

# Social information in nest colonisation and occupancy in a long-lived, solitary breeding bird

Radovan Václav · Francisco Valera ·  
Teresa Martínez

Received: 5 April 2010 / Accepted: 4 November 2010  
© Springer-Verlag 2010

**Abstract** Recent work increasingly reveals the importance of social information in individual dispersal decisions, population dynamics and conservation. Much of the knowledge gained to date comes from studies on short-lived and/or densely breeding species. In contrast, our understanding of the processes involved in nest-site selection for long-lived, solitary breeding species is insufficient. We increased nest-site availability by nest-box supplementation over a 5-year period in a population of a long-lived, solitary, secondary-cavity nesting bird, the European roller *Coracias garrulus*, breeding in natural cavities and human constructions. We tested the nest limitation and the inadvertent conspecific social information hypothesis in order to study the dynamics and mechanisms of abandonment of previously used nests and the colonisation of new ones. Our data lend support to the nest-limitation hypothesis both in terms of quantity—population and the size of breeding clusters increased, and suitability—the majority of pairs used and re-occupied nest-boxes. Nevertheless, the use of natural cavities did not decrease after 5 years. At the between-patch scale, rollers were revealed to colonise nest-boxes based on conspecific social attraction, namely distance to the nearest neighbour in the same season. Despite the unpredictability of patch productivity, at the within-patch scale, the selection of

previously unoccupied cavities was consistent with the performance-based conspecific attraction hypothesis. Philopatry could account for the repeated use of cavities, because nests that were used for two successive years were more likely to also be reused in the subsequent season.

**Keywords** Nest-site selection · Performance-based conspecific attraction · Social attraction · Inadvertent social information · *Coracias garrulus*

## Introduction

The choice of a nest site is one of the most important determinants of individual fitness, population dynamics and the evolution of bird species (Wiens 1984; Martin 1995). One basic constraint when choosing a breeding habitat patch is nest-site limitation. This is particularly the case for secondary cavity-nesting species. Provided that cavities constitute key resources to some birds (Martin et al. 2004), population declines in secondary cavity-nesting birds are usually attributed to habitat quality deterioration (Holt and Martin 1997) and nest-site limitation (Newton 1998).

Conservation tools directed to increase the population size of secondary cavity-nesting species often rely on the installation of artificial cavities or modification of human constructions (bridges, towers, etc.). Yet, artificial increases of nest site availability can influence the fraction of the population breeding in natural conditions in several ways: (1) natural cavities can be partially or completely abandoned in favour of nest-boxes, (2) changes in the structure of the population may occur, for instance, the proportion of yearlings can increase in the breeding population, and (3) spatial segregation with respect to individual quality can

---

Communicated by Markku Orell.

---

R. Václav (✉)  
Institute of Zoology, Slovak Academy of Sciences,  
Dúbravská cesta 9, 84506 Bratislava, Slovakia  
e-mail: radovan.vaclav@savba.sk

F. Valera · T. Martínez  
Departamento de Ecología Funcional y Evolutiva, Estación  
Experimental de Zonas Áridas (CSIC), Almería, Spain

occur, for instance, when subdominant individuals are sometimes segregated to a certain nest type. Even though these situations may have a deep impact on population dynamics, few nest-box studies have addressed the role of naturally nesting birds in local demography (but see Gauthier and Smith 1987; Petty et al. 1994).

Increasing effort has been recently devoted to understanding how animals assess nest-site quality (Danchin and Wagner 1997). Social information has been shown to be important in several ecological processes, like mate selection (Ophir and Galef 2004), foraging (Valone and Brown 1989; Coolen et al. 2003; Whiting and Greeff 1999) and habitat selection (Danchin et al. 1998; Brown et al. 2000; Doligez et al. 2002). For gregarious species, two main attraction-related hypotheses have been proposed concerning habitat selection: (1) the “conspecific attraction” hypothesis (Stamps 1988; Reed and Dobson 1993) suggests that the number of conspecifics breeding nearby could provide information about patch breeding quality, and (2) the “(breeding) performance-based attraction” hypothesis (Danchin et al. 1998) proposes that individuals perceive the more productive patches as higher quality sites and select them preferentially. These processes can also be seen as behavioural constraints limiting the dispersal behaviour of individuals and the dynamics of populations (Reed and Dobson 1993; Reed 1999; Doligez et al. 2003). Despite economic, sociological and scientific benefits, nest-box programs frequently ignore: (1) the likely role of naturally nesting birds in colonisation success and demography (Pöysä and Pöysä 2002), and (2) the role of conspecific information in nest-site selection (Stamps 1988; Danchin et al. 1998; Reed 1999; Brown et al. 2000; Doligez et al. 2003).

The European roller *Coracias garrulus* L. (hereafter roller) is a migratory, secondary cavity-nesting bird species. It has undergone strong geographical range contraction and fragmentation in its northern limits of distribution, where only small breeding subpopulations persist (BirdLife International 2009). The species is currently categorised as *near threatened* by the IUCN. Nest-box programs have dramatically increased local population size in Spain (Avilés and Sánchez 2000). Yet, a recent nest-box study by Parejo et al. (2005) has suggested that rollers do not use conspecific information to colonise new nest-boxes.

Over a period of 5 years, we progressively increased nest-site availability in a roller population to address demographic predictions derived from two hypotheses:

(a) *Nest-site limitation* hypothesis. Provided that secondary cavity-nesting birds are commonly constrained by nest-site limitation, we predicted that a gradual increase in nest-site availability will: (1) increase population size and/or local density of breeding birds,

and (2) increase the proportion of birds breeding in new cavities. Because we observed a high rate of breeding failure in suboptimal natural nest sites (large cavities easily accessible to predators), and reproductive output affects future habitat selection (Switzer 1997), we predicted that providing more secure nesting opportunities (nest-boxes) will (3) result in higher reoccupancy rates of the new cavity type.

(b) *Conspecific attraction* hypothesis. We first tested the assumptions of the *performance-based conspecific attraction* hypothesis that there is significant heterogeneity in productivity among patches and that patch productivity between years is autocorrelated. In line with the hypothesis and after controlling for the confounding effects of nesting success and fledgling productivity, we predicted that (4) the probability of reoccupancy of a cavity in  $t + 1$  increases with patch reproductive success (PRS) in  $t$ . Moreover, for the occupancy in  $t$  of previously unoccupied cavities, we predicted that birds will settle closer to cavities that (5) succeeded in producing young and (6) were more productive in  $t - 1$ . Also, (7) the occupancy probability in  $t$  of previously unoccupied nests should increase with PRS in  $t - 1$ , and (8) the relative change in the size of breeding clusters in year  $t$  should be higher in patches that were more productive in year  $t - 1$ . If birds select their nest sites based on *conspecific attraction* not influenced by the breeding success of conspecifics, we predicted that birds should occupy cavities as a function of conspecific local density or distance to conspecifics, and not to conspecific individual or patch reproductive success.

