IBIS The International Journal of Avian Science
BOU
Ibis (2011), **153**, 37–45

Mechanisms of colony selection by first-year Lesser Kestrels *Falco naumanni*

GUSTAU CALABUIG,[1]*† JOAQUÍN ORTEGO[2] & JOSÉ MIGUEL APARICIO[1]
[1]*Grupo de Investigación de la Biodiversidad Genética y Cultural, Instituto de Investigación en Recursos Cinegéticos – IREC (CSIC, UCLM, JCCM), Ronda de Toledo s/n, E-13005 Ciudad Real, Spain*
[2]*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, E-28006 Madrid, Spain*

In colonial species, first-time breeders may use the number of settled conspecifics in colony selection, but such a relationship is confused by the correlation between colony size and nest-site availability. To distinguish conspecific attraction from neutral colony selection, we experimentally increased nest availability for first-year Lesser Kestrels *Falco naumanni*, allowing us to dissociate the number of vacant nest-sites from colony size at the arrival time of first-year birds. Under natural conditions, the number of first-year birds settling was positively correlated with both the number of philopatric and the total number of breeding pairs (colony size) already settled. However, the probability of occupation of experimentally manipulated nests by first-year birds was independent of colony size. In experimental colonies, the number of first-year birds settling was positively correlated with the number of manipulated nest-sites but not with the number of conspecifics. Overall, these results support a neutral colony selection by first-year Lesser Kestrels based on nest-site availability.

Keywords: conspecific attraction, conspecific cues, first-year birds, nest-site availability, nest-site selection, neutral selection, public information, social information.

The study of settlement decisions by first-time breeders is necessary for understanding the dynamics of animal populations. Several studies have shown that individual decisions about habitat choice and settlement are based on information about habitat quality, which is gathered by watching the success or failure of conspecifics (Templeton & Giraldeau 1996, Danchin *et al.* 1998, Brown *et al.* 2000, Doligez *et al.* 2002, Aparicio *et al.* 2007, Calabuig *et al.* 2008b). This kind of information is called 'public information' (Valone 1989). In birds, public information used for selection of breeding habitat is usually obtained by prospecting conspecific nests during the nestling period (Cadiou *et al.* 1994, Boulinier *et al.* 1996, Schjorring *et al.* 1999, Ottosson *et al.* 2001, Doligez *et al.* 2004, Ward 2005, Parejo *et al.* 2008). As productivity is a cue only available for a short period at the end of the breeding season (Boulinier *et al.* 1996), first-year birds are less likely to obtain information about the productivity of conspecifics in other breeding patches in their year of birth and this is expected to be particularly important in species breeding synchronously (Nocera *et al.* 2006). Thus, the question arises of what kind of information first-year birds are using to select a breeding location.

A neutral hypothesis of random occupation predicts that first-year birds select breeding habitats irrespective of quality, simply occupying available nest-sites where settlement is not constrained by conspecific competition. Alternatively, individuals could be using the presence of conspecifics breeding in a given patch as a source of information. This could be assessed from early stages of the breeding season (Serrano *et al.* 2004) and may indicate habitat suitability (Stamps 1988, Reed & Dobson 1993, Muller *et al.* 1997, Ward & Schlossberg 2004, Hahn & Silverman 2006). This conspecific

*Corresponding author.
Email: Gustau.Calabuig@uclm.es

†Present address: CNRS, UPS; EDB (Laboratoire évolution et Diversité Biologique); UMR5174; 118 route de Narbonne, F-31062 Toulouse cedex 9, France.

attraction hypothesis predicts that the number of individuals attracted to a given breeding patch is positively associated with the number of conspecifics previously settled.

Previous studies have shown that public information cues (i.e. all the cues inadvertently produced by the behaviour of conspecifics that inform about the quality of resources; Danchin *et al.* 2004) are usually strongly intercorrelated, so that experimental approaches are required to discern between alternative hypotheses about settlement decisions (Valone & Templeton 2002). To the best of our knowledge, experimental studies of conspecific attraction have been limited to experimental simulation of the presence of conspecifics using song playback or artificial decoys (Podolsky & Kress 1989, Ward & Schlossberg 2004, Ahlering *et al.* 2006, Hahn & Silverman 2006, Nocera *et al.* 2006). However, these studies did not distinguish between experienced and first-breeding individuals. The apparent preference of first-year birds for larger colonies has been found in colonial species such as the American Cliff Swallow *Petrochelidon pyrrhonota* (Brown & Brown 1996) and the Purple Martin *Progne subis* (Davis & Brown 1999). This preference for more densely occupied plots has also been found in first-year birds of territorial species such as the American Redstart *Setophaga ruticilla* (Hahn & Silverman 2006).

