	-1.195	1.652
COLONY SIZE \times		
BREEDING SUCCESS	-0.011	0.001
BREEDING SUCCESS	1.506	0.881
COLONY SIZE	0.034	0.025
Residual deviance	31.117	
d.f.	39	
r^2	25.43	
Р	< 0.001	

even some from the older cohort, were still alive at the end of the study. Nonetheless, for both kinds of individuals in the four older cohorts (1988-91), we compared the age when last resighted to check whether differences could already be detected. The comparison was undertaken using the Euring age code (Ceballos et al. 1984), which was utilized to assign age categories in our data files. The mean Euring code for philopatric birds was 10.17 (n = 85), while that for dispersers was 10.39. The difference was not significant (Mann–Whitney U test, P = 0.55). In Euring, a code of '9' corresponds to 3 calendar years of age, while '11' would be 4 years. Therefore, the average returning individual, irrespective of its dispersal status, survives a minimum of ≈ 3.5 years.

Discussion

The validity of our results would be compromised if a significant fraction of individuals dispersed out of the study area. We think that this possibility is unlikely. First, the distribution of resights is markedly leptokurtic, and, despite the large size of the study area, over 90% of resights occurred within 30 km of the natal colony. We must also take into account

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Fig. 3. Probability of dispersal in relation to the absolute increase of the natal colony during the study period. A line was fitted for each cohort (years 1988–94).



Fig. 4. Dispersal distance in relation to the size (number of pairs) of the natal colony in the year of hatch. A different line was fitted for different potential values of breeding success (number of chicks/laying pair) within the study area (0.5-2.5).

that the bulk of ringing was conducted in the central portion of the study area and this minimizes the problem of individuals hatched in the periphery escaping detection.

In addition, observed population trends in recent years are in close agreement with those predicted from a demographic model (Hiraldo *et al.* 1996), which utilized the same data set that we have used in the analysis of dispersal. This result implies that survival of juveniles from fledging to the next breeding season (one of the crucial parameters in the model) was correctly assessed. It also indicates that recruitment was from local birds, and thus the population in the study area is neither a source nor a sink of individuals (Matthysen, Adriaensen & Dhondt 1995). Only four birds were recovered outside the study area and, even though lesser kestrels were ringed in large numbers in other areas in Spain (around 10 000 individuals in 1973–95, Cantos & Manzaneque 1994; authors'

© 1997 British Ecological Society Journal of Animal Ecology, **66**, 640–648 unpublished data), we have detected only one immigrant in our population.

Lesser kestrels, even though they migrate to distant wintering sites, tend to return to their natal colonies or nearby. This remarkable philopatry is present in other raptorial birds (Newton & Marquiss 1983; James, Warkentin & Oliphant 1989; Poole 1989), and constitutes the basis of the widely used reintroduction technique called 'hacking' (Newton 1979), which relies on 'the tendency of young raptors to imprint on the region they see as fledglings' (Poole 1989).

Philopatry was the predominant strategy among returning lesser kestrels, but an important fraction of individuals dispersed. In contrast to most avian species (Greenwood 1980), including raptors (Newton 1986; Poole 1989; James *et al.* 1989), lesser kestrels did not show sex-biased dispersal. It has been hypothesized that sex-biased dispersal is linked to the mating system and to the effort expended by each sex in

mate or resource defence (Arcese 1989 and references therein). Our results are in accordance with this hypothesis: lesser kestrels are largely monogamous (Negro *et al.* 1992; Negro *et al.* 1996), both members of the pair defend the nest site vigorously against intruders (authors' unpublished data). Under this mating system organization, equality of dispersal distances in the two sexes is predicted (Arcese 1989). It has to be noted, however, that other raptors (Sparrowhawk *Accipiter nisus* and Hobby *Falco subbuteo*, Newton 1979) show sex-biased dispersal and both members of the pair defend the nest site.

NATAL DISPERSAL, HERITABILITY OF DISPERSAL AND INBREEDING AVOIDANCE

Whether siblings tend to behave similarly is important because most siblings following the same strategy (either philopatry or dispersal) might point to a genetic basis of the dispersal character (Howard 1960), while an excess of siblings practising opposite strategies would provide some support to the inbreeding avoidance hypothesis. Returning siblings dispersed or were philopatric independently of each other. In the few cases where two siblings dispersed, they did so to different distances and directions. These results make it unlikely that the decision to disperse had a genetic basis. In addition, whether lesser kestrels dispersed was not related to the presence of the parent of the opposite sex in the natal colony. These results do not support the hypothesis that individuals disperse to avoid inbreeding.

