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Colony foundation in the lesser kestrel: patterns and consequences of the occupation of empty habitat patches

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Understanding the process of colonization of new habitat patches is critical to clarify the proximate mechanisms involved in the distribution of a species and particularly in the formation of breeding aggregations. We studied the process of colony foundation in a long-term monitored population of lesser kestrels, *Falco naumanni*. For this purpose, we first analysed which habitat/demographic features influence the occupation of empty habitat patches experimentally supplied with nestboxes. Second, we studied the individual characteristics of founders and the reproductive consequences of occupation of new breeding patches in comparison with individuals settled in already established colonies. We found that the probability of occupation of experimental breeding patches increased with the relative cover of cereal crops. Regardless of sex, founders and individuals that settled in pre-existing colonies did not differ in body condition or age. However, there was a higher proportion of unringed kestrels in new than in pre-existing colonies, suggesting that founders are mostly immigrants from distant populations. Founders and nonfounders had similar breeding success, but the former had a lower parasitic burden of feather lice, indicating that occupying new breeding patches could reduce parasite pressure and/or transmission. Our results suggest habitat characteristics influence settlement decisions in the absence of pre-existing social cues, but do not support the idea that founders are suboptimal individuals unable to gain access to previously established colonies.

The colonization of new breeding patches is an important factor determining the dynamics and maintenance of metapopulations and the spatial range of a species' distribution (Ebenhard 1991; Hanski 1991). Despite the amount of research carried out on dispersal and habitat selection, the ecological factors involved in the occupation of empty patches and the mechanisms of population or colony foundation remain poorly understood in comparison with other topics on habitat preferences (Kharitonov & Siegel-Causey 1988).

The process of occupation of new habitats is especially intriguing for species in which individuals assess breeding habitat suitability on the basis of the reproductive performance of conspecifics and select their future breeding site according to this information (Shields et al. 1988; Danchin et al. 1998; Brown et al. 2000; Doligez et al. 2002; Aparicio et al. 2007; Boulinier et al. 2008). This hypothesis of habitat copying requires the presence of previously settled conspecifics and explains the selection of occupied patches and also their growth dynamics (Danchin et al. 1998; Brown et al. 2000; Aparicio et al. 2007). However, it fails to explain the proximate mechanism of colony/population foundation, suggesting that several mechanisms of habitat selection could coexist (Siegel-Causey & Kharitonov 1990). One potential explanation for the foundation of new breeding patches is related to the failure of some individuals to gain access to preferred and saturated sites, if previously established colonies are despotically and hierarchically occupied by dominant individuals following an ideal despotic distribution (Fretwell & Lucas 1970). In this case, and according to the 'individual quality hypothesis', colony foundation events should presumably be carried out by young, inexperienced or suboptimal individuals and founder phenotypes should show certain characteristics related to a low competitive ability (Brown et al. 1990; Holmes et al. 1996; Rendon et al. 2001; Kildaw et al. 2005). This could be the case for several colonial bird species in which a greater percentage of young and first-time breeders settle in new or recently founded colonies compared to older ones (Storey & Lien 1985; Tims et al. 2004).

The presence of conspecifics, their abundance or reproductive performance can be used as a source of reliable information for future habitat choice (e.g. Shields et al. 1988; Muller et al. 1997;

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Brown et al. 2000; Ward 2005; Calabuig et al. 2008a). A lack of social information in empty habitat patches could result in unsuitable habitat assessment and might increase the probability of selecting unsafe or unproductive habitats. According to this hypothesis, founders would experience lower reproductive performance than individuals breeding in already existing colonies because of the unpredictable quality of new sites. On the other hand, a higher parasite load has been identified as one potential cost of breeding aggregations (Shields & Crook 1987; Côté & Poulin 1995; Møller et al. 2001). In this way, the colonization of new patches would allow individuals to avoid the density-dependent costs of crowded breeding and/or to obtain alternative high-quality habitats (Alexander 1974; Wittenberger & Hunt 1985). Environmental and structural cues from empty habitat patches could also be used to choose a breeding patch, which may ultimately have important consequences for fitness (Shields 1984; Smith & Shugart 1987; Orians & Wittenberger 1991).

We studied the pattern of colony foundation by lesser kestrels, *Falco naumanni*, a facultatively colonial bird species which uses social information to choose a breeding colony (Aparicio et al. 2007; Calabuig et al. 2008a, b). We first analysed the influence of social (connectivity) and habitat characteristics (crop composition) on the probability of foundation of new breeding patches, manipulated by adding nestboxes suitable for this species. Second, we examined the phenotypic characteristics (weight, wing length and age) of founder and colonial individuals with the aim of testing whether founders are low-quality individuals. Finally, we studied the consequences of colony foundation for breeding performance and degree of parasitism in comparison with a colonial breeding strategy.

