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Causes, consequences and mechanisms of breeding dispersal in the colonial lesser kestrel, *Falco naumanni*

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Dispersal is a common phenomenon in animals, with important consequences for individual fitness and the genetics and structure of populations. We studied the causes and consequences of breeding dispersal from an individual perspective using as a model organism the colonial lesser kestrel. For this purpose, we gathered information on 235 birds that attempted to breed in 2 consecutive years (2004–2006) in any of the 22 colonies monitored in the study area. Eighty-two per cent of kestrels returned to the same breeding colony where they had attempted to breed in the previous year. Probability of dispersal decreased with age and individual reproductive performance in the season previous to dispersal and females dispersed more frequently than males. Dispersers settled in colonies with a higher mean reproductive performance than other available colonies located around their colony of origin. However, the size of the colony selected did not differ between selected and surrounding colonies. Thus, dispersers selected highly productive rather than large colonies. Own body condition or the quality of the mates obtained (estimated by their pectoral thickness and size) did not change for individuals that dispersed or for philopatric individuals in subsequent seasons. Although dispersers greatly increased their own breeding performance after dispersal, it did not exceed that of their philopatric counterparts. These results help to explain the coexistence of dispersal and philopatric behaviours within a population and suggest that dispersal may be an adaptive behaviour that increases reproductive performance, particularly for individuals that have suffered a bad breeding experience.

Keywords: breeding dispersal; colony selection; *Falco naumanni*; fitness; lesser kestrel; reproductive performance

Dispersal may have important consequences for the fitness of individuals, the dynamics and genetics of populations, and species distribution (Greenwood 1980; Greenwood & Harvey 1982; Johnson & Gaines 1990; Forero et al. 1999; Clobert et al. 2001; Danchin & Cam 2002; Steiner & Gaston 2005). There are two types of dispersal movements: 'natal dispersal', when individuals move from their birth place to the first breeding site (Greenwood et al. 1979), and 'breeding dispersal', when individuals move between breeding sites in two successive breeding episodes (Clobert et al. 2001). Given that the ontogeny of the two types of dispersal is very different, they are generally studied separately (Clobert et al. 2001). In this study, we focused on breeding dispersal, a phenomenon not very well understood and involving complex genetic, ecological and behavioural interactions (Clobert et al. 2001). In fact, breeding dispersal is one of the less well-known processes influencing population dynamics (Cilimburg et al. 2002). Dispersal is assumed to entail certain costs in terms of time and energy devoted by dispersing individuals to finding a new breeding site (Danchin & Cam 2002; Hansson et al. 2004). However, dispersers could also obtain certain benefits that may overcome such costs. At the proximate level, breeding dispersal involves many factors that may affect individual decisions. These can include current and past experience, competence with conspecifics, spatial variation in habitat quality and information on such variation, modes of acquiring it and its reliability. Studies on breeding dispersal

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have been mainly focused on its causes, considering differences between sexes, age classes or populations and, more recently, also paying attention to the cues that individuals use to select a new breeding place (Doligez et al. 2002; Aparicio et al. 2007; Calabuig et al. 2008). However, the whole process of dispersal, including its fitness consequences, has been rarely investigated. An evaluation of the possible adaptive significance of dispersal requires a complete consideration of all these components that may help to answer the following main questions: which individuals disperse and why, where do they go, and what are the fitness consequences of this behaviour?

The first two questions, who and why disperse, are basic to understanding the coexistence of dispersal and philopatric behaviours within a population. This has been explained by variation in the balance of selection pressures imposed on different individuals (Weatherhead & Boak 1986; Ward & Weatherhead 2005). One of these selection pressures could be sex bias in resource defence and acquisition. In birds, it is generally thought that these costs are greater for males than for females because male dispersers must usually compete with other local males to gain a new territory. Therefore, it would be expected that being philopatric is more advantageous for males than for females (Greenwood 1980; Ward & Weatherhead 2005). Also, dispersal may be related to individual characteristics determining competitive ability such as body condition, and age assuming that the probability of dispersal increases with intraspecific competition (Murray 1967; Greenwood & Harvey 1982). Differences in dispersal behaviour could also be associated with an individual's own breeding experience. In this respect, some studies have found that dispersal is promoted by breeding failure or low breeding performance (Greenwood & Harvey 1982; Newton & Marquiss 1982; Oring & Lank 1982; Dow & Fredga 1983; Gratto et al. 1985; Haas 1998; Forero et al. 1999). Moreover, dispersal may be affected by local features of breeding patches. For example, in colonial species dispersal may depend on the characteristics of their own breeding colony (e.g. size, productivity) and the distance to the next one (Serrano et al. 2001).