INTRASPECIFIC COMPETITION FOR RESOURCES (ICR)

In a context of ICR, and for a hole-nesting species such as the lesser kestrel, it can be expected that nestsite availability influenced whether the individuals dispersed or were philopatric. Our GLM supports this idea because it shows that the probability of dispersal was related to the degree of saturation in the natal colonies of the dispersing individuals. The lower the holding ability of a colony, the lower the chance that an individual hatched in that colony was philopatric. The model also showed that the probability of dispersal has increased in recent years, coincidental with a general population increase (authors' unpublished data), and thus a higher saturation in most colonies.

The GLM for dispersal distances also agrees with a scenario of ICR. According to our results, dispersal distances tend to increase with size of the natal colony and breeding success. Dispersal distances are larger when there are more individuals looking for breeding opportunities. It seems logical that a larger pool of individuals would saturate not only their natal colonies but also the neighbouring ones.

A SCENARIO FOR DISPERSAL IN THE LESSER KESTREL

Our results suggest a possible scenario for the dispersal process, which is in fact in accordance with our already favoured hypothesis of resource competition: individuals would try to settle first in their natal colonies, but if they could not secure a nest site or find a mate, they would have to choose between staying as nonbreeders or moving to other colonies where they might have the chance to reproduce. This hypothesis is supported by the observation of individuals (seven females and four males) in two different colonies in the year they first returned. Three individuals were first sighted in their natal colonies, although they eventually settled in a different colony. Seven individuals were sighted in two colonies which were not their natal ones. Only one individual settled in its natal colony after being resighted in another colony.

When yearlings arrive in the colonies, preferred nest sites are already occupied by older birds (Negro & Hiraldo 1993), which are larger on average (Cramp & Simmons 1980). We have observed individuals trying to inspect nest cavities from which they were then evicted by the occupants. Aggression is by no means ritual. We often saw two individuals grabbing each other with the talons in the air and falling to the ground, sometimes losing or breaking feathers. Negro and Hiraldo (1993) suggested that lesser kestrels could be suffering from a shortage of optimal nest sites, and that dominant birds would take the best locations. In this situation, if a newly arrived bird was attacked repeatedly, as we have often observed, it may disperse.

Another factor that may trigger dispersal is the operational sex ratio in the colony: if there are no available individuals of the opposite sex, or the individual is rejected by potential mates, dispersal would again be a best-of-a-bad-job strategy. Whether due to lack of mating opportunities or aggression from other adults, dispersal in the lesser kestrel would have an environmental component (Howard 1960).

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References

- Alberico, J.A.R., Reed, J.M. & Oring, L.W. (1992) Nonrandom philopatry of sibling spotted sandpipers *Actitis* macularia. Ornis Scandinavica, 23, 504–508.
- Arcese, P. (1989) Intrasexual competition, mating system

and natal dispersal in song sparrows. *Animal Behaviour*, **38**, 958–979.

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- Baker, R.R. (1978) The Evolutionary Ecology of Animal Migration. Hodder & Stoughton, London.
- Biber, J.P. (1990) Action Plan for the Conservation of Western Lesser Kestrel Falco naumanni populations. ICBP Study Report no. 41. International Council for Bird Preservation, Cambridge.
- Bustamante, J. & Negro, J.J. (1994) The post-fledging dependence period of the lesser kestrel *Falco naumanni* in southwestern Spain. *Journal of Raptor Research*, 28, 158–163.
- Cantos, F.J. & Gómez-Manzaneque, A. (1994) Informe sobre la campaña de anillamiento de aves en España. Año 1993. *Ecología*, 8, 285–357.
- Ceballos, P., Molina, J., Franco, A. & Palacios, B. (1984). *Manual del Anillador*. Instituto Nacional para la Conservación de la Naturaleza, Madrid.
- Cramp, S. & Simmons, K.E.L (eds) (1980) The Birds of the Western Palearctic, Vol. 2, Oxford University Press, Oxford.
- Dobson, A.J. (1983) *Introduction to Statistical Modelling*. Chapman and Hall, London.
- Greenwood, P. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28, 1140– 1162.
- Greenwood, P.J., Harvey, P.H. & Perrins, C.M. (1979) The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. *Journal* of Animal Ecology, 48, 123–142.
- Hiraldo, F., Negro, J.J. & Donázar, J.A. (1991) Aborted polygyny in the lesser kestrel *Falco naumanni* (Aves, Falconidae). *Ethology*, **89**, 253–257.
- Hiraldo, F., Negro, J.J., Donázar, J.A. & Gaona, P. (1996) A demographic model for a population of the endangered lesser kestrel in southern Spain. *Journal of Applied Ecol*ogy, **33**, 1085–1093.
- Howard, W.E. (1960) Environmental and innate dispersal of individual vertebrates. *American Midland Naturalist*, 63, 152–161.
- James, P.C., Warkentin, I. & Oliphant, L.W. (1989) Turnover and dispersal in urban merlins *Falco columbarius*. *Ibis*, **131**, 426–429.
- Johnson, M.L. & Gaines, M.S. (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, 21, 449–480.
- Keppie, D.M. (1980) Similarity of dispersal among sibling male spruce grouse. *Canadian Journal of Zoology*, 58, 2102–2104.
- Koenig, W.D. & Pitelka, F.A. (1979). Relatedness and inbreeding avoidance: counterplays in the communally nesting acorn woodpecker. *Science*, **206**, 1103–1105.