The presence of conspecifics as a cue attracting first-time breeders has also been suggested for the colonial Lesser Kestrel *Falco naumanni* (Serrano *et al.* 2003). In this species, the number of first-year birds settled in the colonies is associated with colony size (Aparicio *et al.* 2007). However, in Lesser Kestrel colonies, the absolute number of unsuccessful breeding pairs is also positively correlated with colony size (Aparicio *et al.* 2007). Pairs failing to breed emigrate frequently to other colonies in the following season (Aparicio 1997, Serrano *et al.* 2001, Calabuig *et al.* 2008b), thus leaving more available nest-sites in larger colonies where the absolute number of breeding failures is always higher (Aparicio *et al.* 2007). Consequently, there may be a greater opportunity to settle in large colonies than in small ones and first-year birds could settle preferentially in those colonies with lower intraspecific competition. This complex relationship between colony size and the factors determining nest-site availability suggests that an experimental approach is necessary to test neutral and 'conspecific attraction' hypotheses of habitat selection by first-year Lesser Kestrels. Specifically, because first-year birds arrive later than older birds when most of the nest-sites are already occupied, an experimental design manipulating the availability of nesting sites during the later phase of the settlement period is necessary to discriminate between these alternative hypotheses.

In this study, we first examined under natural conditions the intercorrelations between a number of variables related to colony demography, such as colony size, the number of first-year birds settling in a colony, the number of philopatric Kestrels (i.e. ringed adult birds which had returned to the same colony) and the number of unsuccessful breeding attempts. Secondly, we performed an experiment to dissociate nest-site availability from colony size and measure the settlement of first-year birds irrespective of colony size. For this purpose, we blocked off some nest-sites, and provided additional, blocked nestboxes in some small colonies, before the arrival of adult Lesser Kestrels, to create nest-sites that could not be occupied by returning adult birds. These experimental nest-sites were opened when the earliest first-year bird was seen in the area and most adult Lesser Kestrels were already settled, thus providing first-year birds with the chance to select a nest-site with less competition from adults. This experimental manipulation allowed us to assess whether the probability that a nest-site is occupied by first-year birds is greater in colonies with more settled conspecifics, in support of the conspecific attraction hypothesis, or if it is independent of colony size, in support of the neutral hypothesis. We also assessed whether the total number of first-year birds settled was associated with the number of conspecifics settled in the colony or with the number of experimentally provided nest-sites.

METHODS

Species and study area

The study area is located in La Mancha, central Spain (600–800 m above sea level), and extends over about 1000 km^2. We have been monitoring a Lesser Kestrel population in this area since 1991 (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 with 300–400 mm of rainfall mainly concentrated in spring and autumn (data available from AEMET;

http://www.aemet.es). The area is extensively cultivated with barley *Hordeum vulgare*, wheat *Triticum* spp. and vines *Vitis vinifera*.

The Lesser Kestrel is a small migratory falcon that forms colonies in old farmhouses and other buildings, placing its nests under tiled roofs or inside holes in walls (Aparicio & Bonal 2002). Our population has experienced growth in recent years after a severe decline in the second half of the 20th century (Ortego *et al.* 2007). Second-year and older individuals arrive in the study area from their winter quarters in Africa between January and March (depending on the year). First-year birds arrive, together with the last few adults, about 40 days later. For instance, in the year previous to the experiment, the first first-year male was detected 41 days after the first adults arrived at the colonies (see Calabuig *et al.* 2008a for details of censuses; Fig. 1). First-year birds are subordinate individuals and adults usually displace them in nest contests (Serrano & Tella 2007). About 40–50% of individuals attempt to breed in their first year of life (Aparicio *et al.* 2007). On arrival, males take a nest 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 (Negro *et al.* 1997). The earliest clutches are laid at the end of April and the latest in the first week of June (Aparicio & Bonal 2002). Both sexes contribute equally to incubation and feeding of nestlings (Aparicio *et al.* 2007).