The third question concerns where dispersers go. When there is enough variance in the quality of breeding patches, information on alternative breeding places may become relevant to deciding where to settle after dispersal. Such information could be actively obtained by assessing directly the availability and/or quality of local resources or using social information. Dispersers may use the presence of conspecifics to select a particular breeding place. A large number of breeders in a particular place may be a guarantee of its suitability (Stamps 1988; Muller et al. 1997). Individuals could also cue on conspecific breeding performance to make decisions based on this information, as the 'public information hypothesis' predicts (Valone & Brown 1989; Templeton & Giraldeau 1996; Giraldeau et al. 2002; Danchin et al. 2004). In fact, some studies have shown that more productive breeding patches receive more immigrants than less productive ones (Doligez et al. 2002; Aparicio et al. 2007). In a recent study we also found that colonies with higher mean reproductive success were occupied faster in the subsequent season than less productive ones (Calabuig et al. 2008). Although these studies suggest that breeders use public information to select breeding habitat, they have only examined how many individuals, including those that are philopatric and first breeders, are attracted to a given breeding place. However, the question of where dispersing individuals go remains unresolved and requires a more specific analysis such as comparing characteristics of selected and available places for dispersers.

With respect to the consequences of dispersal, an individual is expected to improve its breeding performance by obtaining a better territory and/or mate (Greenwood & Harvey 1982; Daniels & Walters 2000; Blakesley et al. 2006). The possible adaptive significance of breeding dispersal has been evaluated by taking into account the trade-offs of this behaviour. The advantages of dispersal have been demonstrated in some empirical studies showing a positive effect of breeding dispersal on breeding performance (Pärt & Gustafsson 1989; Forero et al. 1999). However, these benefits are not always clear as other studies have found no such relationship (Newton & Marquiss 1982; Payne & Payne 1993) or even an opposite trend (Dow & Fredga 1983; Gavin & Bollinger 1988). Furthermore, most studies have been conducted on territorial species (Payne & Payne 1993; Byholm et al. 2003; Blakesley et al. 2006; Fisher & Wiebe 2006) but the causes of breeding dispersal, and hence its possible consequences, may differ between territorial and colonial species in several aspects, mainly because divorce in territorial species necessitates at least one of the pair members dispersing. Thus, colonial species allow us to study breeding dispersal regardless of divorce.

We investigated the breeding dispersal behaviour of the lesser kestrel, a colonial species in which around a fifth of the breeding individuals change their colony between successive years. The causes of dispersal and cues attracting immigrants to a colony have been considered in previous studies on this species (Serrano et al. 2001; Aparicio et al. 2007; Calabuig et al. 2008). Nevertheless, little is known about the fitness consequences of breeding dispersal and the individual process of taking decisions. Our aim was to examine the process of dispersal from an individual perspective, investigating which individuals disperse and why, where they go, and the consequences for individuals of this behaviour.

METHODS

Study Area and Species

The study was carried out in La Mancha, central Spain (600–800 m above sea level), in an area covering approximately 1000 km^2. The climate is meso-Mediterranean with mean temperatures ranging from 24–26 °C in July to 4–6 °C in January and 300–400 mm of rainfall concentrated mainly in spring and autumn. The area is extensively cultivated with barley, *Hordeum vulgare*, wheat, *Triticum* spp., and vineyards, *Vitis vinifera*. Other minor habitats include scattered olive groves, *Olea europaea*, some recent pine plantations, *Pinus* spp., and noncultivated areas covered with pastures.