## Materials and methods

### Study area and species

The study area ( $\sim 50 \text{ km}^2$ ) lies in the Desert of Tabernas (Almería, SE Spain,  $37^\circ 05' \text{N}$ ,  $2^\circ 21' \text{W}$ ). The landscape mostly consists of badlands and “ramblas” with olive and almond groves interspersed among numerous dry stream channels. The climate in this area is semi-arid with long, hot summers and high annual and seasonal variability of rainfall (mean annual rainfall ca. 218 mm).

The roller is a common avian breeder local to the area with nesting opportunities restricted to natural cavities excavated by other birds (European bee-eaters *Merops apiaster* L.) and by erosion in sandstone banks (Manrique 1996; Casas-Crivillé and Valera 2005). Such cavities are also actively sought and used by other secondary cavity-nesting species such as the jackdaw *Corvus monedula* L.,

common kestrel *Falco tinnunculus* L., little owl *Athene noctua* Scopoli, rock sparrow *Petronia petronia* L., and feral pigeon *Columba livia* L. Thus, in our study area, the use of suboptimal natural cavities (either too small or too large) occurs. The only exceptions to this main nesting resource are human constructions, such as stone cavities in bridges and building crevices in isolated country houses. In contrast to the natural cavities, these nest sites are currently not occupied by jackdaws, pigeons or rock sparrows. Kestrels, little owls and scops owls (*Otus scops*) breed sporadically in bridges. In our study, we monitored cavities in three bridges (50, 100 and 100 m long), which had also been used by rollers before our first study year, 2005. Only jackdaws (*C. monedula* L.) have been detected evicting rollers from natural cavities in our study area. In contrast, rollers were observed expelling small passerines (house sparrows *Passer domesticus* L. and spotless starlings *Sturnus unicolor* L.) that attempted to breed in nest-boxes. Rollers are migratory birds that arrive at breeding grounds when resident, secondary cavity-nesting birds are already settled. Rollers can breed for the first time in their first or second year of life, and rear a single brood per year (Cramp 1998). In our population incubation takes ca. 21 days and nestling rollers fledge approximately 20–22 days after hatching (R. Václav, unpublished data).

#### Field methods and parameters studied

Roller breeding habitat patches were defined as distinct geomorphological units: (1) ramblas (dry stream channels with steep sandstone banks), which are linear, continuous geographical units separated from neighbouring ramblas by hills and human settlements, (2) individual bridges with numerous, densely spaced cavities (~2–3 m apart), and (3) spatial aggregations of suitable nesting places—trees, small sandstone banks and isolated country houses. We monitored 11 habitat patches with a median length of 1,400 m (range 50–2,950 m). Roller breeding clusters were defined as socially and geographically coherent groups located in individual habitat patches. It is unlikely that the number of pairs in the monitored patches were underestimated, because we consistently examined all possible nest sites within the patches.

From the first observations of rollers in early April, the study area with a population of 36–56 breeding pairs was monitored each year at least three times per week. After sighting first copulations, potential nest cavities were inspected regularly until hatching. Thereafter, active nests were monitored until fledging. Each year, we invested a similar search effort to locate roller nests in sandstone banks and human constructions within our study area.

We recorded the following parameters: nest type (NT; sandstone burrows, bridge cavities, and nest-boxes),

nearest neighbour distance (NND), local breeding density (BD; high/low density), the number of pairs in a patch (CS; cluster size), cluster size change (the relative increase/decrease in the number of pairs per patch between two successive years), nest occupancy (NO; occupied/unoccupied), nest reoccupancy (NR), nest success (NS; success/failure), nest productivity (NP; the number of fledglings per nest), and patch reproductive success (PRS; the mean number of fledglings per nest produced in a patch by all pairs including failed pairs).

Depending on the spatial scale of analysis, we considered either the nearest neighbour (prediction 7; between-patch scale) or two nearest neighbours (prediction 1 and 5; within-patch scale) for each focal nest. Mean NND was used for prediction 1, whereas both NND values were used for prediction 5. In order to increase the statistical power of the analysis of the probability of nest reoccupancy (prediction 4), we log-transformed the mean NND and used the median (90 m) to designate NND as low and high density categories. This density classification takes into account local roller densities and is consistent with density characteristics described by other authors for populations where breeding density was not limited by nest-box distribution (Cramp 1998; Butler 2001). Also, the categorisation of breeding dispersion data accords with the natural propensity of rollers to breed either solitarily or in groups (see Cramp 1998).

In the analysis of prediction 5, we determined distances from the focal nest to the nearest successful and failed nest. Only those successful and failed nests that were located within the same patch as the focal nests were considered for the analysis. Focal nests were not included in the analysis if no pair failed in the corresponding patch in the previous season.

Only nest-boxes with the nearest neighbours nesting in sandstone burrows and nest-boxes were considered in the analysis of prediction 7; three nest-boxes with the nearest neighbours nesting in bridge cavities were excluded from the analysis.

#### Nest-site availability and its increase

It is not possible to unambiguously classify an unoccupied hole as the nest site solely based on its dimensions or height from ground. For example, sandstone burrows can change between but also within seasons, and some apparently unsuitable bridge or building crevices were occupied in single years. Instead, breeding density per patch can be used as a surrogate of nest-site availability in our study site. Consequently, nest-site availability appears to be highest for rollers nesting in bridges (mean density = 6.53 pairs/100 m, 95% CI = 5.21–7.86,  $n = 3$ ) compared to ramblas (mean density = 0.61 pairs/100 m, 95% CI = –0.54 to

1.76,  $n = 4$ ) and patches including only nest-boxes and building cavities (mean density = 0.47 pairs/100 m, 95% CI = -0.82 to 1.76,  $n = 4$ ).

We conducted a long-term manipulation of the availability of nest sites for rollers by installing nest-boxes within the study area, progressively increasing their numbers from 2005 at 2-year intervals (2005, 2007, and 2009). Nest-boxes were installed during winter/early spring on trees, sandstone banks and isolated country houses. The number of nest-boxes available for breeding in 2005, 2006, 2007, 2008, and 2009 was 13, 13, 23, 23, and 54, respectively. All nest-boxes were designed for rollers and had the same dimensions, with the exception that boxes installed in 2005 and 2007 were made of wood, whereas the ones installed in 2009 were made of cork. We did not detect significant differences in clutch size and fledgling numbers between wooden and cork nest-boxes (GLMM,  $P > 0.73$ ). From 2005, we kept cavities in bridges unblocked during all breeding seasons (i.e. availability of bridge cavities did not differ between years) after agreeing with local inhabitants.