Field methods and the experimental treatment

At the end of January of 2006 and 2007, before the arrival of Kestrels, we blocked off the entrance of a randomly selected number of nest-sites (range = 1–5) in 12 and 10 colonies, respectively (34 nest-sites were blocked in 2006 and 27 nest-sites in 2007). Of these colonies, three were manipulated only in the 2006 breeding season, one only in 2007, and nine in both years. We erected additional nest boxes in the colonies where the random number of holes to be blocked was equal to or greater than the number of natural nest-sites registered in that colony in the previous breeding seasons. This avoided blocking all the nest-holes in such colonies. All blocked nest-holes and additional nestboxes remained closed and inaccessible to breeding individuals during the early stages of the settlement period. These experimental nest-sites were opened at the end of March, just after the first first-year bird was observed in the study area, thus increasing the number of available nest-holes at the end of the adult settlement period. Each colony was monitored at least once a week to record the number of Kestrels in the colony and nest occupation (see Calabuig *et al.* 2008a for details of censuses). A total of 157 breeding pairs in 2006 and 159 in 2007 were captured by hand in the nest during incubation, ringed and measured in these colonies (see Aparicio 1997, Aparicio & Cordero 2001). The age of many individuals was accurately known because most of them had been captured and ringed as nestlings in previous breeding seasons. We aged unringed males as first-year individuals by their unambiguous immature plumage characteristics. We aged unringed females as first-year or older individuals on the basis of their 11th secondary strip pattern and other plumage characteristics. In particular, first-year females exhibit a more abraded and striped plumage than second-year or older females (J. M. Aparicio unpubl. data). We defined colony size as the number of females that laid at least one egg in non-manipulated nest-sites.

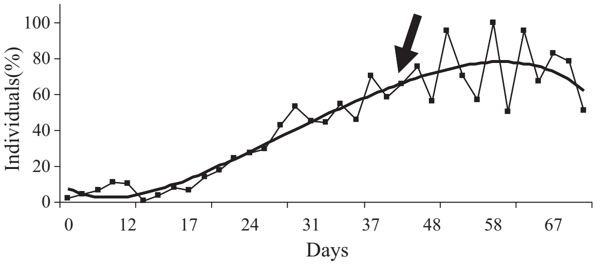

Figure 1. Arrival date of Lesser Kestrels in the study area in the year prior to the experiment. The arrow indicates the arrival date of the first 1-year-old individual. Third-order polynomial regression line is shown.

Variables and statistical analyses

For the analyses in unmanipulated conditions, we used data from colonies monitored intensively since the 2000 breeding season (85 colony-years; range 3–28 colonies per year). For these analyses, we used data from those colonies in which at least 75% of the breeding birds were ringed. In these colonies, we determined colony size (as the number of females that laid at least one egg), nest failure rate, proportion of first-year birds breeding in the colony relative to the number of individuals breeding in the current year and proportion of philopatric birds relative to the number of ringed birds breeding in the previous breeding season. Accordingly, we estimated absolute numbers of failed nests, first-year birds and philopatric Kestrels for each studied colony. We also estimated the number of vacant nest-sites in a given year (*t*) as twice the number of breeding pairs settled in the colony (i.e. the total number of individuals) in year *t*–1 minus the number of philopatrics in the current season.

We used generalized linear mixed models (GLMMs) implemented with the GLIMMIX macro of SAS (SAS Institute 2004) to analyse the relationship between the number of first-year birds settled and the number of philopatric Kestrels, between the number of first-year birds and the number of adults settled, as well as between the number of failed nests and colony size. In all these analyses, we used a Poisson error distribution and log link function. We verified these relationships using data from five breeding seasons (2000–2005) prior to the experiment and included year as a random effect in all these analyses to control for potential differences among years.

We tested the efficiency of our experimental manipulation on stimulating the settlement of first-year individuals in two ways. First, we used a paired *t*-test to compare the percentage of first-year individuals settled in manipulated nests with those settled in non-experimental nest-sites. Secondly, we used Fisher's exact test to compare the number of first-year individuals settled in manipulated nests with the number of first-year birds that settled in the same nest-sites in the year before the experiment.

A GLMM was used to test the conspecific attraction hypothesis analysing the probability of occupation of a given manipulated nest by at least one first-year bird in relation to the number of conspecifics settled in the colony. In this analysis, the presence or absence of first-year birds in a manipulated nest was analysed using a binomial error structure and logit link function. The number of breeding pairs settled in the colony and the number of manipulated nests were fitted as covariates. Year, colony identity and nest identity (nested within colony) were included as random effects to control for nest-site quality and possible differences among colonies and years in occupation rates. Finally, we performed an additional GLMM with Poisson distribution of errors and log link function to determine whether the number of first-year birds settled in manipulated nests in a given colony is associated with colony size, the number of philopatric Kestrels or the number of manipulated nests. Because several nests were manipulated in each colony and most colonies were monitored in both years, we fitted colony identity and year as random effects in this analysis.