The lesser kestrel is a small, migratory and colonial bird of prey. In our study area lesser kestrels form colonies of 2–60 pairs located in abandoned farmhouses where they nest under tiled roofs and inside holes in walls. They normally arrive in this area from their winter quarters in Africa between January and March (Aparicio et al. 2007). Lesser kestrels are mainly monogamous. Males arrive earlier, take a nest site by competing with other males for its possession and try to attract females. Once the pair is formed, the female cooperates with her mate in nest defence. Close to egg laying, females spend progressively more time in the colony and are fed by males. Egg laying lasts from the end of April to the first week of June (Aparicio & Bonal 2002). Females lay a single clutch per year (range 1–6 eggs) with rare replacement clutches (ca. 0.5%). Both parents incubate their eggs and feed the young, but only the female incubates at night (Donázar et al. 1992). The return to the winter quarters usually begins in September, about a month after the kestrels have left the breeding colonies.

Field Procedures

We monitored 22 lesser kestrel colonies during the 2004–2006 breeding seasons. We recorded the positions of the colonies using a global positioning system to calculate distances between them. The minimum distance between two colonies ranged between 180 m and 3200 m. In these colonies, we routinely collected information about breeding performance and adult and chick characteristics. From May onwards, each potential nest was examined every 6 days until the clutch was completed. In these visits we recorded the identity of breeding birds, clutch size and the number of fledglings. Breeding adults were caught by hand in their nests during incubation. We checked nests around hatching and we measured the chicks within the first week of age to estimate hatching date. To avoid confusion caused by nest switching, nestlings were marked at hatching with a waterproof felt-tip pen, and banded 5–7 days later. The chicks fledge at around 30 days after hatching and we measured them at 29–30 days before they left the nest. Adults and chicks (at 29–30 days) were weighed (±0.1 g) with a portable electronic balance and their wing length was measured (±1 mm) with a rule. We measured the pectoral thickness of adults and chicks as an indicator of body condition (Aparicio 1997; Aparicio & Cordero 2001). For this purpose, we used a portable ultrasonic meter, a Krautkrämer USM22F (accuracy 0.1 mm, Krautkrämer, Hürth, Germany), especially designed to measure animal tissues. This trait has been used in previous studies as a measure of body condition in several bird species (Bolton et al. 1991; Newton 1993); it is highly repeatable (Aparicio 1997) and considered a more reliable measure of condition than residuals of body mass on tarsus length (Bolton et al. 1991; Newton 1993).

To study breeding dispersal, we also considered other variables that could influence this behaviour in lesser kestrels. These included: (1) previous experience in a given colony, defined as the number of years that an individual attempted to breed in that colony in the last 5 years; (2) number of fledglings reared (surviving to 30th day); (3) colony size, sum of pairs that laid at least one egg; (4) distance (km) to the nearest colony; (5) number of breeding pairs in neighbouring colonies within a radius of 4 km, approximately the double of the median dispersal distance in our population; (5) mean reproductive success (MRS) per colony, measured as the average number of young produced per pair attempting to breed in a given colony.

Statistical Analyses

We defined $t-1$ as the year previous to dispersal and t as the year in which dispersal occurred. To examine which factors influenced breeding dispersal, we used a generalized linear mixed model (GLMM) 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. Probability of dispersal was analysed using a binomial error structure and a logit link function, including as predictors parameters related to individual breeding performance (covariate: number of fledglings reared in year $t-1$) and the characteristics of individuals (fixed factor: sex; covariates: age, number of years the individual had been breeding in the colony of origin). We also analysed variables related to the characteristics of the colony of origin (covariates: colony size in year $t-1$, mean reproductive success in the colony in year $t-1$), and variables related to the social environment around the colony of origin (covariates: number of breeding pairs within a radius of 4 km around the colony in year $t-1$, distance to the nearest colony). The year of study was included as a fixed factor to account for possible interannual differences in dispersal probability. Furthermore, the identity of the colony of origin was included as a random factor to control for the potential nonindependence of dispersal probability between colonies, in the manner of a randomized complete block design to avoid pseudoreplication (Krackow & Tkadlec 2001). For individuals captured in more than one breeding attempt we randomly chose a unique data point per individual to avoid pseudoreplication, because the model did not converge after including individual identity as a random factor (SAS Institute 2004). Final models were selected following a backward stepwise procedure, by progressively eliminating nonsignificant variables ($P < 0.05$). 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.

