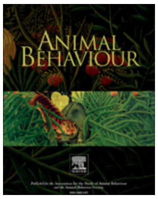
Animal Behaviour 79 (2010) 811–817

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Intercolony movements and prospecting behaviour in the colonial lesser kestrel

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ARTICLE INFO

Article history:
Received 3 July 2009
Initial acceptance 10 September 2009
Final acceptance 23 November 2009
Available online 4 February 2010
MS. number: 09-00444

Keywords:
dispersal
Falco naumanni
habitat selection
lesser kestrel
nest visiting
public information

The exploratory activity of individuals aimed at collecting information about potential future breeding sites is known as prospecting. We studied prospecting behaviour in the colonial lesser kestrel, *Falco naumanni*, using detailed information from radiomarked individuals, whose breeding attempts we terminated at the chick stage, and intensive videotape recording of nests. Half of the radiomarked individuals actively prospected nests in both their own and foreign colonies and they visited colonies up to 7400 m away from their own breeding colony. The presence and number of prospectors arriving at a given nest were influenced by parameters at both the colony and the nest scale. Prospector visits per nest increased with colony productivity and decreased with colony size. The latter does not necessarily mean that prospectors avoid large colonies but rather may be consequence of a dilution effect in colonies where more potential nests can be prospected. The number of prospectors attracted per nest was positively associated with colony connectivity, indicating that both high spatial colony isolation and a small number of breeding pairs in nearby colonies reduced the arrival of prospectors at a given nest. Finally, prospector visits per nest increased and then decreased with parental feeding rates, indicating this parental activity can attract prospectors up to a certain threshold at which nest owners visit their nests frequently enough to keep prospectors away. Overall, this study suggests that prospecting is the mechanism of acquiring public information that could ultimately determine breeding dispersal decisions and the growth and dynamics observed in breeding aggregations.

Owing to the large influence of habitat selection on fitness, habitat assessment mechanisms such as the use of public information may have evolved to reduce the considerable uncertainty associated with breeding site selection (Valone & Templeton 2002). Sampling the activity of conspecifics to obtain information about the quality of potential future breeding sites has been called prospecting. Prospecting activities are likely to have important fitness consequences as the amount of information gathered can decisively increase the chance of identifying and obtaining high-quality breeding sites (Schjorring et al. 1999; Bruinzeel & van de Pol 2004). Accordingly, Boulinier & Danchin (1997) suggested that prospecting behaviour could have evolved to obtain public information useful for future breeding habitat selection. This has been supported by some correlational (Brown & Brown 1996; Danchin et al. 1998; Schjorring et al. 1999; Brown et al. 2000; Doligez et al. 2004; Ward 2005) and experimental studies (Doligez et al. 2002; Pärt & Doligez 2003; Aparicio et al. 2007; Parejo et al. 2008).

Apart from conspecific breeding performance as a source of public information, other cues potentially related to breeding site quality could also influence the attraction of prospectors. These include the presence and number of conspecifics settled (Stamps 1988; Smith & Peacock 1990; Danchin & Wagner 1997), the feeding rate of breeding pairs (Pärt & Doligez 2003) and the age of nest owners (Nordell & Valone 1998). The latter may influence the attractiveness for prospectors if individuals with low discrimination capability cue in particular on experienced conspecifics which can offer more reliable information (Nordell & Valone 1998). Obtaining a general view of the quality of available options for future breeding patch selection also requires that individuals prospect numerous nest sites within different breeding patches. For this reason, the quantity of information gathered (e.g. number of patches/nests visited) can also determine the accuracy of the habitat quality assessment and the future fitness consequences of breeding patch selection (Boulinier & Danchin 1997). However, prospecting is also likely to be a costly behaviour which requires time and energy to travel between patches, increases the risk of predation derived from visiting unfamiliar areas (Reed et al. 1999),

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doi:10.1016/j.anbehav.2009.12.007

and exposes prospectors to injuries derived from attacks and chases from nest owners (Stutchbury & Robertson 1987; Schjorring et al. 1999; van der Jeugd 2001).