METHODS

Study Area

The study was carried out in La Mancha, central Spain (600–800 m above sea level), in an area covering approximately 1000 km^2. This area is extensively cultivated with cereals (*Hordeum vulgare*, *Triticum* spp.), vineyards (*Vitis vinifera*) and olive groves (*Olea europaea*). Other minor crop types include recent pine plantations (*Pinus* spp.) and uncultivated farmed areas and pastures. 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 study area holds a metapopulation of lesser kestrels, a small migratory falcon that forms colonies of up to 60 pairs in old farmhouses, placing their nests under tiled roofs or inside holes in walls. Second-year and older individuals arrive in this area from their winter quarters in Africa between January and March (depending on the year) whereas yearlings arrive around 40 days later (G. Calabuig, J. Ortego & J. M. Aparicio, unpublished data). About 40–50% of individuals try to breed in their first year of life (Aparicio et al. 2007). On arrival, males take a nest site, 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. The earliest clutches are started at the end of April and the latest in the first week of June (Aparicio & Bonal 2002).

Field Methods

In the 2005 and 2007 breeding seasons, we surveyed the study area looking for abandoned buildings with similar characteristics to those containing lesser kestrel colonies but not occupied by this species. We considered as a colony the lesser kestrel breeding pairs settled in the same building. We confirmed the absence of breeding lesser kestrels in these patches/buildings by: (1) inspecting all holes that could have been used as nesting sites; (2) searching for the presence of feathers or pellets that could indicate the presence of old nests used in previous years or early failed undetected nests in the current breeding season; (3) surveying each building with a telescope from a distance where we would not disturb the birds, for up to 30 min in the period when the parents feed the chicks and are easily detectable. In mid-February of 2006 and 2008, before lesser kestrels had arrived, we erected two nestboxes in each of 30 unoccupied buildings (18 in 2006 and 12 in 2008; Fig. 1). These nestboxes were the same type we have previously used in the study area and show an optimal occupation rate by lesser kestrels. As occurred in pre-existing colonies in the area, some nestboxes were placed under the roof ($N = 26$) or in walls ($N = 34$). The occupation rate and breeding performance in the two nestbox models is similar (J. M. Aparicio, unpublished data). We defined as founders those individuals breeding in these experimental sites. We considered an experimental breeding site was colonized when one nestbox was occupied and the breeding pair laid at least one egg in the year of nestbox installation. When both nestboxes of an experimental site were occupied by breeding pairs, we only considered as founders the first pair to lay eggs. This conservative criterion allowed us to avoid confounding social attracting factors influencing settlement decisions (Calabuig et al. 2008a).

We examined several variables that might influence colony foundation. We recorded habitat characteristics surrounding the experimental breeding sites by carrying out four linear transects from each site following the main cardinal points. In these transects we recorded the crop composition and habitat types at 10 m intervals within a radius of 1 km around the experimental breeding sites. To evaluate the influence of the social environment on the probability of colonization, we calculated the connectivity of each experimental breeding site. Connectivity (S) of colony i was calculated following the formula proposed by Hanski (1998) as: $S_{i,t} = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_{j,t}$, where $N_{j,t}$ is the number of breeding pairs

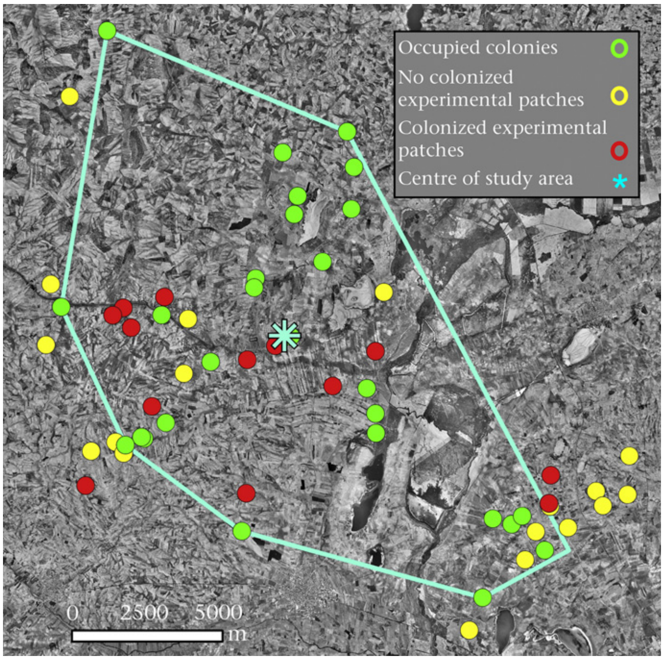

Figure 1. Spatial distribution of experimental breeding patches (colonized and not colonized) and pre-existing, occupied colonies in the study area. The polygon linking the outermost occupied colonies is also shown.