#### Data analysis

Generalised and general linear mixed models (GLMM) were used to study variation in response variables (Table 1). Statistics were calculated with SAS 9.1 (SAS 2002 Institute, Cary, NC, USA) using the PROC GLIMMIX procedure (Littell et al. 2006). As the same cavities and patches could have been occupied in successive years by the same individuals, and observations from such subjects may be temporally autocorrelated, we tried to fit covariance structures with first-order autoregressive AR(1) or compound symmetry parameters to account for the correlation between repeated measurements within cavities or patches (i.e. nest ID or patch ID were treated as random factors; Littell et al. 2006). For repeated measures models, years were used as a measure of time with equal time intervals, and nest ID or patch ID was assigned, depending on the spatial scale of analysis, as a subject variable. When appropriate, the residual random effect was included in models as an overdispersion parameter and the Satterthwaite approximation was used to determine the denominator degrees of freedom (Littell et al. 2006). The likelihood ratio test was used to compare models with different covariance structures (Littell et al. 2006). In the analysis of nest reoccupancy and occupancy probability, the likelihood ratio test was used to assess whether the removal of fixed parameters (one at a time) significantly improves the fit of reduced models (e.g. Quinn and Keough 2007). To account for multiple comparisons within individual models, Šidak-adjusted  $P$  values and adjusted 95% CI were used when appropriate (Littell et al. 2006). The model structures are summarised in Table 1.

## Results

### Nest-site limitation and population structure

Over the 5-year study period, we recorded 242 breeding attempts in 129 different cavities. In line with the nest-site limitation hypothesis, population size increased in 4 years by 56% (from 36 to 56 breeding pairs) after a progressive increase in nest-site availability (Fig. 1). Likewise, the number of pairs per patch (i.e. cluster size) increased after 2005 (Table 2a), though this result was only marginally significant. At the nest scale, NND did not differ among years for rollers nesting in sandstone burrows and nest-boxes but differed for those nesting in bridge cavities (Table 2a; year effect sliced by nest type: bridges,  $F_{4,156.6} = 7.28$ ,  $P < 0.001$ ; sandstone,  $F_{4,166.8} = 0.74$ ,  $P = 0.56$ , nest-boxes,  $F_{4,138} = 0.28$ ,  $P = 0.89$ ). Specifically, for bridges, rollers' distances between nearest neighbours in 2009 were longer compared to those in 2005, 2006 and 2007 (adjusted- $P < 0.019$ ; mean estimates of log NND and adjusted 95% CI: 2005 = 2.55, 1.68–3.43; 2006 = 2.78, 1.92–3.64; 2007 = 2.57, 1.71–3.43; 2008 = 3.34, 2.47–4.22; 2009 = 3.78, 2.89–4.67).

In accordance with the nest-site limitation hypothesis, after the increase in nest-site availability, the proportion of pairs nesting in nest-boxes increased between 2005 and 2009 ( $G_1 = 20.27$ ,  $P < 0.001$ ; Fig. 1). Even though the absolute number of pairs breeding in sandstone burrows was comparable among years, the proportion of pairs breeding in sandstone burrows and bridge cavities decreased between the first and the last year of the study (sandstone,  $G_1 = 4.29$ ,  $P = 0.038$ , bridge,  $G_1 = 3.73$ ,  $P = 0.053$ ).

We found differences in the reoccupancy rate between three types of nests. Excluding (due to small sample sizes) the nests that were used four and five times, by comparison with individual sandstone burrows, which were most often used once in 5 years, individual bridge cavities were most often used up to three times and nest-boxes up to four times over the 5 years ( $G_4 = 11.02$ ,  $P = 0.026$ ; Fig. 2). The probability of nest reuse in  $t + 1$  was higher for nest-boxes compared to bridge cavities or sandstone burrows, but this nest type effect disappeared if nests were used in  $t - 1$  (Table 2b; nest type effect sliced by nest occupancy in year  $t$ : nests unoccupied in  $t$ ,  $F_{2,148.4} = 7.48$ ,  $P < 0.001$ ; nests occupied in  $t$ ,  $F_{2,46.82} = 0.27$ ,  $P = 0.77$ ; Fig. 3). The moderating effect of nest occupancy in  $t - 1$  was due to sandstone burrows and bridge cavities, the occupancy of which increased significantly if they were used in  $t - 1$  (the effect of nest occupancy in  $t$  sliced by nest type: sandstone,  $F_{1,91.14} = 16.56$ ,  $P < 0.001$ ; bridge,  $F_{1,102.7} = 4.49$ ,  $P = 0.037$ ; nest-box,  $F_{1,137.3} = 0.84$ ,  $P = 0.36$ ; Fig. 3).