Prospecting has been mainly inferred from the presence of nonbreeding individuals at active reproductive areas during the breeding period (Reed et al. 1999). It is widely accepted that prospecting mainly occurs at the end of the breeding season (Boulinier et al. 1996; Cadiou 1999; Schjorring et al. 1999; Doligez et al. 2004) and it is mostly performed by nonbreeder immature individuals and failed breeders (Eadie & Gauthier 1985; Cadiou et al. 1994; Doligez et al. 2004). Prospecting behaviour is generally less frequent among successful breeders, probably because they have to care for their progeny when public information on breeding performance is available (Zicus & Hennes 1989; Cadiou et al. 1994; Reed et al. 1999; Doligez et al. 2004; Piper et al. 2006). Given that failed breeders are more likely to prospect other breeding patches and disperse (Ward 2005), experimental manipulation of breeding performance of marked individuals offers an interesting approach to monitor and study prospecting behaviour (Boulinier et al. 2008). Experimental approaches are likely to maximize the information gathered to extract general conclusions applicable to natural populations if the manipulation mimics natural conditions (e.g. breeding failure by predation; Boulinier et al. 2008). Accordingly, experimental breeding failure has been used to study dispersal (Haas 1998) and nest attendance by marked individuals (Boulinier et al. 2008).

Although breeding site/patch selection during prospecting has become a topic of increasing scientific interest in recent years, most studies have generally been performed at a small spatial scale often restricted to a single breeding patch (Bradley et al. 1999; Schjorring et al. 1999; Dittmann et al. 2007; but see Dittmann et al. 2005; Hénaux et al. 2007). A major reason is probably the technical difficulties of identifying prospectors and/or monitoring their behaviour simultaneously in patches/colonies located several kilometres away. Owing to this limitation, prospecting has rarely been quantified in terms of the number of nests or breeding patches visited, time invested or distances travelled. Furthermore, prospecting has rarely been analysed from an individual perspective and its costs as well as the factors modulating it remain scarcely known. All these questions are relevant because individual decisions such as dispersal could be determined by the acquisition of this information. On the other hand, the dynamics of breeding patches, including their growth/decline and persistence, can also ultimately depend on the number of prospectors/dispersers attracted.

In this study we dealt with these questions using the colonial lesser kestrel, *Falco naumanni*, as a model system. Previous studies have found that poor reproductive performance induces breeding dispersal in this species and that dispersers generally settle in more productive colonies (Aparicio et al. 2007; Calabuig et al. 2008a, b). These findings, together with anecdotal field observations of prospecting activity (Aparicio et al. 2007), suggest that lesser kestrels use public information for breeding habitat selection (Aparicio et al. 2007; Calabuig et al. 2008a, b). We analysed the process of prospecting by individuals and studied the factors influencing the attraction of prospectors in several breeding patches at a large spatial scale. For this purpose, we used two different approaches. We first experimentally mimicked natural breeding failure of previously radiomarked birds to track them and document the process of prospecting from an individual-level perspective. This experimental approach allowed us to focus the radiotracking effort on failed breeders, that is, on just the fraction of the population more likely to perform active prospecting activities. Second, we analysed the factors determining the attraction of prospectors at the colony and nest scale by means of intensive videotape recording of nest activity in 14 breeding colonies.

METHODS

Study Population and General Field Procedures

The study area is located in La Mancha, central Spain (600–800 m above sea level) and extends over about 1000 km^2 (39°20′N, 3°15′W; Hernández et al. 2007). 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 mainly concentrated 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 uncultivated pastures.

In the study area, lesser kestrels form colonies of up to 60 pairs in abandoned farmhouses where they nest under tiled roofs or inside holes in walls (Aparicio & Bonal 2002). The lesser kestrel breeds exclusively in human buildings in the study area as other natural breeding substrates such as cliffs are absent. Two-year-old and older individuals arrive at the study area from their winter quarters in Africa between January and March, depending on the year, whereas yearlings return about 40 days later (G. Calabuig, unpublished data). Egg laying lasts from the end of April to the first week of June and females generally lay a single clutch per year (range 1–6 eggs; modal clutch size in our population = 4 eggs) (Aparicio & Bonal 2002) with rare replacement clutches (ca. 0.5%). Both parents incubate the eggs and feed the young which leave the nest around 30 days after hatching.

