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The heterospecific habitat copying hypothesis: can competitors indicate habitat quality?

Deseada Parejo,[a,b] Etienne Danchin,[a] and Jesús M. Avilés[c,d]
[a]Laboratoire de Fonctionnement et Évolution des Systèmes Écologiques, Université Pierre et Marie Curie, CNRS-UMR 7625, Paris, France, [b]Cátedra de Biología y Etología, Facultad de Veterinaria, Universidad de Extremadura, 10071 Cáceres, Spain, [c]Laboratoire d'Écologie Évolutive Parasitaire, Université Pierre et Marie Curie, CNRS-UMR 7103, Paris, France, and [d]Estación Experimental de Zonas Áridas, C.S.I.C., c/ General Segura 1, 04001, Almería, Spain

According to the "habitat copying" hypothesis, animals use the reproductive performance of conspecifics to assess habitat suitability and choose their future breeding site. This is because conspecifics share ecological needs and thus indicate habitat suitability. Here, we propose the "heterospecific habitat copying" hypothesis, which states that animals should use public information (i.e., information derived from the performance of others) from con- and heterospecifics sharing ecological needs. In a correlational approach we test some assumptions and predictions of this hypothesis with a data set from two sympatric bird populations, rollers (*Coracias garrulus*) and kestrels (*Falco tinnunculus*), using the same nest-boxes and exploiting similar food resources. Since kestrels are residents and breed earlier, we assumed that they are dominant over rollers for nest-box acquisition. The environment appears to be patchy for both species and temporally predictable for kestrels only. Two results suggest that the use of heterospecific public information in breeding habitat selection may be at work: (1) an increase in the reoccupancy probability by kestrels of previous roller nests with increasing nest success, and (2) an increase in roller breeding population with increasing local kestrel success. Most of the other observed patterns could be explained by alternative mechanisms such as natal philopatry, breeding fidelity, conspecific attraction, intraspecific habitat copying, and the effect of interspecific competition. *Key words:* breeding habitat selection, conspecific cueing, habitat copying, heterospecific cueing. *[Behav Ecol]*

Whenever habitat varies in space and/or time, animals are expected to select among potential patches of habitat (Wiens, 1976). That process may involve no information gathering if individuals (1) settle at random (Dale and Slagsvold, 1990) when the environment is completely unpredictable or (2) return to their natal patch, natal philopatry (e.g., Pärt, 1991; Schjørring et al., 2000), when the environment is highly predictable (Doligez et al., 2003). Other strategies may involve information gathering about local habitat quality using cues such as: (1) the various components of habitats (vegetation structure; Orians and Wittenberger, 1991), food availability (Brown and Brown, 1996), presence of parasites (Boulinier et al., 2001), or (2) more parsimoniously, integrative cues revealing the effect of local environment suitability on individuals already using the habitat (Boulinier and Danchin, 1997; Danchin et al., 1998). Such cues may be conspecific density, presence (Brown and Brown, 1996; Müller et al., 1997), or success (Boulinier and Danchin, 1997; Danchin et al., 2001). The latter option is supported by evidence that breeders use components of their own fitness (i.e., personal information; Nager et al., 1996; Serrano et al., 2001) or the average reproductive success of conspecifics on a patch (i.e., public information; Boulinier and Danchin, 1997; Danchin et al., 1998, 2001; Doligez et al., 2002; Valone, 1989; Valone and Templeton, 2002). The occurrence of information-based strategies of habitat selection is supported by the widespread existence of prospecting in birds (Reed et al., 1999).

The hypothesis that animals use public information to select breeding habitats has been called the "habitat copying hypothesis" (Danchin et al., 2001; Wagner et al., 2000). Theoretical approaches showed that a strategy using public information is evolutionarily stable as long as the environment is not constant and does not vary randomly (Boulinier and Danchin, 1997; Doligez et al., 2003). This hypothesis is supported by correlative and experimental evidence from various species such as kittiwakes (*Rissa tridactyla*; Boulinier et al., 2002; Danchin et al., 1998), cormorants (*Phalacrocorax carbo*; Schjørring et al., 1999, 2000), house wrens (*Troglodytes aedon*; Müller et al., 1997), cliff swallows (*Petrochelidon pyrrhonota*; Brown et al., 2000), and collared flycatchers (*Ficedula albicollis*; review in Danchin et al., 2001; Doligez et al., 1999, 2002).

The heterospecific habitat copying hypothesis

Here we propose the "Heterospecific Habitat Copying Hypothesis," which states that animals may also use public information from other species with similar ecological requirements. For instance, in birds, species sharing diet and/or nest requirements may indeed provide valuable public information on habitat suitability and more precisely on the resources that are shared. However, if one of the species is dominant over the other, interspecific competition is likely to strongly influence the capacity of the subordinate species to use such information.

The idea that heterospecific cues can influence breeding habitat selection is not new (Cody, 1985). However, most studies involving heterospecific cues focused on heterospecific avoidance through interspecific competition (Gustafsson, 1987; Martin and Martin, 2001a,b), and less frequently on heterospecific attraction (Forsman et al., 1998, 2002; Mönkkönen et al., 1990; Whiting and Greeff, 1999). All these studies analyze the effect of variations in the presence or abundance of one species on population dynamics of another species. Experimental studies on European passerines have

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Address correspondence to D. Parejo. E-mail: dparejo@unex.es.