**Table 1** GLMM model structures

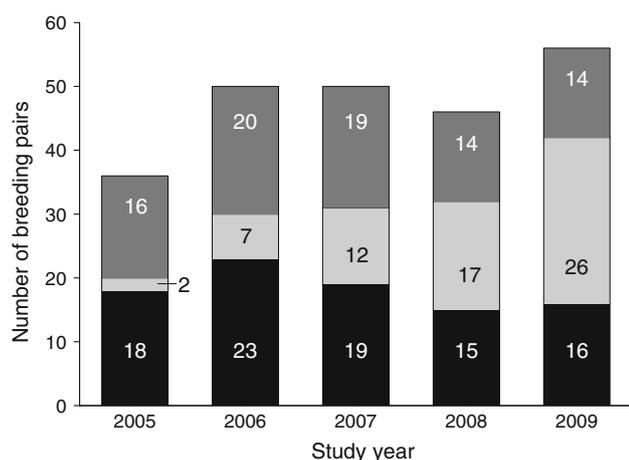
Response variable	Fixed predictors	Covariance parameters	Autoregressive covariance term	Response distribution	Link function
(a) Cluster size (CS) $n = 51$ patch-years	Year '05/'06/'07/'08/'09		Year <i>Patch ID</i> ( $n = 11$ )	Poisson	Log
(b) Log mean NND $n = 236$ breeding attempts	Year '05/'06/'07/'08/'09 Nest type (NT) <i>bridge/sandstone/nest-box</i> Year $\times$ NT	Patch ID ( $n = 11$ )	Year <i>Nest ID</i> ( $n = 124$ )	Gaussian	Identity
(c) Fledglings per nest (NP) $n = 196$ breeding attempts	Year '05/'06/'07/'08/'09	Patch ID (Year) ( $n = 11$ ) Overdispersion term		Poisson	Log
(d) Nesting success (NS) <i>success/failure</i> $n = 236$ breeding attempts	Year '05/'06/'07/'08/'09	Patch ID (Year) ( $n = 11$ ) Overdispersion term		Binomial	Logit
(e) PRS in $t + 1$ $n = 40$ patch-years	Patch reproductive success (PRS) in $t$ Year '05-'06/'06-'07/'07-'08/'08-'09 PRS in $t \times$ Year		Year <i>PatchID</i> ( $n = 11$ )	Gaussian	Identity
(f) NR in $t + 1$ <i>occupied/unoccupied</i> $n = 150$ nest occupancies	NT Year '05/'06/'07/'08 Breeding density (BD) in $t$ <i>low/high</i> Nest occupancy in $t - 1$ <i>occupied/unoccupied</i> PRS in $t$ NP in $t$ NT $\times$ Nest occupancy in $t - 1$ BD in $t \times$ PRS in $t$ NP in $t \times$ PRS in $t$		Year <i>Nest ID</i> ( $n = 93$ )	Binomial	Logit
(g) Log NND to focal nests in $t - 1$ $n = 76$ neighbour distances	Neighbours' NS in $t - 1$ <i>success/failure</i> Year '05-'06/'06-'07/'07-'08/'08-'09 NT	Focal nest ID ( $n = 38$ )		Gaussian	Identity
(h) Neighbours' NP in $t - 1$ $n = 122$ neighbour NPs	Neighbours' nest position relative to focal nest <i>nearest/second nearest</i> Year '05-'06/'06-'07/'07-'08/'08-'09 NT	Focal nest ID ( $n = 61$ )		Poisson	Log
(i) Nest-box occupancy in $t$ <i>occupied/unoccupied</i> $n = 61$ nest-box occupancies	Year '06/'07/'08/'09 Log NND in $t$ Neighbours' NT in year $t$ Log NND in $t \times$ Neighbours' NT in $t$	Patch ID ( $n = 9$ )	Year <i>Nest ID</i> ( $n = 51$ )	Binomial	Logit
(j) Cluster size change in $t$ $n = 40$ patch-years	Year '05-'06/'06-'07/'07-'08/'08-'09 PRS in $t - 1$ CS in $t - 1$ Year $\times$ PRS in $t - 1$		Year <i>Patch ID</i> ( $n = 11$ )	Gaussian	Identity

Italics below response variables and fixed predictors denote category levels. Italics below autoregressive parameters denote subjects. Round brackets under covariance parameters mean that patch identity was nested in years

### Patchiness and predictability

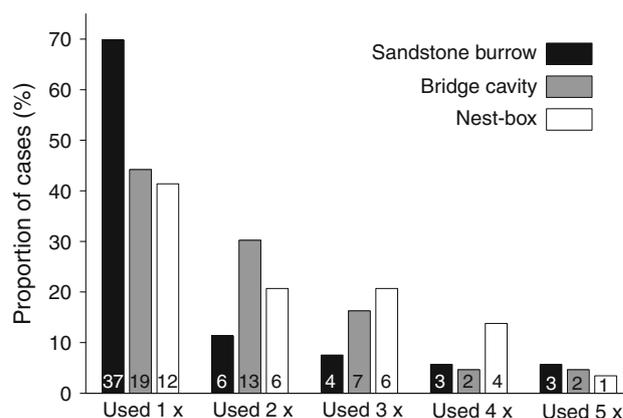
Mean fledgling numbers fluctuated among years and patches (Table 3a; mean estimates of fledgling numbers

and adjusted 95% CI: 2005 = 3.06, 2.65–3.53; 2006 = 3.99, 3.51–4.53; 2007 = 3.24, 2.84–3.69; 2008 = 3.00, 2.63–3.43; 2009 = 3.16, 2.79–3.58). The probability of nesting failure did not differ among years, but seemed to



**Fig. 1** Number of roller *Coracias garrulus* pairs nesting in three different nest types over 5 years. Black, pale grey and dark grey colours represent sandstone burrows, nest-boxes and bridge cavities. Values in the boxes represent sample sizes for respective nest types. For simplicity, four breeding attempts detected between 2008 and 2009 in building holes were not included

depend on patch ID [Table 3b; mean estimates of probability (in %) of successful breeding and adjusted 95% CI: 2005 = 88.46, 71.07–95.99; 2006 = 87.87, 72.34–95.26;



**Fig. 2** Occupancy (times used) of individual nests. Proportions are calculated for each nest type. Values in the boxes represent sample sizes for respective nest types and occupancy rate categories

2007 = 82.90, 65.80–92.43; 2008 = 83.17, 66.24–92.57; 2009 = 85.78, 70.44–93.85].

With the exception of years 2006 and 2007, PRS did not correlate significantly between two successive years (Table 3c; slope ± SE for the effect of PRS in  $t - 1$  sliced by years, 2006–2007:  $0.77 \pm 0.29$ ,  $t_{22} = 2.67$ ,  $P = 0.014$ ; other years:  $-0.03 < \text{slope} < 0.12$ ,  $P > 0.59$ ).