To analyse the characteristics of the colonies selected for breeding in the year after dispersal (t), we carried out a paired t test comparing the size and mean reproductive success of the colony of destination in the year $t-1$ (supposedly the year when selection of a colony for subsequent breeding is made) and that of the available colonies within a radius of 4 km around the colony of origin. We took this distance because it is approximately the double of the median distance of dispersal and it covers 75% of dispersal distances recorded in this population.

The consequences of dispersal for individual physical condition (pectoral thickness), mate characteristics (pectoral thickness, wing length), and reproductive performance (number of fledglings, fledgling pectoral thickness averaged per brood) were analysed using GLMMs. All dependent variables were analysed using a normal distribution of errors and an identity link function with the exception of number of fledglings which was analysed using a Poisson error structure and a log link. Models included dispersal status (philopatric versus disperser) in interaction with season (year $t-1$ versus year t) as predictors (Valcu & Kempenaers 2008). We also included year as a fixed factor in all models. Furthermore, the models for reproductive performance also included laying date and age as additional covariates. Because the observations are not independent (i.e. the same individual was measured in two breeding seasons) we included individual identity as a random effect. We also included colony identity as a random effect to control for possible differences in the analysed variables between colonies. As done in other studies, we developed separate models for males and females because the consequences of dispersal may differ between the sexes (Forero et al. 1999; Valcu & Kempenaers 2008). Furthermore, this avoids both pair members contributing twice in the same analysis. All tests are two tailed.

Ethical Note

The study was done under licence from the Spanish institutional authorities (Environmental Agency of the Community of Castilla-La Mancha (JCCM) and the Ringing Office of the Ministry of Environment) that provided permits for capturing and ringing kestrels. All 235 breeding adults were caught by hand during incubation and 774 chicks were banded a week after hatching. Lesser kestrels are accustomed to human presence and our trapping and handling caused no obvious nest desertion or other harm to the individuals, their nests or breeding colonies.

RESULTS

Who Disperse and Why ?

From 2004 to 2006 we caught 105 males and 130 females as breeders in two consecutive breeding seasons. A total of 20 individuals in 2005 (seven males and 13 females) and 21 in 2006 (six males and 15 females) dispersed from their breeding colony in year $t-1$. The mean age of breeders ± SE was 2.30 ± 0.78 years for philopatric birds and 2.02 ± 0.71 years for dispersers. Ten per cent of philopatric individuals and 21% of dispersers were yearlings. Average breeding failure was 28.7% and 73.4% in 2004 and 16.1% and 62% in 2005 for philopatric individuals and dispersers, respectively. Sex, age and number of fledglings produced in year $t-1$ all significantly explained breeding dispersal (Table 1): dispersal probability was greater for females and decreased with both age and number of fledglings reared. This model accounted for 34% of the original deviance (Table 1). No any other analysed variable relative to individual or colony characteristics had any effect on dispersal probability (Table 1).

Table 1. GLMM for probability of breeding dispersal

	Estimate±SE	Test	*P*
Explanatory terms			
Intercept	2.099±1.101		
Sex	0.945±0.423	$F_{1,172}=4.98$	0.027
Age	−0.836±0.311	$F_{1,177}=7.22$	0.008
Number of fledglings reared	−1.025±0.187	$F_{1,183}=30.16$	<0.001
Year	−1.288±0.492	$F_{1,181}=6.84$	0.010
Rejected terms			
Previous experience		$F_{1,169}=0.08$	0.774
Distance to nearest colony		$F_{1,13}=0.75$	0.423
Mean reproductive success		$F_{1,46.6}=2.65$	0.111
Colony size		$F_{1,17.2}=0.00$	0.967
Number of breeding pairs within 4 km		$F_{1,27.3}=0.74$	0.395
Covariance parameter estimates			
Colony of origin	5.029±2.612	$Z=1.93$	0.027

Parameter estimates ± SE for the levels of fixed factors were calculated considering a reference value of zero for the 'male' level in the variable 'sex' and for the '2005' level in the variable 'year'.