Population-monitoring tasks included the capture and banding of breeding adults, recording of breeding parameters and intensive ringing of nestlings in all the studied colonies (Aparicio & Cordero 2001; Calabuig et al. 2008b). During the 2005–2007 breeding seasons we intensively monitored a mean ± SE of 21 ± 2.53 colonies per year (range 18–26) where we captured a mean ± SE of 288 ± 19.97 adults per year and ringed 1740 chicks (mean ± SE = 490 ± 74.14 per year). Colony size was 2–47 breeding pairs (mean ± SE = 12.49 ± 1.69). We located nest sites before the onset of egg laying and each potential nest was examined every 6 days to determine laying date (defined as the date when the first egg was laid, Aparicio & Bonal 2002). Adult lesser kestrels were trapped with a noose carpet or by hand during incubation, measured and individually marked with metallic and coloured plastic rings for further identification. Around one-third of captured individuals were ringed as fledglings in previous breeding seasons and so we knew their exact age. All other unringed individuals captured for the first time were considered to be yearlings or adults (2 years and older) on the basis of their plumage characteristics (Aparicio & Cordero 2001).

Prospecting Behaviour in Lesser Kestrels

During the breeding seasons of 2005 and 2006 we captured and radiotagged 26 individuals from 15 breeding pairs (2005: three males and four females; 2006: eight males and 11 females). We failed to capture both pair members in four cases (one male in 2005 and three males in 2006). In all other cases both pair members were radiotagged. Each individual was equipped with a 2.7 g radiotransmitter (Biotrack, Wareham, U.K.) glued and tied to the base of the two central tail feathers. In open landscapes, like our study area, the signal emitted by these transmitters can be detected at a distance of up to 6 km. We mimicked natural breeding failure of these individuals 2 days after both pair members were radiomarked. For this purpose, we removed all the chicks from their nests (see Ethical note below for more details).

We tracked radiomarked individuals from the day after the experimental breeding failure to mid-July, when most chicks had already fledged. We tracked the birds by car using a portable receiver and a hand-held flexible Yagi antenna (Lintec Antennas Ltd, Worthing, U.K.). To determine the position of radiomarked individuals and detect their presence in the colonies, we performed circular transects covering the entire study area and all the colonies. We started each transect from different points every day, automatically scanning for the signal of all radiomarked individuals. When any radiomarked individual was detected, we followed it to determine its exact position using triangulation or direct observation with a telescope. Then, we resumed the transect from the point where we left it until a new individual was detected. Two radiomarked birds (one male and one female) were not located after release, probably because of failure of the transmitter and so the data presented below are based on the remaining 24 marked individuals. Location was determined at least 6 days per week at intervals between 0730 and 2130 hours. On average, individuals were localized on a mean ± SE of 7.71 ± 0.91 days (range 3–16) and 1.46 ± 0.18 times per day (range 1–13). When individuals were seen, we observed them (1) until they left the colony or (2) until we observed them performing an unambiguous active prospecting behaviour (see below). We noted the identity of the bird, the colony where it was located and the behaviour of those individuals that we were also able to see. The geographical coordinates of all colonies and of each location obtained for radiomarked individuals were registered using a global positioning system. This allowed us to determine the frequency of prospecting behaviour and to quantify the intensity of prospecting in both the birds' own and foreign colonies, the number of colonies visited and the distances travelled. We routinely sampled all known colonies in the study area and covered an area of around 450 km^2 around the origin colonies to detect radiomarked individuals accurately. We are confident that our data set is not substantially biased towards short prospecting distances because the area we covered around the origin colonies (12 km radius; 450 km^2) is much longer than the observed median distance travelled between origin and foreign prospected colonies (females: 3.3 km; males: 2.3 km; see below).