**Table 2** GLMM examining nest-site limitation and nest reoccupancy predictions

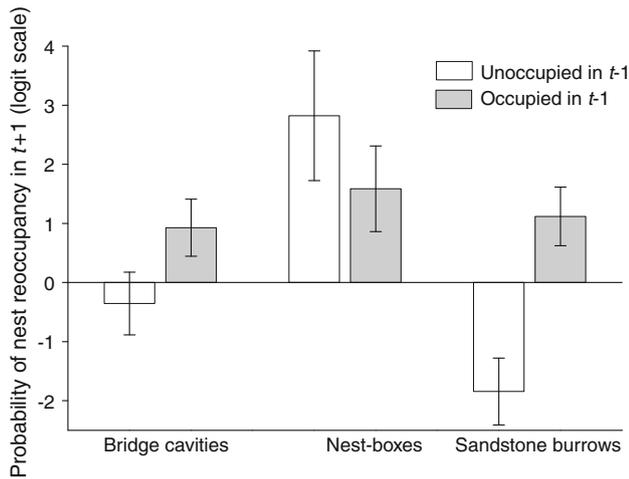
Fixed effects	df	F	P	Covariance parameters	Z	P
<b>(a)</b>						
Cluster size						
Year	4, 42.23	2.63	<b>0.048</b>	AR(1), subject = nest ID <sup>(+)</sup>	27.70	<b>&lt;0.001</b>
Log mean NND						
Year	4, 148.8	2.93	<b>0.023</b>	Patch ID	1.88	0.060
Nest type (NT)	2, 86.39	24.24	<b>&lt;0.001</b>	AR(1), subject = nest ID <sup>(+)</sup>	9.16	<b>&lt;0.001</b>
Year × NT	8, 153	2.72	<b>0.008</b>			
<b>(b)</b>						
Nest reuse in $t + 1$						
Year	3, 123.2	0.03	0.994	AR(1), subject = nest ID <sup>(-)</sup>	1.23	0.219
Nest productivity (NP) in $t$	1, 145.6	2.40	0.123			
PRS $t$	1, 148.8	3.61	0.059			
Breeding density (BD) in $t$	1, 134.2	6.47	<b>0.012</b>			
Nest occupancy (NO) in $t - 1$	1, 147.2	3.36	0.069			
NT	2, 82.26	6.23	<b>0.003</b>			
NP × PRS $t$	1, 149.4	3.13	0.079			
BD × PRS $t$	1, 145.2	6.85	<b>0.010</b>			
NO × NT	2, 135	4.12	<b>0.018</b>			

(a) Cluster size and log mean nearest neighbour distance (NND) between years. The effect of nest type was used to control for nest type dependent variation in NND

(b) The probability of nest reoccupancy. This is the reduced model, achieving the best fit as assessed by log likelihood ratio test. Only interaction terms were removed from the saturated model, starting with higher order interactions

Specifically, NP × NO, NP × NT, NP × Year, PRS  $t$  × NO, PRS  $t$  × Year, BD × NP, BD × NO, BD × NT, and NO × Year. Note that the use of nest success instead of nest productivity consistently produced models with worse fit

P values in bold are significant at  $\alpha = 0.05$ . The sign in parentheses denotes the value of autoregressive parameter estimate



**Fig. 3** Probability of nest reoccupancy in  $t + 1$  with respect to nest type and nest occupancy in  $t - 1$ . SE and mean are shown

**Table 3** GLMM examining the assumptions of the public information hypothesis about inter-patch differences and inter-annual predictability with respect to patch breeding performance

Fixed effects	df	F	P	Covariance parameters	Z	P
<b>(a) Nest productivity</b>						
Year	4, 46	3.19	<b>0.022</b>	Patch ID (Year)	2.21	<b>0.027</b>
<b>(b) Nest success</b>						
Year	4, 46	0.18	0.950	Patch ID (Year)	1.66	0.097
<b>(c) PRS t</b>						
PRS $t - 1$	1, 22	1.38	0.250	Year, subject = nest ID	4.00	<b>&lt;0.001</b>
Year	3, 22	1.98	0.150			
PRS in $t - 1$	3, 22	1.59	0.220			
1 × Year						

P values in bold are significant at  $\alpha = 0.05$

### Public information and nest reoccupancy

In contrast with the performance-based hypothesis, the probability of nest reoccupancy in  $t + 1$  decreased with increasing PRS in  $t$  while the PRS effect was stronger for nests occupied under high local breeding density in  $t$  (Table 2b; slopes  $\pm$  SE for the effect of PRS in  $t$  sliced by breeding density, high density:  $-3.08 \pm 1.31$ ,  $t_{149.2} = -2.35$ ,  $P = 0.020$ ; low density:  $-1.53 \pm 1.19$ ,  $t_{147.8} = -1.29$ ,  $P = 0.20$ ). The probability of nest reoccupancy in  $t + 1$  was higher if rollers nested under higher density in  $t$  (Table 2b; mean estimates of probability (in %) of reoccupancy and adjusted 95% CI: low density = 65.98, 47.65–80.51; high density = 68.06, 47.87–83.17), but this density effect was moderated when PRS in  $t$  was high. In other words, if PRS in  $t$  was low, rollers

were more likely to reoccupy nests in  $t + 1$  if they bred under high instead of low density in  $t$ .

### Public information and occupancy of previously unoccupied nests

In accordance with the performance-based hypothesis, after controlling for year and nest type effects, pairs nesting in  $t$  in nests that were not occupied in  $t - 1$  settled nearer those nests within the same patch that fledged at least one young in  $t - 1$  compared to nests that failed to fledge any young in  $t - 1$  (Table 4a, Fig. 4a).

Correspondingly, when considering two nearest nests from which at least one nestling fledged in  $t - 1$ , pairs nesting in  $t$  in previously unoccupied nests settled nearer those nests within the same patch where rollers fledged relatively more chicks in year  $t - 1$  (Table 4a; Fig. 4b).

In contrast with the performance-based hypothesis, our results did not reveal a significant effect of PRS in  $t - 1$  on the probability of nest occupancy in  $t$  of previously unoccupied nest-boxes. The probability of nest-box occupancy in  $t$  was higher if the nearest nest occupied by roller in  $t$  was a sandstone burrow, not a nest-box [Table 4b; mean estimates of probability (in %) of nest-box occupancy and adjusted 95% CI: sandstone burrow = 57.25, 30.29–80.50; nest-box = 47.04, 9.75–76.23]. In accordance with the conspecific attraction hypothesis, the probability of nest-box occupancy in  $t$  increased as a function of decreasing distance to the nearest neighbour in  $t$ , but this effect was stronger if the nearest roller nested in sandstone burrow, and not in a nest-box (Table. 4b; slope  $\pm$  SE for the effect of log-NND sliced by nest type: sandstone:  $-1.03 \pm 0.47$ ,  $t_{55.79} = -2.20$ ,  $P = 0.032$ ; nest-box:  $0.09 \pm 0.25$ ,  $t_{54.29} = 0.39$ ,  $P = 0.70$ ).

We did not find support for the performance-based hypothesis in that the change in the relative number of pairs breeding in patches in  $t$  should be positively related to patch productivity in  $t - 1$ . After controlling for cluster size in  $t - 1$ , the relative cluster size in  $t$  decreased with increasing PRS in  $t - 1$  only in 2007 (Table 4c; slope  $\pm$  SE for the effect of PRS in  $t - 1$ , 2007:  $-38.25 \pm 14.60$ ,  $t_{21} = -2.62$ ,  $P = 0.016$ ; other years:  $10.87 < \text{slope} < 24.48$ ,  $P > 0.16$ ). The result for the autoregression covariance parameter implies that relative cluster size consistently increased/decreased between successive years for individual patches (Table 4c).