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shown that the number of species and the abundance of migrant birds increase with increasing resident titmice densities (*Parus* spp.; Mönkkönen et al., 1990), and this was true even for potential titmice competitors (Forsman et al., 1998). Moreover, heterospecific attraction seems to be selectively advantageous; pied flycatchers (*Ficedula hypoleuca*; migrants) were attracted to and got fitness benefits from the presence of titmice (Forsman et al., 2002). These results strongly suggest the existence of interspecific information use. However, a game-theoretical approach suggests that the evolutionary implications of social attraction (i.e., settlement based on the presence of others) and strategies based on conspecifics' reproductive success are likely to differ strongly (Doligez et al., 2003); when the environment is somewhat autocorrelated, a strategy based on conspecifics' reproductive success performs better than the presence strategy. However, when pitted against another strategy, the strategy based on conspecific presence often manages to persist at low frequency because it parasitizes the information inadvertently produced by individuals of the other strategy (Doligez et al., 2003). This implies that if the assumptions of this model are sound, we may also expect that heterospecific attraction is less likely to be observed in nature than heterospecific habitat copying. Furthermore, recent work has focused on positive interactions in various taxa. For example, the use of heterospecific public information has been experimentally shown in a fish, in a foraging context, (*Gasterosteus aculeatus*; Coolen et al., 2003) and in a plant as a way to improve defenses against herbivory (*Nicotiniana attenuata*; Karban and Maron, 2002). Hence, evidence suggests that positive interspecific interactions may be more general than previously thought.

In this study we use a correlative approach to tentatively test some of the assumptions and predictions of the heterospecific habitat copying hypothesis. We use data from two sympatric territorial hole-nesting bird species (the roller *Coracias garrulus* and the kestrel *Falco tinnunculus*) using nest-boxes in an area with low nesting opportunities (lack of trees and holes). The breeding biology of the two species allowed us to assume that kestrels are dominant over rollers for nest-box occupation. In our populations no bird was individually marked, so we only tested demographic predictions of the hypothesis because this can be done without individual monitoring.

Heterospecific public information is likely to be a secondary cue in breeding habitat selection, because it is a rather indirect cue of habitat suitability relative to conspecific public information and other more direct cues. This is because the similarity of ecological needs is likely to be much weaker than when spying on conspecifics. In particular, heterospecifics cannot inform about potential mate quality. Thus, only a carefully designed experiment, such as that in Doligez et al. (2002), can allow a proper testing of this hypothesis, disentangling the respective roles of the different cues.

Assumptions and predictions

In southern Europe most kestrel populations are resident (Village, 1990), whereas rollers are migratory (Cramp and Simmons, 1988). Therefore, kestrels have free access to nest-boxes, and we assumed that kestrels dominate rollers in nest-box acquisition. Rollers arrive to the breeding area later than kestrels, which breed earlier than rollers every year (mean laying dates ± SD [day 1 = 1 January]: kestrels 128.91 ± 10.33, $N = 80$; rollers 145.61 ± 9.40, $N = 111$). All years pooled, laying dates were affected by the interaction between the year and the species (ANOVA model, interaction term: $F_{3,183} = 19.14$, $p = .001$ [in every year laying dates differed between both species]).

We first tested two assumptions of the habitat copying hypothesis: (1) environmental patchiness (environment must be patchy to induce meaningful patch selection) and (2) temporal autocorrelation of breeding habitat quality (patch quality must be predictable from one year to the next to make information gathered during the previous breeding season valuable; Boulinier and Danchin, 1997; Danchin et al., 1998; Doligez et al., 2003). We expect the autocorrelation of the measure of environmental quality (the local reproductive success) to be more detectable in kestrels than in rollers, because the latter species is constrained by competition in nest-box acquisition. Only a few rollers may be able to breed in their preferred nest-boxes if kestrels occupy them first, which should lead rollers to seem to be less driven by habitat suitability than kestrels. By creating some noise, this may reduce the apparent autocorrelation of the local reproductive success in rollers.

Thus, we test the following predictions of the heterospecific habitat copying hypothesis:

1. The occupation of formerly unoccupied nest-boxes by each species should increase with the local reproductive success of kestrels and of rollers. However, for rollers we expect the situation to be made more complex by competition, and roller occupation probability in a given year may be less related to previous local reproductive success of rollers and/or kestrels.
2. Similarly, nest-box occupation of previously used boxes is expected to increase with nest-box former success, whatever the species occupying it before, and with local kestrel and roller reproductive success. As for occupancy, we also expect a more complex situation in rollers as a result of competition.
3. Population trends between successive years should be related to local reproductive success in the same way as for nest-box occupancy and reoccupancy. We expect population trends to be influenced by local kestrel and roller reproductive success in kestrels, but less so in rollers because of the effect of competition. When only considering nest-boxes that are not occupied by kestrels, however, we expect roller population trends to be influenced by local kestrel and roller reproductive success.