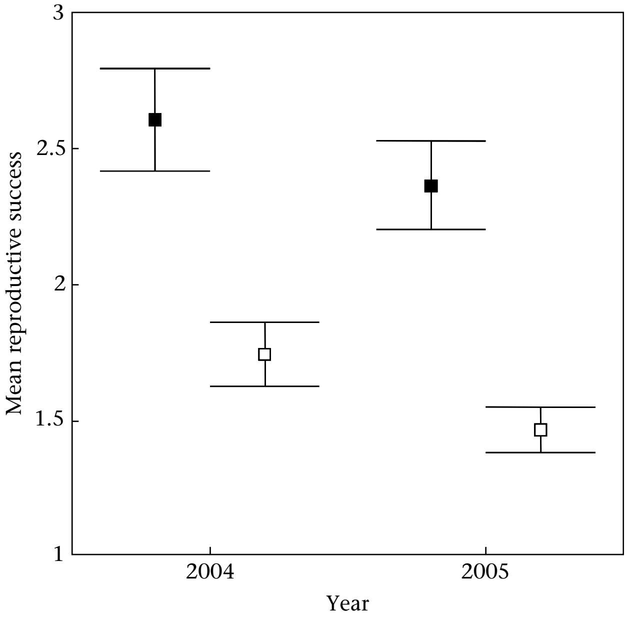

Figure 1. Mean reproductive success in predispersal year ($t-1$) for destination (■) and available colonies within a radius of 4 km around the colony of origin (□). Figures are presented separately for the two study years. Means ± SE are shown. $N = 17$ for each category of colony in each year.

Where do Dispersers go?

To analyse colony features that dispersers could use for settlement, we used mean reproductive success of the colonies and colony size. We used paired *t* tests to compare these parameters in year $t-1$ between the colony selected after dispersal and the available colonies within a radius of 4 km around the colony of origin. Mean reproductive success was higher in the colony of destination (paired *t* test: 2004: $t_{16} = 4.63$, $P < 0.01$; 2005: $t_{16} = -4.76$, $P < 0.01$; Fig. 1) but we found no difference in relation to colony size (2004: $t_{16} = 1.93$, $P = 0.07$; 2005: $t_{19} = 1.76$, $P = 0.1$).

Consequences of Dispersal

GLMM analyses showed that own body condition and the quality of the mates obtained (estimated by their pectoral thickness and wing length) did not change between year $t-1$ and t, for individuals that dispersed or for philopatric individuals (Table 2). Although dispersers of both sexes greatly increased their own breeding performance (estimated as the number of chicks that survived to fledgling) after dispersal it did not exceed that of philopatric individuals in year *t* (Table 2, Fig. 2). Finally, average fledgling pectoral thickness did not change between year $t-1$ and year *t*, for individuals that dispersed or for philopatric individuals of either sex (Table 2).

DISCUSSION

Who Disperse and Why?

Three main factors accounted for breeding dispersal: number of fledglings reared in year $t-1$, sex and age. Lesser kestrels that reared fewer fledglings than average dispersed more frequently than more successful individuals. A higher dispersal rate after a poor breeding performance has been described in several taxa including other bird species (Newton & Marquiss 1982; Dow & Fredga 1983; Shields 1984; Gratto et al. 1985; Weatherhead & Boak 1986; Switzer 1997; Forero et al. 1999). Our study also showed that age negatively influenced the probability of dispersal. In a previous study on another lesser kestrel population, Serrano et al. (2001) found that the main factor determining dispersal was the lack of previous breeding experience in a given colony. This apparent discrepancy between studies could be because the

Table 2. GLMMs for changes in individual physical condition (pectoral thickness), mate characteristics (pectoral thickness, wing length), and reproductive performance (number of fledglings, fledgling pectoral thickness averaged per brood) between seasons (year $t-1$ versus year *t*) and dispersal status (philopatric versus disperser)