in colony j, d_{ij} is the distance between colonies i and j, and $1/\alpha$ is the average dispersal distance. This is a relatively fair way to estimate the chance that individuals arrive at a given site, considering the size and distance of neighbouring colonies as well as the average dispersal distance of the study species (Hanski 1998). We set dispersal distance to 3.022 km based on previous research in the study population (Ortego et al. 2008).

Once a week, we checked nestboxes installed in experimental breeding sites and potential nest sites in already established colonies to record their occupation and to determine the phenotypic characteristics and breeding performance of both founders and colonial individuals. During these visits, we trapped breeding individuals by hand during incubation and recorded the reproductive parameters laying date, clutch size and number of fledglings. We defined laying date as the date the first egg was laid (Aparicio & Bonal 2002). Clutch size was the maximum number of eggs in the nest. We considered the number of fledglings raised as the number of surviving chicks day 30 posthatch (Aparicio & Cordero 2001). The burden of the ectoparasitic dipteran *Carnus hemapterus* was also determined in nestlings around the 10th day after hatching. Ectoparasite burden was determined by counting the *C. hemapterus* under the wing surface, the body part where these ectoparasites generally congregate (Valera et al. 2003). For each nest, we calculated the average parasite burden per brood. This fly parasitizes only nestlings and has never been recorded infesting adult birds (Dawson & Bortolotti 1997). For each individual, we measured its weight (to the nearest 0.1 g) with an electronic scale and wing length (to the nearest 1 mm) with a stopped ruler. These measures of weight and size could account for the competitive ability of individuals in direct interactions with conspecifics during nest site acquisition and/or its defence during the settlement period (Serrano & Tella 2007). We also determined the burden of feather lice, *Degeeriella rufa*, counting these parasites by direct visual examination of all rectrix and primary feathers as described in Ortego et al. (2007). These parasites are known to be harmful to other bird species (e.g. Cannings 1986; Booth et al. 1993; Barbosa et al. 2002) and constitute the most frequent ectoparasites infesting lesser kestrels during the breeding season (G. Calabuig, unpublished data). The age of many kestrels was accurately known because they had been captured and ringed as nestlings in previous breeding seasons. To calculate the age of unringed male birds, we assumed that individuals captured for the first time were in their first year if they had yearling plumage or in their second year or older if they had adult plumage (Aparicio & Cordero 2001). We determined the age of unringed females by the stripe pattern of their 11th primary and plumage wear characteristics: compared with adults, yearlings have more stripes and their plumage looks more worn (G. Calabuig, unpublished data).

Statistical Analyses

We analysed the factors influencing the probability of occupation of the experimental empty breeding sites using a generalized linear mixed model (GLMM) implemented with the GLIMMIX macro of SAS (SAS Institute 2004). GLMMs allow analyses of data where the response variable is determined by both random and fixed effects. The probability of occupation was analysed using a binomial error structure and logit link function. The percentage of different crop types within 1 km radius around each experimental breeding site and patch connectivity were included as covariates. Habitat types included the relative cover of cereal cultures, ploughed land, fallow land, olive groves, vineyards and other minor habitat types. Nestbox type and year were included as random effects to control for their potential influence on the probability of occupation of the experimental breeding sites. Proportions of habitat types within a defined area are generally strongly intercorrelated, because when one habitat type is more abundant other ones are necessarily scarcer. For this reason, the potential influence of structural habitat parameters on the probability of occupation of the experimental empty breeding sites was also analysed using a compositional analysis (Aebischer et al. 1993). This analysis considers the log-ratio differences of used and available habitat proportions to determine habitat use preferences (Lurz et al. 2000). In the compositional analysis, a statistically significant Wilkś lambda value ($P < 0.05$, with $df =$ number of habitat types $- 1$) indicates a nonrandom use of the available habitat types. Negative and positive values in the matrix of compared variable pairs indicate avoidance or selection of the numerator habitat type over the denominator habitat type. The statistical significance of these pair comparisons was assessed by computing t values (Aebischer et al. 1993).