RESULTS

Settlement under natural conditions

The number of first-year birds breeding in a given colony was positively correlated with the number of adult breeding pairs ($F_{1,50} = 10.32$, $P = 0.002$, Fig. 2a) and with the number of philopatric Lesser Kestrels settled in the same season ($F_{1,27} = 6.74$, $P = 0.015$, Fig. 2b). These results appear to support the conspecific attraction hypothesis. In contrast, similar analyses including as predictors either the number of failed nests in the previous

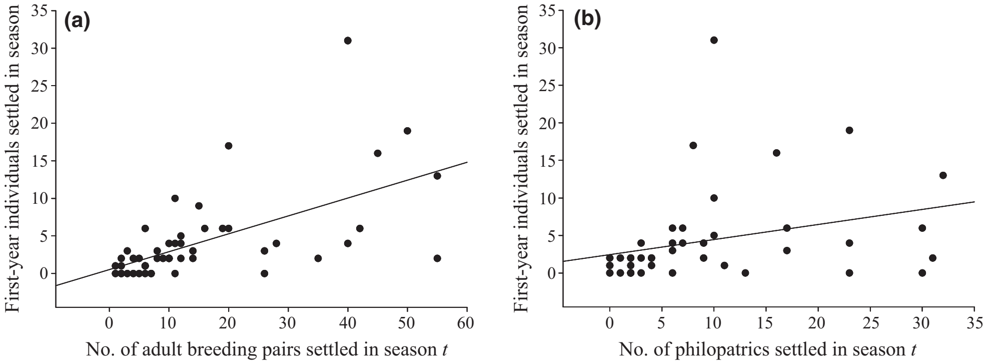

Figure 2. Relationship between the number of first-year birds settled and (a) colony size and (b) the number of philopatrics settled in the colony in the current breeding season. Regression lines are shown.

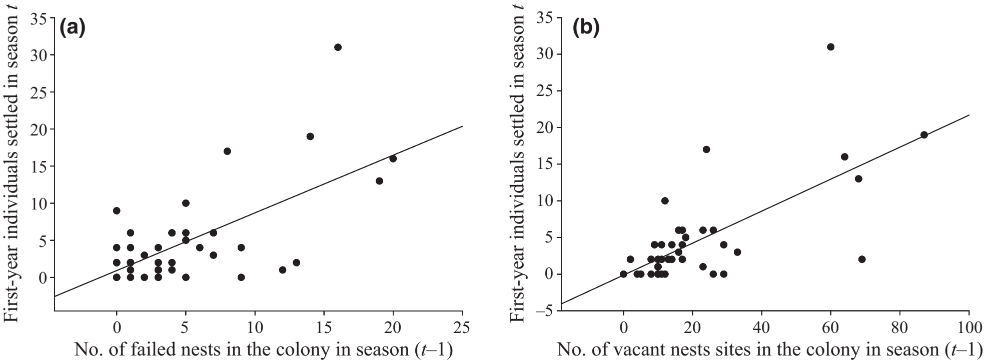

Figure 3. Relationship between the number of first-year birds settled and (a) the number of failed nest-sites in the previous breeding season and (b) the number of vacant nests sites in the settlement season. Regression lines are shown.

year (*t*–1) ($F_{1,39} = 28.02$, $P < 0.001$, Fig. 3a) or the number of vacant nest-sites (i.e. twice the colony size in year *t*–1 minus the number of philopatric Kestrels in year *t*) ($F_{1,23} = 43.39$, $P < 0.001$, Fig. 3b) also showed that both variables are positively correlated with the number of first-year birds settled in year *t* in agreement with the neutral hypothesis. In addition, we performed a GLMM analysis including colony size in year *t*–1 and number of philopatric Kestrels in year *t* as predictors. The number of first-year birds breeding in a colony in year *t* was positively associated with colony size in year *t*–1 ($F_{1,26} = 49.16$, $P < 0.001$) and negatively associated with the number of philopatric Kestrels in year *t* ($F_{1,26} = 12.41$, $P = 0.002$). Given that Lesser Kestrels do not examine foreign colonies in their hatching year (Calabuig *et al.* 2010), the number of kestrels breeding in a colony in year *t*–1 cannot be considered a conspecific attraction cue but a variable related to the number of suitable nest-sites in a given colony. This analysis suggests that first-year birds settle more frequently where there are more available nest-sites and fewer, competitive older individuals. However, the variables relating to colony size in year *t*–1, number of philopatric Kestrels in year *t*, number of failed nests in year *t*–1 and number of first-year birds settling in year *t* were all strongly intercorrelated (Table 1), and the correlation of the response variable with these multicollinear parameters may be either to true synergistic relationships among the variables or to spurious correlations (Graham 2003).

Table 1. Correlations between different social parameters in Lesser Kestrel colonies.