Factors Influencing Prospector Attraction

During the 2007 breeding season we studied potential factors affecting nest attractiveness for prospectors. For this purpose we recorded the activity of 109 nests located in 14 colonies. The parental and prospecting activity of these nests was recorded using a video camera (JVC Model GRD320E) hidden near the entrance of the targeted nest. Each nest was recorded two to seven times for 1.5 h each time, always after the chicks were 10 days old. We analysed all videotapes using Adobe Premiere Pro 2.0 software (Adobe Systems Inc, San Jose, CA, U.S.A.). The attractiveness of a given nest for prospectors was calculated by determining the presence/absence of prospectors (1 = presence of one or more prospectors; 0 = absence of prospectors) in that nest during each recording. We also quantified this attractiveness by considering the number of prospectors visiting the nest during each recording.

Prospectors could be differentiated from nest owners by the absence/presence and position of numbered and/or colour rings. Although numbered rings could not be read from videotape recordings, all nest owners were ringed and prospectors could be unambiguously identified (1) if they were unringed or (2) when their coloured/numbered rings were on a different tarsus or in a different combination to that of the same-sex nest owner. Prospectors could be also differentiated from nest owners by phenotypic traits (plumage pattern) and by their conspicuous and characteristic behaviour during prospecting. Prospectors usually land in the vicinity of conspecifics' nests and approach the nest entrance by walking in a characteristic position with the head bowed and the neck stiff. On most occasions prospectors remain perched at the nest entrance or over the nest cavity and they seem to respond to chick activity by turning their head towards the origin of the nestling begging sounds. Prospectors frequently look into the nests by putting their head or even the entire body into the nest and, on most occasions, they arrive at a given nest a short time after the arrival of one of the breeders (G. Calabuig, personal observation; see Supplementary Material). Prospectors are also repeatedly chased by nest owners and they never bring prey to the nest (van der Jeugd 2001; Tobler & Smith 2004). The number of prospectors was defined as the number of foreign individuals per nest that we were able to discriminate unambiguously on the basis of the above criteria. To measure one of the potential costs of prospecting behaviour, we recorded the number of chases of prospectors by nest owners, assuming that the attacks on prospectors by nest owners could be harmful if they do not avoid the encounter.

We considered 10 variables that could potentially influence the attraction of prospectors: (1) the time when the recording started to account for potential daily variability of prospector activity; (2) date of recording to control for potential temporality of information availability as the breeding season advances; (3) the age of the male nest owner; (4) the age of the female nest owner; (5) the number of chicks at the time of recording; (6) the mean age of nestlings; (7) parental feeding rates, calculated as the number of visits per min; (8) colony size, defined as the number of active breeding pairs in the colony at the time of recording; (9) mean reproductive success in the colony, defined as the average number of fledglings raised by successful breeding pairs in a colony; (10) colony connectivity (Hanski 1998). Connectivity (S) of colony i is calculated as: $S_i = \Sigma_{j \neq i} \exp(-\alpha d_{ij}) N_j$, where N_j is the number of breeding pairs in colony j, d_{ij} is the distance between colonies i and j, and $1/\alpha$ is the average dispersal distance, set to 3.022 km based on previous research in the study population (Ortego et al. 2008).

Statistical Analyses

To analyse the factors influencing whether a given nest was prospected we used generalized linear mixed models (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. We analyzed the probability that a given nest is prospected (i.e. presence/absence of prospectors) in each videotape recording using a binomial error structure and logit link function whereas the number of prospectors in each nest and recording was analysed using a Poisson error structure and log link function. For each of these two dependent variables we constructed two separate models fitting colony (covariates: number of nestlings at recording, mean age of nestlings, feeding rate; fixed factor: age class of nest owners) as explanatory variables. The time of each recording was included as an additional covariate to control for its potential influence on the activity pattern of lesser kestrels. As each nest was recorded several times and numerous nests were recorded in each colony, we included colony identity and nest identity nested within colony identity as random effects. By doing so, we controlled for the potential nonindependence of prospector attraction within colonies and nests, in the manner of a randomized complete block design to avoid pseudoreplication (Krackow & Tkadlec 2001).

Initially, each GLMM was constructed with all explanatory terms fitted, including quadratic effects to account for potential nonlinear relationships. We did not include interactions between independent variables because we did not have an a priori hypothesis about them. Final models were selected following a backward procedure, by progressively eliminating nonsignificant variables. The significance of the remaining variables was tested again until no additional variable reached significance. The result is the minimal most adequate model for explaining the variability in the response variable, where only the significant explanatory variables are retained. Denominator degrees of freedom were computed using the Satterthwaités method (SAS Institute 2004). Hypotheses were tested using F statistics and all P values refer to two-tailed tests. Means are given ±SE.