## Discussion

### Nest-site limitation

We used a quasi-experimental approach to examine how a progressive increase in nest-site availability affected the

**Table 4** GLMM examining nest occupancy predictions

Fixed effects	<i>df</i>	<i>F</i>	<i>P</i>	Covariance parameters	<i>Z</i>	<i>P</i>
(a)						
Distance from focal nest in <i>t</i> to nest in <i>t</i> - 1						
Nest success of nest in <i>t</i> - 1	1, 38	52.21	<b>&lt;0.001</b>	Nest ID	0.32	0.749
Year	3, 38	0.58	0.632			
Nest type of <i>t</i> focal nest	2, 38	33.74	<b>&lt;0.001</b>			
Nest productivity of nests in <i>t</i> - 1						
Nest position in <i>t</i> - 1 relative to focal nest in <i>t</i>	1, 60	3.95	<b>0.051</b>	Nest ID	~0	1.000
Year	3, 60	0.62	0.606			
Nest type of <i>t</i> focal nest	2, 60	0.19	0.825			
(b)						
Nest-box occupancy probability in <i>t</i>						
Log nearest neighbour distance in <i>t</i> (NND)	1, 56.50	2.91	0.093	Patch ID	0.71	0.478
Nest type of nearest neighbour in <i>t</i> (NT)	1, 58.71	4.57	<b>0.037</b>	AR(1), subject = nest ID <sup>(-)</sup>	1.32	0.187
Year	3, 53.75	1.65	0.190			
NND × NT	1, 55.92	4.80	<b>0.033</b>			
(c)						
Cluster size change in <i>t</i>						
PRS in <i>t</i> - 1	1, 21	0.19	0.669	AR(1), subject = patch ID <sup>(+)</sup>	1.92	0.056
Year	3, 21	3.42	<b>0.036</b>			
Cluster size in <i>t</i> - 1	1, 21	3.20	0.088			
PRS in <i>t</i> - 1 × Year	3, 21	3.96	<b>0.022</b>			

(a) Differences in distances between nearest successful and failed nests as well as in productivity between two nearest nests in *t* - 1, relative to the position of focal nests in *t*. The interaction between year and nest type was removed from the models in both analysis, because it did not improve the model fit. Patch ID was not included as a random effect in the analysis, because each focal pair and its two neighbours were from the same patch

(b) The probability of nest-box occupancy in *t* with respect to distance from the nearest occupied nest in *t* and *t* - 1. Only previously unoccupied nest-boxes were included in the analysis. This is the reduced model after the removal of fixed parameters that did not significantly improve the model fit. Specifically, we refer to the log nearest distance to neighbour in *t* - 1, nest type of nearest neighbour in *t* - 1, and the interaction between the two parameters

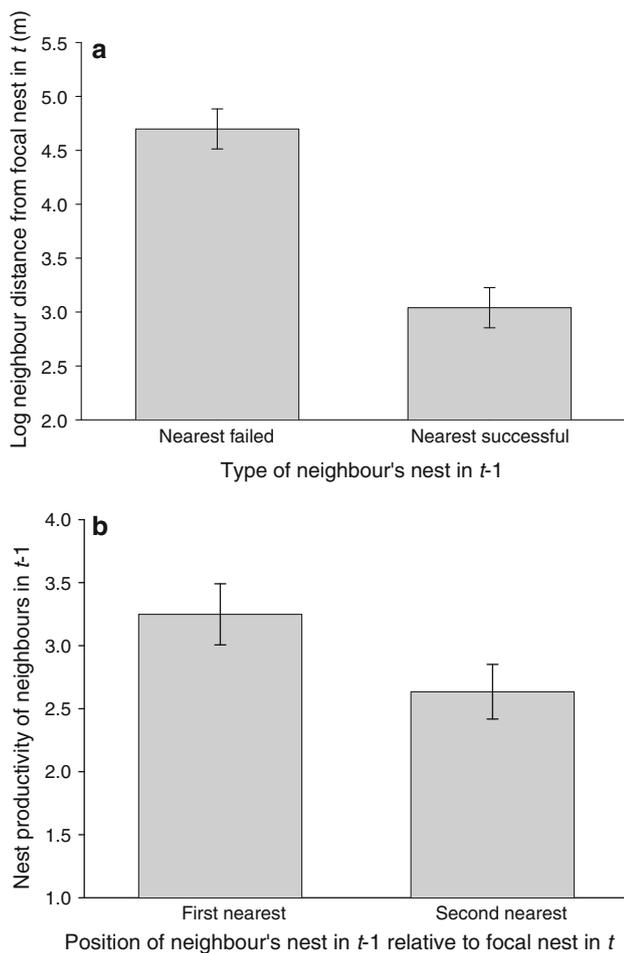
(c) The change in cluster size in *t* with respect to patch reproductive success in *t* - 1. Cluster size in *t* - 1 was included as a covariate to control for the effect of cluster size on the magnitude of cluster size change

*P* values in bold are significant at  $\alpha = 0.05$ . The sign in parentheses denotes the value of autoregressive parameter estimate

socio-ecological parameters of rollers over the course of 5 years. During this period, the population gradually increased by more than 50%. Similarly, the number of pairs per patch (cluster size) increased during the study period. As we monitored the fraction of the population nesting in natural cavities, the increase in population fraction nesting in nest-boxes does not simply reflect the abandonment of natural cavities and colonisation of new ones (Gauthier and Smith 1987; Pöysä and Pöysä 2002; Petty et al. 1994). Therefore, our study suggests that nest-site availability can be one of the limiting factors responsible for local population increase in rollers.

Studies traditionally interpret the high success of nest-box programs as a support for nest-site limitation (Pöysä and Pöysä 2002). Our results show a large increase in the fraction of the population nesting in nest-boxes. However, they also point to the fact that the success of nest-box

schemes can be due to a lower suitability of natural nest sites. Namely, we found that the reoccupancy rate of nest-boxes was higher than that of other nest types. Moreover, while the number of birds nesting in sandstone burrows was comparable among years, apparently unsuitable sandstone burrows that were barely larger than the roller or relatively enormous sandstone cavities (enlarged by mammals) were abandoned after the first year of nest-box installation. High nest-box occupancy could be related to the safety they provide to rollers from their main nest-site competitors (namely the jackdaw) and predators, because the hole entrance does not allow these to enter the nest. Also, rollers are migratory birds that arrive at the breeding grounds when other cavity-nesting species are already established. Thus, nest-boxes could be more suitable nest sites solely because they are the most abundant vacant nesting resource when rollers arrive in the spring.