We used GLMMs to analyse the characteristics of individuals in relation to their founder or colonial breeding status (hereafter referred to as ‘settlement strategy’). Weight and wing length were analysed using a normal error structure and an identity link function whereas age class was analysed using a binomial distribution of errors and a logit link function. In all these analyses we included settlement strategy (founder/colonial breeding individual) and sex as fixed factors whereas colony size was included as covariate. Age (yearling or adult) was included as an additional fixed factor in the models of weight and wing length. Year and colony identity were included as random effects to control for possible differences in the studied parameters between breeding seasons and colonies.

We also analysed the reproductive performance of breeding pairs in relation to their settlement strategy using GLMMs. Laying date was analysed using a normal error structure and an identity link function whereas clutch size and number of fledglings were analysed using a Poisson distribution of errors and a log link function. In all these analyses we included settlement strategy and maternal and paternal age class (yearling or adult) as fixed factors whereas colony size was included as a covariate. Laying date was included as an additional covariate in the models of clutch size and number of fledglings to control for the expected decline in breeding performance as the season advances (Perrins 1970). Year and colony identity were included as random effects to control for possible differences in the studied breeding performance parameters between breeding seasons and colonies.

Finally, using GLMMs, we analysed the consequences of settlement strategy by studying the factors that determine the parasite burden of adults and chicks in relation to their settlement strategy. The burden of feather lice was analysed using a Poisson distribution of errors and a log link function. The average burden of *C. hemapterus* per nest was analysed using a normal distribution of errors and an identity link function. In these analyses, we included settlement strategy (founder/colonial breeding individual or parents) as a fixed factor and laying date and colony size as covariates. In the analysis of feather lice burden, we included individual age (yearling or adult) as a fixed factor, whereas chick age (in days) was included as a covariate in the analysis of *C. hemapterus*. Year and colony identity were included as random effects to control for possible differences in parasite burden between breeding seasons and colonies. As feather lice are transmitted by direct contact among individuals, we included nest identity as an additional random effect to control for the potential effect of breeding pair on parasite burden. In all the analyses, we randomly selected a unique data point per individual captured in more than one breeding season to avoid pseudoreplication (e.g. Calabuig et al. 2008b). We did this because the models did not converge after including individual identity as a random factor (SAS Institute 2004; e.g. Calabuig et al. 2008b). Initially, each GLMM was constructed with

Table 1
GLMM for influence of habitat composition on probability of colonization of experimental breeding sites

	Estimate±SE	Test	*P*
Explanatory terms			
Intercept	−3.21±1.34		
% Cereal crops	0.13±0.05	$F_{1,27}=5.67$	0.024
Rejected terms			
% Ploughed land		$F_{1,26}=0.42$	0.524
% Pastures and fallow land		$F_{1,26}=0.02$	0.895
% Vineyard		$F_{1,26}=0.01$	0.920
% Olive groves		$F_{1,26}=1.12$	0.299
Connectivity		$F_{1,26}=0.08$	0.785
Covariance parameter estimates			
Year	0	—	—
Nestbox type	0	—	—

Parameter estimates ± SE are indicated only for the variables included in the final model.

all explanatory terms fitted, including first-order interactions and quadratic effects to account for potential nonlinear relationships. Final models were selected following a backward 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. Denominator degrees of freedom (*ddf*) were computed using Satterthwaite's method. This method provides a numerical approximation of *ddf*, so the reported *ddf* are not necessarily whole numbers (SAS Institute 2004). Hypotheses were tested using *F* statistics and all *P* values refer to two-tailed tests.

To avoid potential problems derived from unbalanced sample sizes in the analyses in which we compared founders and colonial individuals, we performed additional analyses including all founders and a different randomly selected subsample of colonial individuals of equal size ($N = 21$, 10 females and 11 males). This allowed us to reduce the problem caused by the inequality of sample sizes and the probability of obtaining an unrepresentative subsample of colonial individuals by chance. After repeating the same routine 30 times, we recorded the number of times that each variable was retained as significant in the final model (1) or it was eliminated in the backward variable selection procedure (0). Finally, we tested with a binomial test whether the number of significant and nonsignificant results obtained for each variable was distributed at random with a probability of 95%.

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) which provided permits for capturing and ringing kestrels. All these activities were performed following general ethical guidelines for animal welfare and nature conservation. All the 381 breeding adults were caught by hand during incubation and 570 chicks were banded a week after hatching. Lesser kestrels are accustomed to the presence of people, and our trapping and handling did not cause any harm, nest desertion or any other damage to the individuals, their nests or breeding colonies.

RESULTS

Of the 30 experimental buildings, 13 provided with two nestboxes were occupied by at least one breeding pair of lesser kestrels in the year of nestbox installation. In three experimental houses, both nestboxes were occupied. Five experimental sites were occupied in 2006 and eight in 2008. Seven of these colonization events (i.e. 54%) resulted in successful breeding attempts whereas the other six failed to produce any fledglings.