Ethical Note

The Environmental Agency of the Community of Castilla-La Mancha (JCCM) and the Ringing Office of the Ministry of Environment provided necessary licences for capturing and manipulating lesser kestrels. All 26 radiotagged individuals were captured by hand in the nests and immediately released after radiotagging in their breeding colony. Radiotransmitters weighted 2.7 g which is only 2.44% of the body weight of the smallest radiomarked bird, lower than the maximum 5% recommended for migratory birds (Kenward 2000). These transmitters were tied and glued to the base of one or two central tail feathers, so the glue did not come into contact with the skin. This system also ensured that birds lost the transmitters relatively quickly (around 30–40 days) because lesser kestrels start to moult at the end of the breeding phase. A previous study also showed that tail-mounted radiotransmitters similar to those used in the present study do not have significant effects on the reproductive performance, survival, copulatory behaviour or prey delivery rate to the bird's mate or chicks in this species (Hiraldo et al. 1994). We mimicked breeding failure in only one or two pairs per colony, which, on average, is 1.7% and 6.0% of the breeding pairs studied in 2005 and 2006, respectively. These percentages are relatively small compared with the natural breeding failure rates observed in the lesser kestrel population studied (2005: 37.6% of failed pairs, $N = 239$; 2006: 19.5% of failed pairs, $N = 149$). This experimental manipulation mimics the natural conditions in the lesser kestrel colonies we studied, where total breeding failure, mostly attributable to predation, is frequent. The chicks of radiotagged pairs were immediately assigned to other nests in the same colony with appropriate brood size and chick age (Aparicio et al. 2007). Adoption of nestlings is common in this species (Tella et al. 1997), recognition of alien chicks is rare (Bonal & Aparicio 2009) and the growth and survival of adopted broods or translocated chicks are similar to those raised in natural conditions (J.M Aparicio, unpublished data). Thus, our experimental breeding failure mainly modified the identity of failed breeding pairs and does not imply a disproportionate disturbance from a population-level perspective. Lesser kestrels are accustomed to human presence and our trapping, handling and videotape-recording tasks caused no obvious nest desertion or other harm to the individuals, their nests or breeding colonies. The birds returned to their breeding colonies shortly after we left them.

RESULTS

Prospecting Behaviour in Lesser Kestrels

Radiotracking data revealed that individuals visited foreign breeding colonies and inspected conspecific nests. Of the radiomarked individuals 54.16% (eight females and five males) were found at least once in a foreign breeding colony. In 34% and 38% of all localizations individuals were found in a foreign colony or in their own colony, respectively. Each individual was found in a foreign colony in 28.97 ± 7.04% of the radiolocalizations obtained. This percentage increased to 53.48 ± 8.13% when we considered only individuals found in at least one foreign colony. The remaining locations involved individuals during foraging activities or found perched outside the colonies. We observed kestrels 80 times (36 in their own colonies and 44 in foreign colonies). These observations involved 16 radiomarked individuals which were sighted at least once. Each individual was observed in 1.82 ± 0.81 colonies, including their own. In 60% of cases when we saw individuals in their own colony, they performed active prospecting such as looking into or even entering occupied alien nests. Radiomarked individuals were never observed in their own nests after the experimental breeding failure. A similar behaviour was recorded in 70.1% of the cases when birds were detected in foreign colonies. These observations involved 10 individuals which were observed in 1.7 ± 0.64 foreign colonies. We saw 12 radiomarked individuals performing active nest prospecting in their own or in foreign colonies. The remaining observations ($N = 22$) included individuals that were apparently resting or performing activities other than active prospecting. Individuals recorded prospecting outside their own breeding colony visited 2.38 ± 0.43 foreign colonies (range 1–6). The maximum distance travelled between the bird's own and the prospected colonies averaged 3600 ± 2034 m (females: 3078 ± 1216 m; males: 1860 ± 896 m) and ranged between 310 and 7400 m (females: 2420–7400 m; males: 310–7400 m). After we controlled for year and colony of origin, males and females did not differ in the number of foreign colonies visited ($F_{1,11} = 0.53$, $P = 0.48$) or in the maximum distance travelled ($F_{1,11} = 0.44$, $P = 0.52$).