**Fig. 4** Distances from focal nests in  $t$  ( $n = 38$ ) to the nearest successful and nearest failed nests in  $t - 1$  (**a**), and productivity of the first and second nearest nests in  $t - 1$  with respect to the position of focal nests in  $t$  ( $n = 61$ ) (**b**). Means and SE are shown

Therefore, caution should be exercised before any conclusion about the quality of nest-boxes is made, because this nest type is still novel and may be temporarily more attractive for other reasons (e.g. higher availability, lower nest parasite loads).

The results obtained, which are not underestimated by neglecting birds breeding in natural cavities (Pöysä and Pöysä 2002), show striking differences in NND with respect to nest type. Pairs nesting in bridges nested under higher local densities (up to 13 breeding pairs/500 m<sup>2</sup>) than rollers nesting in sandstone burrows or nest-boxes. Such high densities suggest that, if suitable nest sites are highly limited and concentrated, rollers can create quasi-colonies. Though territoriality in this species seems to be important (e.g. Cramp 1998), our results suggest that it can be highly patch dependent. The unexpected dense aggregations observed in bridges could be due to the fact that the costs derived from breeding in high density (infanticide and clutch destruction; personal observation) are compensated

by the benefits of outcompeting rollers' nest-site competitors. In contrast to other sites, no jackdaws bred in bridges.

### Social information

Our study has revealed the role of conspecific information in nest colonisation and use. Based on correlational data, we found mixed evidence for the performance-based attraction hypothesis (Danchin et al. 1998). In accordance with this hypothesis, we found that at the intermediate level, within-patch spatial scale, newly selected nests were closer to nests that were successful and more productive nests in the previous year. However, contrary to the performance-based attraction hypothesis, we found that (1) the propensity of rollers to colonise nest-boxes increased with decreasing distance to the nearest nest occupied in the same rather than in the previous season, (2) the relative number of pairs per patch in  $t$  decreased, and not increased, with PRS in  $t - 1$ , (3) the probability of nest reoccupancy in  $t$  decreased, rather than increased, with PRS in  $t - 1$ , and (4) nest reoccupancy was not related to nest success or productivity.

Evidence against the performance-based attraction hypothesis was detected at two spatial scales: between-patch (large) and within-cavity (small) scales. At the large scale, in accordance with the conspecific attraction hypothesis, we found that rollers colonised nest-boxes that were closer to conspecifics nesting nearby in the same year, though this relationship was significant only considering neighbours breeding in natural cavities. This result is important because the role of birds breeding in natural cavities is usually neglected (e.g. Roy et al. 2009). The relative change in the number of pairs per patch was not related to PRS in the previous year. This can reflect the inconsistent auto-correlation in PRS between successive years. Moreover, despite significant autocorrelation in PRS between 2006 and 2007, we found a negative relationship between PRS in  $t - 1$  and relative cluster size in  $t$ . Several reasons can explain this: (1) instead of cueing on the performance of conspecifics, rollers use the presence of conspecifics (social attraction) to choose the patch (see above), and (2) nest-site limitation and/or intra-specific interactions prevent the establishment of new birds in the patches.

At the within-nest scale, we did not find support for the performance-based attraction hypothesis because we found no relationship between nest reoccupancy and nest success or productivity. Moreover, we found that, if PRS in  $t$  was low, rollers were more likely to reoccupy a nest in  $t + 1$  if they bred under high breeding density in  $t$ . Parejo et al. (2005) found a similar result for rollers, namely that the reoccupancy probability was negatively related to PRS in  $t - 1$  under certain socio-ecological conditions (patches with low kestrel PRS in  $t - 1$ ). We propose that low

heterospecific nest-site competition in patches with locally high breeding density could be the reason why rollers reoccupy nests even if the patches were less productive in the previous year (cf. Forsman et al. 2008).

At this same scale, we found some evidence in favour of philopatry. The probability of cavity reoccupancy in  $t + 1$  was positively influenced by the use of the cavities in year  $t - 1$ . Nevertheless, we found that reoccupancy probability increased with previous use only for natural nests and bridge cavities. Therefore, sandstone burrows and bridge cavities were not only reused less frequently than nest-boxes but, in contrast to nest-boxes, their reuse was dependent on their long-term use. The greater physical variability among sandstone burrows and bridge cavities compared to nest-boxes could be one explanation for this finding.

Evidence in favour of the performance-based attraction hypothesis was detected only at the within-patch scale. Even though the assumption about autocorrelation in PRS was not met in our study system (cf. Parejo et al. 2005), our study implies that, if PRS differs between patches but it is not predictable between years, cavity selection criteria based on performance-based attraction can still operate at the within-patch scale (see also Parejo et al. 2006).

#### Implications for conservation

The implications of studies on the role of social information in habitat selection are skewed towards short-lived and/or densely breeding species. Our study reveals that various mechanisms, including opposite responses, can be involved in nest-site selection at different temporal and spatial scales in a long-lived, solitary breeding species. For example, at the between-patch scale animals might avoid patches with high density to reduce resource competition, but once they select a patch they can be attracted to the vicinity of conspecifics as a means of protection against predators. Thus, different measures should be employed at different scales to achieve the same goal, i.e. bird settlement in a patch. At the between-patch scale, attraction of individuals could be accomplished by the use of decoys and adult song playback (Ward and Schlossberg 2004; Hahn and Silverman 2006). However, the recruitment of the birds to the patch would require that prospecting birds can gather additional information about conspecific breeding performance, e.g. by using nestling decoys or nestling call playbacks.

Combined with factors like nest-site availability or low heterospecific competition, social attraction can result in dense aggregations even in a solitary species such as the roller. Some seemingly suitable holes were unoccupied by any bird in every patch even before nest-site manipulation. Yet, population size increased only after further increases in nest-site availability and subsequent growth of clusters.

Therefore, our study implies that nest-site limitation might not affect population growth only directly, but also by constraining the use of social information. Consequently, artificial constructions (e.g. towers), where the socio-ecological factors can be readily manipulated, can be useful conservation tools to create breeding and information hot spots in a short time (Smiddy and O'Halloran 2004; Franco et al. 2005).

Short-lived birds breeding under high densities and using social cues in habitat selection were suggested to be sensitive to habitat fragmentation (Reed and Dobson 1993; Ward and Schlossberg 2004; Ahlering and Faaborg 2006; Fletcher 2006). Our study implies that conservation plans should also consider and reduce the effects of habitat fragmentation for solitary species such as rollers. As social information is naturally scarcer in solitary breeding species, the impact of habitat fragmentation, as well as the disruption of information webs (Holt 2007; Schmidt et al. 2010), on this system is likely to be even greater than for densely breeding species.