		No. of philopatrics (*t*)	No. of breeding pairs (*t*–1)	No. of failed nests (*t*–1)
No. of breeding pairs in (*t*–1)	*r*	0.912		
	P	< 0.001		
	n	31		
No. of failed nest-sites in season (*t*–1)	*r*	0.791	0.710	
	P	< 0.014	< 0.001	
	n	31	31	
No. of first-year birds in season (*t*)	*r*	0.389	0.594	0.696
	P	0.030	< 0.001	< 0.001
	n	31	34	39

Settlement in the experiment

The number of manipulated nest-holes in a given colony (mean ± se = 2.77 ± 0.23, $n = 22$) was independent of colony size (Pearson correlation 2006: $r = 0.23$, $n = 12$, $P = 0.4$; 2007: $r = 0.386$, $n = 10$, $P = 0.27$), indicating that the manipulation was efficient at breaking the relationship between colony size and late nest availability. After controlling for colony identity and year, laying dates of breeding pairs nesting in manipulated and non-manipulated nest-sites did not differ in the breeding season prior to the experiment ($F_{1,160} = 0.207$, $P = 0.65$), suggesting that their quality was similar. Thirty-one (91%) and 21 (78%) of manipulated nest-sites were occupied after being reopened in 2006 and 2007, respectively. A total of 53 individuals (23 males and 30 females) in 2006 and 33 individuals (17 males and 16 females) in 2007 were captured in manipulated nest-sites. Of these, 16 (30.2%) in 2006 and 10 (30.3%) in 2007 were first-year individuals. The efficiency of the experimental manipulation favouring the settlement of first-year birds was supported by the higher percentage of these individuals settled in manipulated nests in comparison with unmanipulated nests in each colony (paired *t*-test, $t = -2.647$, $P = 0.018$). Furthermore, the number of first-year birds settled in manipulated nests in the years of the experiment was higher in relation to the number of first-year birds in the same nest-sites in the year before the experiment (Fisher exact test, $P = 0.003$; Fig. 4).

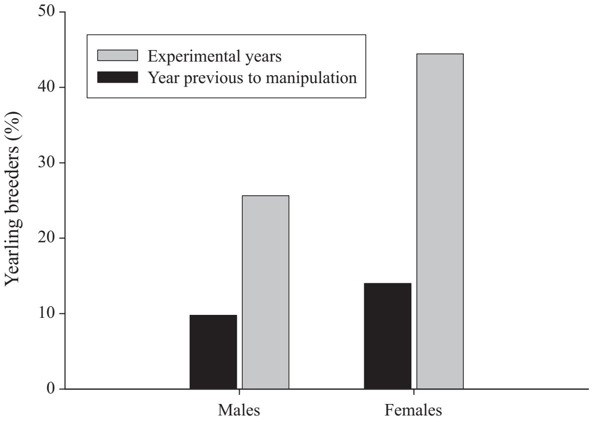

Figure 4. Percentage of male and female first-year birds settled in manipulated nests in the two experimental years (grey bars) compared with the percentage of first-year birds of both sexes settled in these manipulated nests in the 2 years prior to the experiment (black bars).

The probability of a manipulated nest-site being occupied by a first-year bird was not associated with colony size or with the total number of manipulated nest-sites in a given colony (Table 2a). Furthermore, the number of first-year birds settled in manipulated nest-sites was positively associated with the total number of manipulated nest-sites in a given colony but was not related to colony size (Table 2b; Fig. 5). In contrast to the results obtained in natural conditions, under experimental conditions the total number of first-year birds breeding in a colony was positively related to the number of manipulated nests but independent of

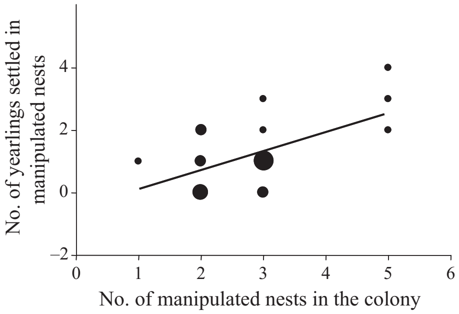

Figure 5. Number of first-year birds settled in manipulated nest-sites in relation to the number of manipulated nest-sites in the colony. Bigger dots represent five, four and two data points. Regression line is shown.

Table 2. GLMMs for (a) the probability of settlement by first-year birds in late available nests (binomial error and logit link function) and (b) the number of first-year birds settled in Lesser Kestrel colonies (Poisson error and log link function) in relation to colony size and nest availability. Estimates ± se are only indicated for variables entered into the final model.