Frequency of Prospecting

We videotaped 647 h of nest activity in 109 nest sites from 14 colonies (Table 1). The mean number of nests recorded per colony was 7.78 ± 2.08 and nests were recorded during 6.11 ± 0.21 h. During the recordings we registered the presence of at least one prospector in 64% of the nests and in 93% of colonies surveyed. Individuals prospecting foreign nests were found in 94 of the 447 tapes recorded for 90 min each. The number of different prospectors unambiguously identified in a given nest ranged from one to seven (mean ± SE = 1.35 ± 0.09). In 26.7% of prospecting events recorded the prospector was evicted by nest owners when they returned to the nest. This defensive behaviour was performed by both breeding owners. Males and females were involved in 68.3%

Table 1
Details of colonies

Colony code	No. of videotaped nests	Colony size	Mean reproductive success	Connectivity
1 AN	11	13	3.10	0.995
2 AS	4	6	4.00	0.976
3 BS	16	29	2.93	0.001
4 CA	5	12	2.50	0.939
5 CB	7	7	3.00	0.000
6 CE	26	38	3.56	1.471
7 CP	6	8	2.00	1.447
8 DE	7	8	2.67	1.861
9 LA	20	24	3.78	0.908
10 NL	1	1	3.00	1.084
11 PN	1	2	3.00	1.258
12 RO	2	2	4.00	1.204
13 RT	1	1	0.00	1.341
14 RW	2	2	4.50	0.977

Code, number of videotape-recorded nests, colony size (number of breeding pairs), mean reproductive success of the colony (average number of fledglings raised per successful breeding pair in the colony) and colony connectivity (S, calculated as $S_i = \Sigma_{j \neq i} \exp(-\alpha d_{ij}) N_j$, where N_j is the number of breeding pairs in colony j, d_{ij} is the distance between colonies i and j, and $1/\alpha$ is the average dispersal distance) for each colony where we monitored prospector activity during 2007 breeding season.

and 31.7% of cases, respectively. Prospectors were chased 23 times by the male owner and 18 times by the female owner.

Factors Influencing Prospector Attraction

The probability that a nest was prospected increased with mean reproductive success of the colony and decreased with colony size (Table 2). It also increased and then declined significantly with the feeding rate of the breeding pairs (Table 2). That is, nests in which owners delivered prey to chicks at an intermediate rate were more likely to be prospected than those whose owners were feeding less or at higher rates. Similarly, the number of prospectors per nest was positively associated with the mean reproductive success of the colony and negatively associated with colony size (Table 2). The number of prospectors per nest was also higher at nests with intermediate feeding rates and increased with colony connectivity (Table 2). However, the probability that a nest was prospected or the number of prospectors attracted was not associated with time, date, chick age, number of chicks or age of nest owners (Table 2). Connectivity was not associated with the probability that a nest was prospected (Table 2). Apart from the quadratic effect of feeding rate, other quadratic terms were not significant in any analysis ($P > 0.1$ in all cases).

Table 2
GLMMs for probability of observing a prospector and number of prospectors attracted per nest in relation to colony, nest and nest owner characteristics