Social and Habitat Characteristics

The GLMM showed that the percentage of cereal within a radius of 1 km was the only physical characteristic of the habitat that influenced colony foundation positively (Table 1). However, connectivity and percentage of cereal crops were positively correlated ($r = 0.41$, $P = 0.03$) and so we reanalysed the data including only connectivity as covariate. We found that colony connectivity was not significant after excluding the percentage of cereal crops from the model ($F_{1,11.7} = 2.18$, $P = 0.167$). Compositional analysis also showed that the colonization of experimental patches was not random, indicating habitat preferences in terms of available habitat types (Wilks's lambda test: $\chi^2_5 = 18.7$, $N = 12$, $P = 0.002$). Cereal was again the preferred habitat type and the difference to the second habitat type in the preference rank (ploughed land) was significant (Table 2).

Founders versus Colonial Individuals

We trapped and measured 21 founders (10 males and 11 females) in 13 experimental breeding sites and 360 colonially breeding individuals (170 males and 190 females) in 20 traditional colonies in the study area. Fourteen per cent ($N = 3$) of founders and 10% ($N = 36$) of colonial breeders were yearlings (Fisher's exact test: $P = 0.463$). Among founders there were more unringed birds (76.2%; $N = 16$) than among individuals breeding in already established colonies (64.1%; $N = 193$; Fisher's exact test: $P < 0.001$). We tested whether this result could be related to a hypothetical peripheral position of experimental breeding sites in the study area, which could facilitate the arrival of immigrants from unmonitored colonies beyond the study area. We analysed the mean distance to the centre of the polygon resulting from linking the outermost occupied colonies (see Fig. 1). Experimental patches were not more peripheral than pre-existing colonies in the study

Table 2
Log-ratio differences (mean ± 1 SE) between used and available habitat surrounding experimental breeding sites

Crop type (denominator)	Crop type (numerator)					Preference rank
	Cereal	Vineyard	Olive groves	Ploughed land	Fallow land	
Cereal						5
Vineyard	0.743±0.346*					1
Olive groves	0.551±0.395*	−0.193±0.467*				2
Ploughed land	0.409±0.192**	−0.334±0.329*	−0.141±0.387*			4
Fallow land	0.485±0.149**	−0.258±0.271*	−0.066±0.364*	0.076±0.190*		3
Other crops	2.954±0.991**	2.211±1.158*	2.404±1.183*	2.545±1.115*	2.470±1.020*	0

$^{*}P < 0.05$; $^{**}P < 0.001$.

Table 3

GLMMs for individual characteristics of lesser kestrels in relation to their settlement strategy and other potentially influential variables

	Estimate±SE	Test	P
Weight			
Explanatory terms			
Intercept	122.65±4.35		
Sex	31.07±2.99	$F_{1,296}=107.81$	<0.001
Rejected terms			
Age class		$F_{1,315}=1.42$	0.234
Settlement strategy		$F_{1,62.7}=0.37$	0.545
Colony size		$F_{1,8.35}=1.28$	0.289
Covariance parameter estimates			
Year	13.17±25.68	$Z=0.51$	0.304
Colony identity	122.55±77.89	$Z=1.57$	0.056
Wing length			
Explanatory terms			
Intercept	220.88±1.60		
Sex	2.55±0.65	$F_{1,288}=15.35$	<0.001
Age class	11.51±1.07	$F_{1,312}=114.63$	<0.001
Rejected terms			
Settlement strategy		$F_{1,82.1}=2.92$	0.092
Colony size		$F_{1,4.95}=0.93$	0.381
Covariance parameter estimates			
Year	2.62±4.08	$Z=0.65$	0.258
Colony identity	0.98±2.02	$Z=0.49$	0.313
Age class			
Rejected terms			
Settlement strategy		$F_{1,67.9}=0.00$	0.981
Sex		$F_{1,302}=0.45$	0.503
Colony size		$F_{1,4.25}=1.45$	0.291
Covariance parameter estimates			
Year	0	—	—
Colony identity	0.21±0.36	$Z=0.57$	0.284

Parameter estimates ± SE for the levels of fixed factors were calculated considering a reference value of zero for the 'female' level in the variable 'sex' and for the 'yearling' level in the variable 'age class'. Parameter estimates ± SE are indicated only for the variables included in the final models.

area (ANOVA: $F_{1,61}=0.19$, $P=0.665$). Furthermore, the distance to the centre of the study area was similar for experimental patches colonized by unringed and ringed individuals (GLMM: $F_{1,11}=0.06$, $P=0.811$) after controlling for the year of nestbox installation.