Marzluff, J.M. & Balda, R.P. (1989) Causes and conse-

quences of female-biased dispersal in a flock-living bird, the pinyon jay. *Ecology*, **70**, 316–328.

- Matthysen, E., Adriaensen, F. & Dhondt, A.A. (1995) Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos*, **72**, 375–381.
- McCullagh, P. & Nelder, J.A. (1983) *Generalised Linear Modelling*. Chapman and Hall, London.
- Negro, J.J. & Hiraldo, F. (1992) Sex ratios in broods of the lesser kestrel *Falco naumanni*. *Ibis*, **134**, 190–191.
- Negro, J.J. & Hiraldo, F. (1993) Nest-site selection and breeding success in the lesser kestrel *Falco naumanni*. *Bird Study*, **40**, 115–119.
- Negro, J.J., de la Riva, M. & Bustamante, J.J. (1991) Patterns of winter distribution and abundance of lesser kestrels (*Falco naumanni*) in Spain. *Journal of Raptor Research*, 25, 30–35.
- Negro, J.J., Donázar, J.A. & Hiraldo, F. (1992) Copulatory behaviour in a colony of lesser kestrels: sperm competition and mixed reproductive strategies. *Animal Behaviour*, 43, 921–930.
- Negro, J.J., Villarroel, M., Tella, J.L., Kuhnlein, U., Hiraldo, F., Donázar, J.A. & Bird, D.M. (1996) DNA fingerprinting reveals a low incidence of extra-pair fertilizations in the lesser kestrel. *Animal Behaviour*, **51**, 935–943.
- Nelder, J.A. & Wedderburn, R.W.M. (1972) Generalised Linear Models. *Journal of the Royal Statistical Society A*, 135, 370–384.
- Newton, I. (1979). *Population Ecology of Raptors*. T. & A.D. Poyser, Calton, U.K
- Newton, I. (1986) *The Sparrowhawk*. T. & A.D. Poyser, Calton, UK.
- Newton, I. & Marquiss, M. (1983) Dispersal of sparrowhawks between birthplace and breeding place. *Journal* of Animal Ecology, **52**, 463–477.
- Poole, A. (1989) *Ospreys. A Natural and Unnatural History.* Cambridge University Press, Cambridge.
- Redmond, R.L. & Jenni, D.A. (1982) Natal philopatry and breeding area fidelity of long-billed curlews (*Numenius americanus*): patterns and evolutionary consequences. *Behavioural Ecology and Sociobiology*, **10**, 277–279.
- Schroeder, M.A. & Boag, D.A. (1988) Dispersal in spruce grouse: is inheritance involved? *Animal Behaviour*, 36, 305– 307.
- Siegel, S. & Castellan, N.J. (1988) Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, Singapore.
- Tella, J.L., Negro, J.L., Villarroel, M., Kuhnlein, U., Hiraldo, F., Donázar, J.A. & Bird, D.M. (1996) DNA fingerprinting reveals polygyny in the lesser kestrel *Falco naumanni*. Auk, **113**, 262–265.
- van Noordwijk, A.J. (1984) Problems in the analysis of dispersal and a critique on its 'heritability' in the great tit. *Journal of Animal Ecology*, **53**, 533–544.

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