	Estimate±SE	Test	P
Probability that a nest is prospected			
Explanatory terms			
Intercept	−3.52±0.92		
Mean reproductive success	0.54±0.27	$F_{1,313}=4.11$	0.043
Colony size	−0.04±0.01	$F_{1,313}=8.15$	0.005
Feeding rate	26.17±6.90	$F_{1,313}=14.39$	<0.001
(Feeding rate)^2	−78.94±29.74	$F_{1,313}=7.05$	0.008
Deleted terms			
Date		$F_{1,312}=0.00$	0.956
Age of male owner		$F_{1,312}=0.51$	0.474
Age of female owner		$F_{1,312}=0.00$	0.975
Age of chicks		$F_{1,303}=0.22$	0.639
Number of chicks		$F_{1,294}=1.31$	0.253
Time		$F_{1,311}=1.4$	0.237
Connectivity		$F_{1,312}=2.05$	0.153
Covariance parameter estimates			
Colony identity	0	—	—
Nest identity	0	—	—
Number of prospectors per nest			
Explanatory terms			
Intercept	−3.54±0.75		
Mean reproductive success	0.45±0.18	$F_{1,310}=6.47$	0.011
Colony size	−0.04±0.01	$F_{1,310}=12.57$	<0.001
Connectivity	0.51±0.26	$F_{1,310}=1.45$	0.045
Feeding rate	20.19±6.18	$F_{1,310}=10.68$	0.001
(Feeding rate)^2	−64.26±28.08	$F_{1,310}=5.24$	0.023
Deleted terms			
Date		$F_{1,309}=0.19$	0.665
Age of chicks		$F_{1,300}=0.95$	0.331
Age of male owner		$F_{1,309}=0.47$	0.496
Age of female owner		$F_{1,309}=0.92$	0.339
Number of chicks		$F_{1,292}=0.88$	0.349
Time		$F_{1,308}=1.80$	0.180
Covariance parameter estimates			
Colony identity	0	—	—
Nest identity	0	—	—

For the probability that a nest is prospected: 1 = presence of one or more prospectors; 0 = absence of prospectors; binomial error and logit link function. For number of prospectors: Poisson error and log link function. Mean reproductive success in a colony is measured as the average number of fledglings raised per successful breeding pair. Colony and nest site identities were included as random effects. in both analyses. Parameter estimates ± SE are only indicated for variables included in the final reduced models. $N = 431$ videotape recordings from 109 nests.

DISCUSSION

In this study we found that prospecting to gather information on conspecific breeding performance is a widespread behaviour in the lesser kestrel. Data on radiomarked individuals revealed that around 50% of failed breeders inspected conspecific nests in at least one foreign colony, a figure probably underestimated because radiotracking tasks did not allow simultaneous locations of all individuals and some visits to foreign colonies would have gone unnoticed. Our experimental manipulation mimicked natural breeding failure, which in lesser kestrels is mostly attributable to predation (Serrano et al. 2004). Thus, there is no reason to think that the observed prospecting behaviour differs between artificially and naturally failed breeders. Failed breeders are, a priori, more prone to select a new breeding site, as a poor reproductive performance often induces breeding dispersal in most species (e.g. Greenwood & Harvey 1982; Dow & Fredga 1983; Forero et al. 1999; Calabuig et al. 2008b). The high occurrence of prospecting among this subset of the population supports the idea that this behaviour is the mechanism by which individuals acquire information on conspecific breeding performance later used in postdispersal breeding patch selection (Brown et al. 2000; Pärt & Doligez 2003; Boulinier et al. 2008; Calabuig et al. 2008b).

Detailed information on prospecting patterns within the studied colonies also revealed that a high percentage of nest sites and almost all colonies were regularly prospected. Furthermore, the presence and number of prospectors attracted were determined by parameters acting at both the breeding patch and the nest site scales. At the breeding patch scale, local productivity was positively related to the probability that a nest was prospected and to the number of prospectors attracted. The higher prospecting activity detected in more productive colonies indicates the important role of conspecific breeding performance as a quality indicator for the habitat assessment process which can ultimately determine the growth and dynamics of breeding patches (e.g. Cadiou 1999; Brown et al. 2000; Doligez et al. 2002; Aparicio et al. 2007; Calabuig et al. 2008a).

Apart from breeding patch productivity, we also found that the number of prospectors attracted was positively associated with colony connectivity. The connectivity of a given colony is a parameter that describes the probability that this colony receives foreign visitors based on the distance and size of other surrounding colonies (Ortego et al. 2008). This pattern is further supported by the relatively short distances travelled by radiotracked individuals, which suggests that prospecting movements are limited to foreign breeding patches located around the colonies of origin. The costs of prospecting could increase with the distance from local breeding patches if entering unfamiliar areas increases the number of attacks received and/or the risk of predation (van der Jeugd 2001; Brown et al. 2008). Also, both prospecting movements and the selection of a future breeding patch could be performed in a restricted geographical area only if alternative patches/nest sites are available within this spatial scale. Overall, the observed pattern of limited prospecting movements is in accordance with the relatively small breeding dispersal distances generally observed in most bird species despite most of them often showing a large movement capacity (Paradis et al. 1998; Serrano et al. 2001; Ortego et al. 2008).