GLMM analyses showed that body mass, wing length and age did not differ between founders and colonial breeders after controlling for the effect of sex and age (Table 3). Other parameters, quadratic terms or interactions between independent variables were all nonsignificant ($P>0.05$; Table 3). Resampling analyses confirmed these results except for wing length, which was marginally significant in the analysis including the pool of nonfounders, but was highly significant in the final models obtained with a random subsample (binomial test: $P=0.003$). This analysis indicated that founders had longer wings than individuals settled in traditional colonies (mean ± SE; colonial individuals: 228.7 ± 1.8 mm; founders: 231.2 ± 1.7 mm).

Breeding Consequences of Colony Foundation

Laying date, clutch size and number of fledglings did not differ between founders and individuals breeding in already established colonies after controlling for age, year and colony identity (Table 4). Older males bred earlier and showed higher breeding performance (clutch size, the number of fledglings raised; Table 4). Both clutch size and the number of fledglings raised were negatively associated with laying date (Table 4). Other parameters, quadratic terms or interactions between independent variables were all nonsignificant ($P>0.05$; Table 4). Resampling analyses with randomized subsamples for colonial individuals confirmed these results for all variables analysed (binomial tests: $P>0.05$ in all cases).

Table 4

GLMMs for breeding performance of lesser kestrels in relation to their colonial or founder status and other potentially influential variables

	Estimate±SE	Test	P
Laying date			
Explanatory terms			
Intercept	130.21±2.07		
Paternal age class	−4.67±1.57	$F_{1,149}=8.92$	0.003
Rejected terms			
Settlement strategy		$F_{1,111}=3.6$	0.06
Maternal age class		$F_{1,111}=2.02$	0.158
Colony size		$F_{1,111}=0.88$	0.349
Covariance parameter estimates			
Year	7.19±10.74	$Z=0.67$	0.251
Colony identity	0	—	—
Clutch size			
Explanatory terms			
Intercept	3.39±0.41		
Paternal age class	0.25±0.07	$F_{1,111}=12.71$	<0.001
Laying date	−0.02±0.003	$F_{1,111}=31.18$	<0.001
Rejected terms			
Settlement strategy		$F_{1,99.8}=0.07$	0.792
Maternal age class		$F_{1,110}=3.55$	0.062
Colony size		$F_{1,6.83}=0.03$	0. 871
Covariance parameter estimates			
Year	0	—	—
Colony identity	0	—	—
Number of fledglings raised			
Explanatory terms			
Intercept	2.34±1.52		
Paternal age class	1.72±0.52	$F_{1,86.9}=3.29$	0.001
Laying date	−0.02±0.01	$F_{1,97}=4.86$	0.029
Rejected terms			
Settlement strategy		$F_{1,52.8}=0.3$	0.585
Maternal age class		$F_{1,90.2}=2.42$	0.123
Colony size		$F_{1,3.49}=0.22$	0.669
Covariance parameter estimates			
Year	0	—	—
Colony identity	0.01±0.02	$Z=0.33$	0.37

Parameter estimates ± SE for the levels of fixed factors were calculated considering a reference value of zero for the 'yearling' level in the variable 'paternal age class'. Parameter estimates ± SE are indicated only for the variables included in the final models.

Parasitism and Colony Foundation

Feather lice burden was lower for founders than for individuals breeding in previously established colonies, although this effect varied between the sexes (Table 5, Fig. 2). Females were the most parasitized sex and founder females showed lower parasite burden (mean ± 1 SE = 1.6 ± 2.4) than colonially breeding females (mean ± 1 SE = 8.6 ± 15.38; Fig. 2). However, the number of feather lice showed a high individual variability and resampling analyses showed that this effect was also highly significant for males when we compared groups of equal size (binomial test: $P<0.001$). The burden of *C. hemapterus* decreased with chick age (Table 5). However, chicks raised by founders and by colonial breeders did not differ in parasite burden (Table 5) and a similar pattern was shown by resampling analyses (binomial test: $P>0.05$). Other parameters, quadratic terms or interactions between independent variables were all nonsignificant in these analyses ($P>0.05$; Table 5).

DISCUSSION

Which Patches are Colonized?