	Estimate ± se	Test	*P*
(a) Probability of settlement by first-year birds			
Intercept	−2.71 ± 6.13		
Colony size		$F_{1,25.8} = 0.23$	0.632
No. of manipulated nests in the colony		$F_{1,26.9} = 0.30$	0.588
Covariance parameter estimates			
Year	0	–	–
Colony identity	0	–	–
Nest-site identity (nested within colony)	118.88 ± 43.69	$Z = 2.72$	0.003
(b) Number of first-year birds settled			
Intercept	−0.75 ± 0.48		
Colony size		$F_{1,17} = 1.91$	0.186
No. of manipulated nests in the colony	0.45 ± 0.13	$F_{1,17} = 12.74$	0.002
Covariance parameter estimates			
Year	0	–	–
Colony identity	0	–	–

the number of adult breeders in the colony (number of manipulated nests: $F_{1,19} = 4.88$, $P = 0.039$; number of adults in the colony: $F_{1,19} = 2.73$, $P = 0.115$) or the number of philopatrics settled (number of manipulated nests: $F_{1,19} = 5.30$, $P = 0.033$; number of philopatrics: $F_{1,19} = 0.58$, $P = 0.457$).

DISCUSSION

The pattern of first-year settlement observed in natural conditions was based on the number of vacant nest-sites, suggesting the use of a neutral breeding site selection mechanism by first-year Lesser Kestrels. We demonstrate that the role of conspecific attraction cannot be discerned from a random pattern of settlement using a non-experimental approach because absolute numbers of first-year birds, philopatric breeders, available nest-sites and breeding dispersers are all strongly and positively intercorrelated in natural conditions (Table 1, Figs 2 and 3). However, this relationship disappeared when we provided a small number of available nest-sites in each colony at the end of the settlement period. Therefore, correlative evidence on the use of public information for habitat selection cannot reject the alternative hypothesis and an accurate analysis of the information actually used requires experimental approaches (Doligez *et al.* 2002, Valone & Templeton 2002).

Settlement decisions based on public information could reduce the time and energy invested in habitat assessment and increase the chance of choosing better breeding places (Valone & Templeton 2002, Danchin *et al.* 2004). In several species, including the Lesser Kestrel, second-year and older individuals use public information based on the breeding performance of conspecifics obtained in the previous year (Aparicio *et al.* 2007, Calabuig *et al.* 2008a,b). However, productivity is a cue only available during a short period at the end of the breeding season and first-year birds are not likely to obtain such information in their year of birth (Boulinier *et al.* 1996). Although fledgling Lesser Kestrels from the earlier breeding attempts could potentially prospect outside their breeding colonies, the time available for this is expected to be highly limited by other activities (e.g. improving hunting techniques) essential to ensure survival during the critical period after independence. Accordingly, intensive videotape recording and colony monitoring in our study population have revealed that Lesser Kestrels never examine foreign colonies in their hatching year (Calabuig *et al.* 2010). Given that first-year birds have no alternative information or previous breeding experience, arrive later at the breeding areas and are time-constrained in selecting a breeding location, they should be especially prone to use public information in their settlement decisions that can be obtained in the current season. Why, then, do first-year individuals not appear to use it? Conspecific attraction would be advantageous if fitness prospects were associated with colony size, and so it was expected that reproductive success would be greater in larger colonies. This seems to be generally true in Lesser Kestrel colonies (Tella 1996). However, variance in breeding performance within a colony may increase with the number of pairs breeding as long as late breeders experience higher costs in large colonies where food depletion is particularly intense at the end of the season (Bonal & Aparicio 2008). Therefore, breeding in a large colony may be advantageous for early breeders but less so for late breeders, which will include almost all first-year birds. It may be that the costs of breeding in large colonies for first-year birds can be high enough to impede the evolution of behavioural mechanisms of colony selection based on social attraction.

Unlike first-year birds, adult Kestrels base their settlement on the productivity of conspecifics (Aparicio *et al.* 2007, Calabuig *et al.* 2008a) but this kind of information seems to be used only at the beginning and not later in the settlement period when the associated costs are probably high due to intraspecific competition. We suggest that nest availability probably shapes colony selection even for individuals with available information on the quality of breeding sites estimated using public information. This emphasizes the importance of considering variation in the conditions experienced at settlement as a potential explanation for the coexistence of different settlement strategies (Muller *et al.* 1997, Baltz & Clark 1999, Schjorring & Bregnballe 2000).

Nest failure promotes breeding dispersal in Lesser Kestrels (Aparicio 1997, Serrano *et al.* 2001, Calabuig *et al.* 2008b) so that breeding colonies suffering a high nest failure rate in a season would have fewer breeding pairs in the subsequent season. However, observation data in our population show that some colonies with productivity close to zero maintain a constant size for years. The neutral colony selection performed by first-year birds offers an explanation for the persistence of low-quality sites where the high number of vacant nesting sites as a result of breeding dispersal and low productivity offer a better chance of nest-site acquisition by first-year birds. This idea is supported by the high number of individuals ringed as fledglings in other colonies and captured as first-year breeders in these very low-productivity colonies (J. M. Aparicio unpubl. data).