Colony size was negatively associated with the probability that a nest was prospected and with the number of prospectors attracted. Most probably prospectors do not avoid large colonies but, rather, the observed association could be a consequence of a dilution effect in large colonies where several potential nests can be prospected. This seems to be confirmed by the fact that colony size was not correlated with the number of prospectors after standardizing for the total time each colony was recorded ($F_{1,12} = 2.03$, $N = 14$ colonies, $P = 0.18$). Thus, if defensive tasks are costly for nest owners (see below), breeding in larger colonies could provide a benefit similar to the reduction of individual predation risk at increasing group size (Hamilton 1971).

Apart from colony characteristics, we also found that the probability that a nest is prospected and the number of prospectors attracted increased and then decreased with the feeding rates of nest owners. A high feeding rate of nest owners may attract prospectors to more productive breeding sites (Lombardo 1987; Pärt & Doligez 2003; Doligez et al. 2004). This cue can be remotely evaluated by birds and this may facilitate the detection of high-quality nests, particularly in larger colonies where many breeding sites can potentially be explored (Parejo et al. 2008). Thus, monitoring feeding activity of nest owners seems to be important for locating high-quality breeding sites (Lombardo 1987). However, a detailed inspection of nests with the highest feeding rates could be difficult as these nests are more efficiently defended because of a recurrent presence of their owners which evict prospectors. Thus, the fact that prospecting activity first increased and then decreased with the feeding rate of nest owners could indicate a trade-off between the interest of a given nest and the costs of prospecting it.

The cost of prospecting for both prospectors and nest owners has been little studied and is one of the less well-known aspects of prospecting behaviour (Eadie & Gauthier 1985; Arcese 1987). The effort invested in prospecting seems to be high as radiomarked individuals visited up to six different colonies and a high proportion of them were detected performing active nest prospecting in the visited colonies. Besides the time and energy required for prospecting, nest owners frequently chased and evicted prospectors which exposes them to injuries from the attacks (Arcese 1987; Pärt & Doligez 2003; Doligez et al. 2004; Tobler & Smith 2004). For the same reason, prospector presence or activity could also be costly for nest owners and the eviction of prospectors should entail certain benefits for them. A possibility is that such defensive behaviour helps to avoid future prospector settlement, reducing future competition for nest sites in their breeding colonies (see also Piper et al. 2006).

Overall, this study has revealed that prospecting is a very frequent behaviour in the colonially breeding lesser kestrel and sheds light on the nest and breeding patch characteristics influencing prospector attraction which have been previously overlooked by studies performed at a reduced spatial scale and restricted to a single breeding patch. The observed patterns can help to explain the proximate mechanism by which individuals select more productive colonies after breeding dispersal and suggest that prospecting is the underlying behaviour translating public information into the growth and dynamics observed in breeding aggregations (Brown et al. 2000; Aparicio et al. 2007; Calabuig et al. 2008a, b).

Acknowledgments

We are indebted to the Councils of Villacañas and Villafranca de los Caballeros and Agrupación Naturalista Esparvel who allowed us to work on their properties. Raúl Bonal and Alberto Muñoz helped to monitor the study population in the past and Sonia Quilón helped us in videotape-recording tasks. Tobias Dittmann, Valentin Amrhein and an anonymous referee provided valuable comments that improved the manuscript. This work received financial support from the projects PAI 05-053 and PCI 08-0130 of the Junta de Comunidades de Castilla-La Mancha (JCCM) and CGL2005-05611-C02-02 and CGL2008-00095BOS of the Ministerio de Ciencia y Tecnología (MCYT). During this work G.C. and J.O were supported by predoctoral fellowships from the JCCM and the European Social Fund. Nowadays J.O enjoys a postdoctoral JAE-Doc (CSIC) contract.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2009.12.007.

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