We found that habitat composition was associated with the probability of colonization, suggesting that habitat characteristics constitute an important factor used for settlement decisions in the

Table 5

GLMMs for parasite burden of the feather louse *Degeeriella rufa* in adults and the dipteran *Carnus hemapterus* in chicks in relation to their colonial or founder status and other potentially influential variables

	Estimate±SE	Test	*P*
Feather louse *Degeeriella rufa*			
Explanatory terms			
Intercept	0.68±0.57		
Sex*Settlement strategy (colonial females)	1.31±0.56	$F_{3,201}$=35.38	<0.001
Sex*Settlement strategy (founder females)	−0.22±0.76		
Sex*Settlement strategy (colonial males)	0.17±0.61		
Rejected terms			
Settlement strategy		$F_{1,127}$=3.25	0.073
Laying date		$F_{1,157}$=0.4	0.527
Age class		$F_{1,277}$=0.2	0.652
Sex		$F_{1,180}$=2.04	0.155
Colony size		$F_{1,4.88}$=1.03	0.359
Covariance parameter estimates			
Year	0	—	—
Colony identity	0.22±0.19	*Z*=1.17	0.121
Nest identity	0.76±0.15	*Z*=5.16	<0.001
Dipteran *Carnus hemapterus*			
Explanatory terms			
Intercept	3.16±1.36		
Mean chick age	−0.19±0.07	$F_{1,80.3}$=6.23	0.015
Rejected terms			
Settlement strategy		$F_{1,65.6}$=3.22	0.077
Laying date		$F_{1,77.7}$=0.44	0.511
Colony size		$F_{1,11.4}$=0.04	0.836
Covariance parameter estimates			
Year	2.73±4.04	*Z*=0.68	0.249
Colony identity	0.37±0.39	*Z*=0.96	0.168

Parameter estimates ± SE were calculated considering a reference value of zero for the 'founder males' level in the variable 'sex*settlement strategy' interaction. Parameter estimates ± SE are indicated only for the variables included in the final models.

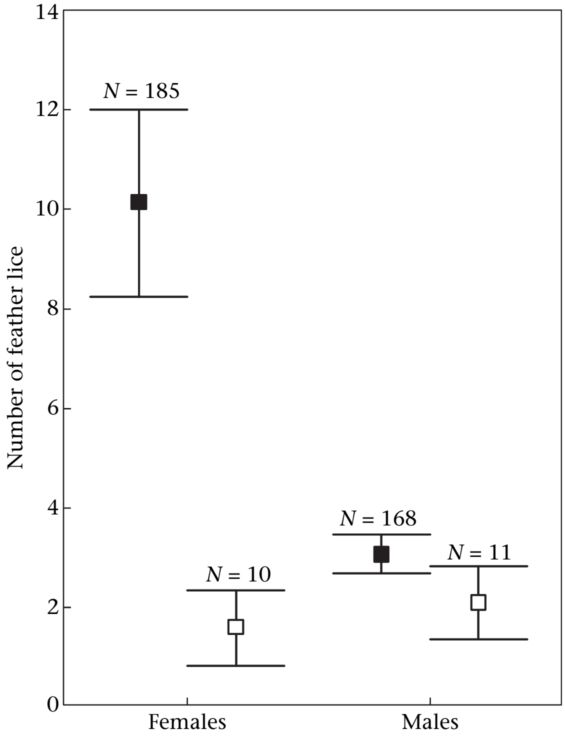

Figure 2. Mean ± 1 SE feather lice burden in relation to the sex and settlement strategy of individuals (filled squares: colonial individuals; empty squares: founders). Numbers above bars indicate sample sizes.

absence of social information on patch quality. Experimental plots with a high cover of cereal crops were particularly preferred. This seems reasonable as cereal crops are one of the most profitable habitats in terms of food supply and foraging efficiency for lesser kestrels (Donázar et al. 1993). Although we expected that the most strongly connected breeding sites would have a higher probability of receiving immigrants from nearby colonies, we did not find any relationship between connectivity of experimental patches and the probability of colony foundation. The fact that most founders were unbanded birds suggests that they were not local dispersers from neighbouring colonies and this may explain why patch connectivity had no effect on colonization probability at the spatial scale we studied (see below).

Who are the Founders?

It has been assumed that colonizing new breeding patches is riskier than breeding in traditional existing colonies. Thus, one would expect that yearlings or low-quality individuals would be more prone to colonize new patches if they arrive later at the breeding areas, are less competitive for obtaining nest sites, or their information on patch quality is incomplete (Calabuig et al. 2008a). In agreement with this pattern, some studies have found a higher percentage of yearlings and first-time breeders in recently founded colonies (Storey & Lien 1985; Kharitonov & Siegel-Causey 1988; Tims et al. 2004). However, we found that the proportion of yearlings did not differ between founded and previously established colonies and both founders and individuals breeding in pre-existing colonies had similar phenotypic characteristics with the exception of wing length, with founders having longer wings than nonfounder individuals. Overall, these results did not support the 'individual quality hypothesis' which suggests that colony foundation would be carried out by suboptimal individuals, for which it would be harder to obtain a presumably better breeding site in a previously established colony.