The factors affecting nest-site suitability are numerous and complex and their direct assessment can be expensive. Thus, managers should protect the most frequently used nest sites, because these nests most likely confer information (both social and environment-related) that can promote patch recolonisation both during the nest-box program and following its cessation. However, since nest-box occupancy and reoccupancy rates can be markedly different from those occurring in natural nests, inference should not be obtained by considering a single nest type.

**Acknowledgments** We thank R.H. Wagner, J.T. Seppänen, M. Orell and an anonymous referee for fruitful comments and suggestions, and J. Manrique for sharing unpublished information with us. M.A. Calero-Torralbo helped with field-work. During the elaboration of this paper the authors received financial support from the Spanish Ministry of Science and Innovation (SB2003-0333), the SAS-CSIC bilateral program (Ref. 2007SK0006), and the Programa de Incentivos de Carácter Científico y Técnico de la Junta de Andalucía (2/2008). F.V. also received financial support from the Spanish Ministry of Science and Innovation (CGL2008-00562) and the European Regional Development Fund.

#### References

- Ahlering MA, Faaborg J (2006) Avian habitat management meets conspecific attraction: if you build it, will they come? *Auk* 123:301–312
- Avilés JM, Sánchez A (2000) Avian responses to nest-box installation in steppes of the south-west of the Iberian Peninsula (Extremadura). *Avocetta* 24:51–54
- BirdLife International (2009) Species factsheet: *Coracias garrulus*. <http://www.birdlife.org> (accessed 05/04/2010)
- Brown CR, Brown MB, Danchin E (2000) Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. *J Anim Ecol* 69:133–142

- Butler S (2001) Nest-site selection of the European Roller (*Coracias garrulus*) in the Vallée des Baux de Provence. MSc report
- Casas-Crivillé A, Valera F (2005) The European Bee-eater (*Merops apiaster*) as an ecosystem engineer in arid environments. *J Arid Environ* 60:227–238
- Coolen I, van Bergen Y, Day LR, Laland KN (2003) Species difference in adaptive use of public information in sticklebacks. *Proc R Soc Lond B* 270:2413–2419
- Cramp S (1998) The complete birds of the Western Palearctic on CD-ROM. Oxford University Press, Oxford
- Danchin E, Wagner RH (1997) The evolution of coloniality: the emergence of new perspectives. *Trends Ecol Evol* 12:342–347
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79:2415–2428
- Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. *Science* 297:1168–1170
- Doligez B, Cadet C, Danchin E, Boulinier T (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim Behav* 66:973–988
- Fletcher RJ (2006) Emergent properties of conspecific attraction in fragmented landscapes. *Am Nat* 168:207–219
- Forsman JT, Hjernquist MB, Taipale J, Gustaffson L (2008) Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Behav Ecol* 19:539–545
- Franco AMA, Marques JT, Sutherland WJ (2005) Is nest-site availability limiting lesser Kestrel populations? A multiple scale approach. *Ibis* 147:657–666
- Gauthier G, Smith JNM (1987) Territorial behaviour, nest-site availability, and breeding density in buffleheads. *J Anim Ecol* 56:171–184
- Hahn BA, Silverman ED (2006) Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biol Lett* 2:334–337
- Holt RD (2007) IJEE soapbox: the unraveling of nature's information webs: the next depressing frontier in conservation? *Isr J Ecol Evol* 53:229–236
- Holt RF, Martin K (1997) Landscape modification and patch selection: the demography of two secondary cavity nesters colonizing clearcuts. *Auk* 114:443–455
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) SAS for mixed models, 2nd edn. SAS Institute, Cary NC
- Manrique J (1996) Corología y ecogeografía de las aves nidificantes en la provincia de Almería (SE ibérico). PhD dissertation, Universidad de Granada, Granada
- Martin TE (1995) Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecol Mon* 65:101–127
- Martin K, Aitken KEH, Wiebe KL (2004) Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106:5–19
- Newton I (1998) Population limitation in birds. Academic, London
- Ophir AG, Galef BG (2004) Sexual experience can affect use of public information in mate choice. *Anim Behav* 68:1221–1227
- Parejo D, Danchin E, Avilés JM (2005) The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? *Behav Ecol* 16:96–105
- Parejo D, Oro D, Danchin E (2006) Testing habitat copying in breeding habitat selection in a species adapted to variable environments. *Ibis* 148:146–154
- Petty SJ, Shaw G, Anderson DIK (1994) Value of nest boxes for population studies and conservation of owls in coniferous forests in Britain. *J Raptor Res* 28:134–142
- Pöysä H, Pöysä S (2002) Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. *J Appl Ecol* 39:502–510
- Quinn GP, Keough MJ (2007) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Reed J (1999) The role of behavior in recent avian extinctions and endangerments. *Conserv Biol* 13:232–241
- Reed JM, Dobson AP (1993) Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends Ecol Evol* 8:253–256
- Roy C, Eadie JM, Schaub EM, Odell NS, Berg EC, Moore T (2009) Public information and conspecific nest parasitism in wood ducks: does nest density influence quality of information? *Anim Behav* 77:1367–1373
- Schmidt KA, Dall SRX, van Gils JA (2010) The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* 111:304–316
- Smiddy P, O'Halloran J (2004) The ecology of river bridges: their use by birds and mammals. In: Davenport J, Davenport JL (eds) The effects of human transport on ecosystems: cars and planes, boats and trains. Royal Irish Academy, Dublin, pp 83–97
- Stamps JA (1988) Conspecific attraction and aggregation in territorial species. *Am Nat* 131:329–347
- Switzer PV (1997) Past reproductive success affects future habitat selection. *Behav Ecol Sociobiol* 40:307–312
- Valone TJ, Brown JS (1989) Measuring patch assessment abilities of desert granivores. *Ecology* 70:1800–1810
- Ward MP, Schlossberg S (2004) Conspecific attraction and the conservation of territorial songbirds. *Conserv Biol* 18:519–525
- Whiting MJ, Greeff JM (1999) Use of heterospecific cues by the lizard *Platysaurus broadleyi* for food location. *Behav Ecol Sociobiol* 45:420–423
- Wiens JA (1984) Resource systems, populations, and communities. In: Price PW, Slobodchikoff CN, Gaud WS (eds) A new ecology. Novel approaches to interactive systems. Wiley, New York, pp 397–436