	Males		Females	
	Test	*P*	Test	*P*
Individual physical condition				
Dispersal status	$F_{1,132}$=0.88	0.350	$F_{1,132}$=0.88	0.350
Season	$F_{1,168}$=3.21	0.075	$F_{1,195}$=3.02	0.084
Dispersal*season	$F_{3,151}$=1.06	0.367	$F_{3,175}$=1.41	0.241
Year	$F_{2,135}$=26.61	<0.001	$F_{2,166}$=31.37	<0.001
Mate pectoral thickness				
Dispersal status	$F_{1,154}$=0.29	0.591	$F_{1,134}$=0.45	0.502
Season	$F_{1,155}$=1.51	0.221	$F_{1,143}$=0.19	0.668
Dispersal*season	$F_{3,153}$=0.60	0.615	$F_{3,140}$=0.30	0.828
Year	$F_{2,158}$=5.46	0.005	$F_{2,127}$=32.42	<0.001
Mate wing length				
Dispersal status	$F_{1,119}$=0.43	0.512	$F_{1,171}$=0. 01	0.931
Season	$F_{1,136}$=0.41	0.524	$F_{1,77.5}$=0.23	0.635
Dispersal*season	$F_{3,136}$=1.09	0.354	$F_{3,96.4}$=0.71	0.551
Year	$F_{2,119}$=1.61	0.203	$F_{12,84.8}$=2.28	0.108
Number of fledglings				
Dispersal status	Not tested		Not tested	
Season	Not tested		Not tested	
Dispersal*season	$F_{3,151}$=8.02	<0.001	$F_{3,164}$=15.28	<0.001
Year	$F_{2,105}$=2.42	0.093	$F_{2,117}$=1.53	0.222
Age	$F_{1,113}$=0.11	0.736	$F_{1,76}$=3.72	0.058
Laying date	$F_{1,143}$=16.88	<0.001	$F_{1,204}$=15.71	0.001
Fledgling pectoral thickness averaged per brood				
Dispersal status	$F_{1,130}$=0.58	0.448	$F_{1,156}$=0.20	0.651
Season	$F_{1,131}$=0.37	0.542	$F_{1,110}$=0.75	0.387
Dispersal*season	$F_{3,129}$=0.28	0.839	$F_{3,134}$=0.42	0.736
Year	$F_{2,118}$=3.61	0.030	$F_{2,136}$=2.38	0.096
Age	$F_{1,70.5}$=0.05	0.821	$F_{1,168}$=2.94	0.088
Laying date	$F_{1,129}$=0.00	0.981	$F_{1,104}$=0.02	0. 886

Main effects were not tested when the interaction was significant.

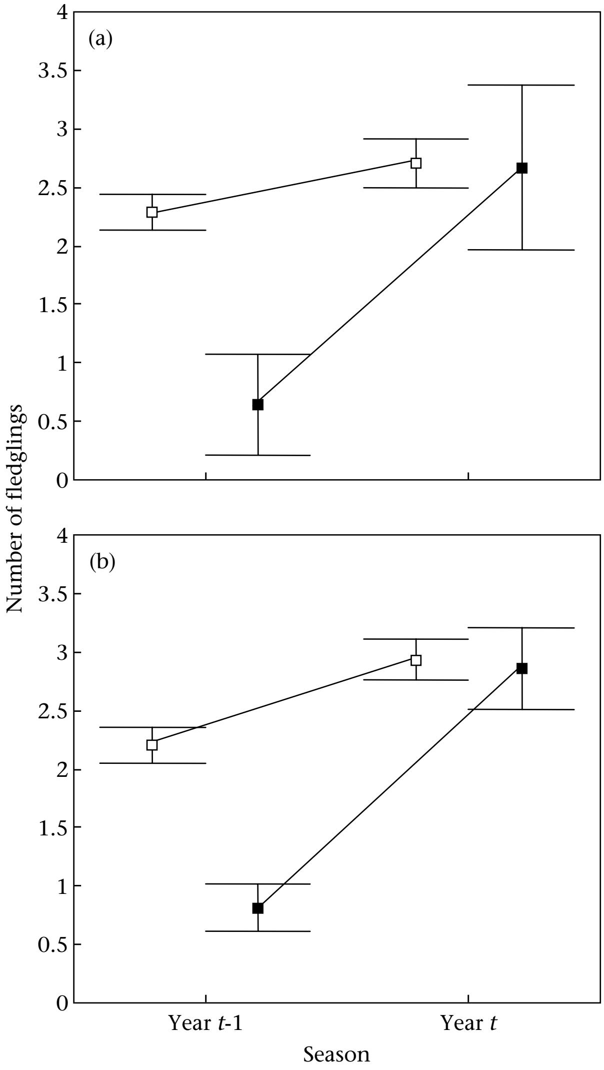

Figure 2. Mean ± SE number of fledglings reared for (a) male and (b) female lesser kestrels of different dispersal status (□: philopatric; ■: dispersers) in seasons *t*−1 (the year previous to dispersal) and *t* (the year of dispersal).