If traditional breeding colonies are despotically occupied, one could expect colonizers to be local individuals from nearby colonies. However, some lines of evidence argue against this possibility: first, individuals occupying experimental empty patches showed similar laying dates to individuals settled in previously established colonies. Under a despotic settlement, we would expect that founders would settle, and lay, later than colonial individuals. Another possibility is that individuals arrive earlier at established colonies, but laying date is later with respect to the arrival date if getting a nest site is harder than in empty breeding patches. Second, despite the intensive ringing work performed in the study area in the last 7 years, we found a significantly higher proportion of unbanded individuals among founder individuals and this result cannot be explained by a peripheral position of the experimental patches in the area. Although some unmonitored colonies exist within the study area, the number of breeding pairs settled there is negligible (<2%) compared with the total size of the studied population. Thus, this is not likely to explain the greater proportion of unringed birds among individuals colonizing empty breeding patches. Finally, founders had longer wings than nonfounders. Wing length has been associated in other species with flight performance, earlier arrival at the breeding grounds after migration and longer migration distances (Møller 1994; Potti 1998). The greater percentage of unringed individuals among colonizers, together with their longer wing length relative to nonfounder individuals of similar age and sex, suggests that the occupation of empty patches could be mainly led by immigrants from distant populations rather than by local dispersers from nearby colonies.

Therefore, our results highlight the role of immigrants in the growth of colonies from their earliest stages and the importance of long-distance immigration not only for colony growth but also for the foundation of new colonies (Porter & Coulson 1987; Brown et al. 2000; Oro & Ruxton 2001; Kildaw et al. 2005; Ward 2005).

Consequences of Colony Foundation

Founders had similar reproductive performance but lower ectoparasite burden than colonial breeders, suggesting that founders gain certain benefits associated with reduced parasite pressure. In particular, feather lice cause plumage damage, which could ultimately compromise flight ability, thermoregulatory capacity and mate selection (Clayton 1990; Booth et al. 1993; Kose & Møller 1999; Barbosa et al. 2002). Feather lice transmission depends on direct body contact between hosts and this may have resulted in the observed pattern of higher parasite pressure in previously established colonies where host density is particularly high (Hoogland & Sherman 1976; Anderson & May 1978; May & Anderson 1978; Brown & Brown 1986). An interaction with sex revealed that the effect of settlement strategy on ectoparasite burden was particularly important in females. This sex difference could be the result of different behaviour during incubation between males and females. In lesser kestrels, only females incubate at night whereas males roost in communal aggregations of up to a hundred individuals. This greater contact among males from different colonies in the early stages of reproduction could reduce any possible difference in feather louse abundance in relation to breeding patch characteristics in males.

Another expected consequence of occupying empty patches is a lower parasitism load of *C. hemapterus* in nestlings, owing to the occupation of unused nest sites. The burden of this parasite decreased with chick age as found in other studies (e.g. Valera et al. 2003). However, we did not find any influence of settlement pattern on parasite burden of *C. haematerus*. In contrast to feather lice (Clayton & Johnson 2003), *C. hemapterus* is a generalist species parasitizing a wide variety of bird hosts (Capelle & Whitwort 1973; Kirkpatrick & Colvin 1989; Valera et al. 2006; Lopez-Rull et al. 2007). Some of these species coexist with lesser kestrels in the same breeding colonies and frequently use the same nest sites in successive years (J. M. Aparicio, unpublished data). Thus, the settlement in a patch previously unoccupied by conspecifics would not prevent infestations by *C. hemapterus*, because the populations of this parasite can be also maintained by several other coexisting bird species (Valera et al. 2003).

In sum, we have found that habitat composition played an important role in the foundation of new breeding patches. Founders and individuals settled in already established colonies did not differ in condition, age class or breeding performance, suggesting that the foundation of new colonies does not impose relatively higher costs on founders nor does it involve low-quality individuals. Founders showed a lower ectoparasite load, indicating that colony foundation may reduce parasite transmission and its related detrimental fitness consequences. Furthermore, individuals settled in experimental patches were unringed and had longer wings, suggesting that they were nonlocal individuals with a higher dispersal ability. Overall, these results support the idea that the foundation of new breeding patches is not necessarily a suboptimal option. Thus, intraspecific competition and the displacement of suboptimal individuals from already established colonies are not likely to be the primary mechanisms involved in colony foundation.

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