First-year Lesser Kestrels mainly attempt to breed where they find vacant nest-sites regardless of public information cues such as the number of conspecifics settled. This kind of public information could be useful to detect adequate breeding places for early breeders, but not for late breeders, including first-year birds. First-year birds and older Kestrels use different strategies to select a breeding colony (Doligez *et al.* 2002, Nocera *et al.* 2006, Parejo *et al.* 2007) and these differences may explain the population dynamics of some colonies showing very low productivity but long persistence. This study highlights the importance of experimental approaches to reveal the preferences, constraints and mechanisms of habitat selection.

We are indebted to the Councils of Villacañas and Villafranca de los Caballeros and Agrupación Naturalista Esparvel which allowed us to work on their properties. Raul Bonal and Alberto Muñoz contributed to monitoring this population in the past. We manipulated and banded Lesser Kestrels under licence from the Spanish institutional authorities (Environmental Agency of the Community of Castilla-La Mancha and the Ringing Office of the Ministry of Environment) and we followed general ethical guidelines for animal welfare and nature conservation. This work received financial support from the projects PCI08-0130 of the Junta de Comunidades de Castilla-La Mancha (JCCM), CGL2005-05611-C02-02 and CGL2008-00095BOS of the Ministerio de Ciencia e Innovación. During this work, G.C. and J.O. were supported by predoctoral fellowships from the JCCM and the European Social Fund. AEMAT provided data on temperature and precipitation (ref. 990081557).

REFERENCES

Ahlering, M.A., Johnson, D.H. & Faaborg, J. 2006. Conspecific attraction in a grassland bird, the Baird's Sparrow. *J. Field Ornithol.* **77**: 365–371.

Aparicio, J.M. 1997. Costs and benefits of surplus offspring in the Lesser Kestrel (*Falco naumanni*). *Behav. Ecol. Sociobiol.* **41**: 29–137.

Aparicio, J.M. & Bonal, R. 2002. Effects of food supplementation and habitat selection on timing of Lesser Kestrel breeding. *Ecology* **83**: 873–877.

Aparicio, J.M. & Cordero, P.J. 2001. The effects of the minimum threshold condition for breeding on offspring sex-ratio adjustment in the Lesser Kestrel. *Evolution* **55**: 1188–1197.

Aparicio, J.M., Bonal, R. & Muñoz, A. 2007. Experimental test on public information use in the colonial Lesser Kestrel. *Evol. Ecol.* **21**: 783–800.

Baltz, A.P. & Clark, A.B. 1999. Does conspecific attraction affect nest choice in Budgerigars (*Melopsittacus undulatus*: Psittacidae: Aves)? *Ethology* **105**: 583–594.

Bonal, R. & Aparicio, J.M. 2008. Evidence of prey depletion around Lesser Kestrel *Falco naumanni* colonies and its short term negative consequences. *J. Avian Biol.* **39**: 189–197.

Boulinier, T., Danchin, E., Monnat, J.Y., Doutreland, C. & Cadiou, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *J. Avian Biol.* **27**: 252–256.

Brown, C.R. & Brown, M.B. 1996. *Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior*. Chicago: University of Chicago Press.

Brown, C.R., Brown, M.B. & Danchin, E. 2000. Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. *J. Anim. Ecol.* **69**: 133–142.

Cadiou, B., Monnat, J.Y. & Danchin, E. 1994. Prospecting in the Kittiwake, *Rissa tridactyla*: different behavioral patterns and the role of squatting in recruitment. *Anim. Behav.* **47**: 847–856.

Calabuig, G., Ortego, J., Aparicio, J.M. & Cordero, P.J. 2008a. Public information in selection of nesting colony by Lesser Kestrels: which cues are used and when are they obtained? *Anim. Behav.* **75**: 1611–1617.

Calabuig, G., Ortego, J., Cordero, P.J. & Aparicio, J.M. 2008b. Causes, consequences and mechanisms of breeding dispersal in the colonial Lesser Kestrel (*Falco naumanni*). *Anim. Behav.* **76**: 1989–1996.

Calabuig, G., Ortego, J., Aparicio, J.M. & Cordero, P.J. 2010. Intercolony movements and prospecting behaviour in the colonial Lesser Kestrel. *Anim. Behav.* **79**: 811–817.

Danchin, E., Boulinier, T. & Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* **79**: 2415–2428.

Danchin, E., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. 2004. Public information: from nosy neighbors to cultural evolution. *Science* **305**: 487–491.

Davis, J.A. & Brown, C.R. 1999. Costs of coloniality and the effect of colony size on reproductive success in Purple Martins. *Condor* **101**: 737–745.

Doligez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science* **297**: 1168–1170.