number of years that an individual breeds in a given colony is strongly correlated with its age, one of the explanatory variables included in our model. Indeed, if we excluded age from our model, previous experience was retained as a significant variable and the explained deviance decreased by only 2%.

In our population, dispersal was more frequent in females than in males, a general pattern found among birds. Sex differences in dispersal rate have been generally explained as a consequence of asymmetrical investment in the acquisition and defence of resources between the sexes (‘the resource competition hypothesis’, Greenwood 1980). However, in lesser kestrels both sexes invest almost equally in nest acquisition and defence (G. Calabuig, unpublished data) and therefore it would be difficult to explain the sexual differences in dispersal found on the basis of this hypothesis. Alternatively, we suggest that sex differences in breeding dispersal could also be related to differences between the sexes in the costs of remaining in a given colony. Adults frequently suffer nest predation (Serrano et al. 2005), and females could be particularly at risk as they spend more time in the nest during egg laying and are the only sex that incubates at night. Thus, staying in a place with a high predation risk is likely to be more costly for females and this may increase their predisposition to disperse. With regard to the characteristics of the colony of origin, none of the variables related to their degree of isolation had any effect on dispersal probability. The lack of effect of the distance to the nearest colony on the probability of dispersal may have resulted from the relatively small distances between colonies in our population which were generally much smaller than the usual breeding dispersal distances in the lesser kestrel. Thus, even the largest distance to the nearest colony was not high enough to constrain dispersal. Finally, we found that neither the mean reproductive success nor the size of the colony of origin had any effect on dispersal probability. Given that dispersers did not select larger colonies after dispersal, colony size would not be expected to have any effect on dispersal probability. The lack of effect of local reproductive success on dispersal probability is unexpected and contrasts with the fact that dispersers select more productive colonies to breed after dispersal. This result could be caused by differences in how individuals perceive the quality of their colony of origin according to their own breeding experience.

Where do Dispersers go?

An important part of the breeding dispersal decision is related to subsequent breeding site selection. Our results show that dispersers selected colonies with higher mean reproductive success than other available colonies around their colony of origin. However, the hypothesis that dispersers preferentially select the largest colonies was not supported by our results. This finding agrees with a previous study showing that the local reproductive success of a colony, but not its size, determines its attractiveness (Calabuig et al. 2008). That study showed that more productive colonies were occupied at a higher rate in the subsequent breeding season than less productive ones. Both studies agree in their conclusions even though they took different perspectives and used different kinds of information. To date, the question of how a colony is selected has been investigated by looking at how many individuals join the colony. However, this approach includes all individuals attracted to a given colony and leads to conclusions that are not easily extrapolated to dispersers. The analysis of colony selection by dispersing individuals requires an analysis of where dispersers go, which is what we did in the present study in which we analysed differences in colony characteristics between selected and available colonies. This analysis, exclusively focused on dispersing individuals, is not affected by nest availability and accurately reflects individual breeding site preferences.

Consequences of Dispersal

Selecting a colony on the basis of the reproductive performance of conspecifics requires local reproductive success to be predictable. This was shown to be true in previous studies on this population (Aparicio et al. 2007). Nevertheless, it is more important to analyse the consequences of colony selection than the repeatability of local reproductive success. In this respect, we found that dispersers greatly increased their own breeding performance after dispersal relative to their previous breeding attempt. However, their breeding performance did not exceed that of their philopatric counterparts, suggesting that dispersal may result in part from a negative perception of the quality of the colony of origin affected by a bad breeding experience. Overall, these results help to explain the coexistence of dispersal and philopatric behaviours within a population and suggest that dispersal may be an adaptive behaviour that increases reproductive performance, particularly for individuals that have suffered a bad breeding experience in the previous season.

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