Doligez, B., Pärt, T. & Danchin, E. 2004. Prospecting in the Collared Flycatcher: gathering public information for future breeding habitat selection? *Anim. Behav.* **67**: 457–466.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**: 2809–2815.

Hahn, B.A. & Silverman, E.D. 2006. Social cues facilitate habitat selection: American Redstarts establish breeding territories in response to song. *Biol. Lett.* **2**: 337–340.

Hernández, J.L., Ortego, J., Calabuig, G., Bonal, R., Muñoz, A., García, G., Cordero, P.J. & Aparicio, J.M. 2007. Casi dos décadas anillando primillas en la mancha. In Casas, F., Arredondo, A. & López-Jamar, J. (eds) *Anuario Ornitológico de Ciudad Real 2004–2005*: 165–170. Ciudad Real: SEO-Ciudad Real.

Muller, K.L., Stamps, J.A., Krishnan, V.V. & Willits, N.H. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *Am. Nat.* **150**: 650–661.

Negro, J.J., Hiraldo, F. & Donázar, J.A. 1997. Causes of natal dispersal in the lesser kestrel: inbreeding avoidance or resource competition? *J. Anim. Ecol.* **66**: 640–648.

Nocera, J.J., Forbes., J. & Giraldeau, L.A. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. *Proc. R. Soc. Lond. B* **273**: 349–355.

Ortego, J., Aparicio, J.M., Calabuig, G. & Cordero, P.J. 2007. Increase of heterozygosity in a growing population of Lesser Kestrels. *Biol. Lett.* **3**: 585–588.

Ottosson, U., Bäckman, J. & Smith, H.G. 2001. Nest-attenders in the Pied Flycatcher (*Ficedula hypoleuca*) during nestling rearing: a possible case of prospective resource exploration. *Auk* **118**: 1069–1072.

Parejo, D., White, J. & Danchin, E. 2007. Settlement decisions in Blue Tits: difference in the use of social information according to age and individual success. *Naturwissenschaften* **94**: 749–757.

Parejo, D., Pérez-Contreras, T., Navarro, C., Soler, J.J. & Aviles, J.M. 2008. Spotless Starlings rely on public information while visiting conspecific nests: an experiment. *Anim. Behav.* **75**: 483–488.

Podolsky, R.H. & Kress, S.W. 1989. Factors affecting colony formation in Leach's Storm-Petrel. *Auk* **106**: 332–336.

Reed, J.M. & Dobson, A.P. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends Ecol. Evol.* **8**: 253–256.

SAS Institute. 2004. *SAS/STAT 9.1 User's Guide*. Cary, NC: SAS Institute Inc.

Schjorring, S. & Bregnballe, T. 2000. Sex difference in criteria determining fidelity towards breeding sites in the great cormorant. *J. Anim. Ecol.* **69**: 214–223.

Schjorring, S., Gregersen, J. & Bregnballe, T. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Anim. Behav.* **57**: 647–654.

Serrano, D. & Tella, J.L. 2007. The role of despotism and heritability in determining settlement patterns in the colonial Lesser Kestrel. *Am. Nat.* **169**: 53–67.

Serrano, D., Tella, J.L., Forero, M.G. & Donázar, J.A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience *vs*. conspecific cues. *J. Anim. Ecol.* **70**: 568–578.

Serrano, D., Tella, J.L., Donázar, J.A. & Pomarol, M. 2003. Social and individual features affecting natal dispersal in the colonial lesser kestrel. *Ecology* **84**: 3044–3054.

Serrano, D., Forero, M.G., Donázar, J.A. & Tella, J.L. 2004. Dispersal and social attraction affect colony selection and dynamics of Lesser Kestrels. *Ecology* **85**: 3438–3447.

Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. *Am. Nat.* **131**: 329–347.

Tella, J.L. 1996. *Ecological constraints, costs and benefits of coloniality in the Lesser Kestrel*. PhD Thesis, University of Barcelona.

Templeton, J.J. & Giraldeau, L.A. 1996. Vicarious sampling: the use of personal and public information by Starlings foraging in a simple patchy environment. *Behav. Ecol. Sociobiol.* **38**: 105–114.

Valone, T.J. 1989. Group foraging, public information and patch estimation. *Oikos* **56**: 357–363.

Valone, T.J. & Templeton, J.J. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **357**: 1549–1557.

Ward, M.P. 2005. Habitat selection by dispersing Yellow-headed Blackbirds: evidence of prospecting and the use of public information. *Oecologia* **145**: 650–657.

Ward, M.P. & Schlossberg, S. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conserv. Biol.* **18**: 519–525.

Received 18 January 2010;
revision accepted 27 September 2010.
Associate Editor: Luc Lens.