METHODS

Study species and area

The roller is a hole-nesting bird that usually nests in sandy banks and human buildings in southern Europe (Cramp and Simmons, 1988). In open habitats, where natural cavities are scarce, they often use nest-boxes (Avilés and Sánchez, 1997). Their main prey is insects and small mammals (Cramp and Simmons, 1988).

The European kestrel is a secondary hole-nesting bird that inhabits a variable range of habitats and nests (Village, 1990). When nest availability is low and food availability is high, kestrels readily use nest-boxes (Avilés et al., 2000; Fargallo et al., 2001). Their diet is highly variable depending on the habitat. They feed mainly on small rodents in northern Europe (Village, 1990) and on insects at southern latitudes (Veiga, 1985).

The diet of both species in the area widely overlaps; kestrels (Avilés JM, Parejo D, unpublished data) and rollers (Avilés and Parejo, 2002) mainly prey on Mediterranean locusts *Dociostaurus maroccanus* during the breeding season. In the study area locusts are the most abundant arthropod prey, with a suitable size for these species (Avilés and Parejo, 2002). During the breeding period, adult rollers clearly prefer locusts among invertebrates, and locusts constituted 73.4% of all consumed prey (Avilés and Parejo, 2002). On the other hand, kestrels are food generalists, and in southern areas grasshoppers are their main prey during the summer (Aparicio, 2000; Gil-Delgado et al., 1995; Avilés JM, Parejo D, unpublished data). Thus, interactions between the two species involve potential competition over both food and nest sites (Avilés et al., 1999, 2000).

Age at first breeding differs in these species. Rollers usually breed for the first time in their second year of life (Cramp and Simmons, 1988). Thus, an effect of local roller reproductive success on local population trends in the following year cannot be the result of natal philopatry unless the environment is still predictable on a two-year time scale or longer. Most kestrels breed for the first time in their first year of life (Village, 1990). However, in another kestrel population, only 5% of marked kestrel nestlings bred subsequently in their natal area (Village, 1990). Though natal philopatry may vary among populations, this suggests that philopatry is relatively low in that species at the scale of a local patch (and even lower at the scale of a nest-box) and is thus unlikely to be the main cause of a role of local reproductive success on future nest-box occupation and reoccupation and local population trends in kestrels.

Incubation in rollers takes 20 days and rearing takes 24 days (Cramp and Simmons, 1988), compared to 34 (Village, 1990) and 32 days, respectively, in kestrels. Because of such differences in the length of the reproductive stages as well as in laying dates, fledging occurs at similar dates in these species. Furthermore, families of both species stay in nesting territory for at least two weeks after fledging. These breeding characteristics favor heterospecific information gathering.

Both species nested in wooden nest-boxes placed on electric poles along lines crossing farmland in Extremadura, Spain. The study area is characterized by the predominance of dry pastures and cereal crops. Habitat types range from pasturelands, fallow lands, cereal croplands, shrublands, and holm-oak lands (*Quercus rotundifolia*). Nest-boxes were set from 1986 to 1991 and increased from 50 in 1986 to 1311 in 1991 (see Appendix). The constant distance between electric poles maintains nest-box density constant (mean ± SD: 9.43 ± 0.26 boxes/km). Power lines are always separated from each other by a minimum of 1.5 km of unsuitable habitat (due to the lack of natural cavities or nest-boxes). We defined a patch as the portion of one power line with nest-boxes that crosses the same type of habitat. Thus, a given power line could be parted in several patches and close boxes could belong to different patches. However, this convention can only diminish our capacity to test the assumptions and predictions of the heterospecific habitat copying hypothesis. Furthermore, it is highly likely that animals perceive changes in habitats and thus would also use close nest-boxes set in different habitats, revealing then the quality of the two different habitats. After the erection of nest-boxes in a patch, no patch was left unoccupied and at least one of the two species colonized it. We were not able to test within-species habitat copying because among the 12 patches that were once occupied exclusively by one species, only five contained the same species in the following year (see Appendix). Further description of the study area can be found elsewhere (Avilés et al., 1999).

Data collection and extraction of relevant parameters

Data were collected from 1988 to 1991. Nest-boxes were monitored weekly from mid April onwards. During the nesting period, visit frequency increased to determine breeding success accurately. Nest-box reproductive success was measured either as a binary variable, failure versus success of the breeding attempt (i.e., no chicks fledged versus at least one chick fledged), or, for successful nests, as the number of fledglings. Nest-box reproductive success represents the smallest piece of public information about habitat suitability (Boulinier et al., 1996; Reed et al., 1999).

As a measure of conspecific and heterospecific public information from a given patch, we used the mean number of chicks fledged per nest of a given patch, including failed nests (patch reproductive success [PRS]). We thus computed two estimators of PRS for each patch: PRSr and PRSk, only accounting for rollers or kestrels, respectively. To estimate population trends we computed the patch difference between the nest-box occupation rates in two consecutive years. Patch occupation rate was defined as the proportion of the available nest-boxes occupied in a season. We used variation in patch occupation rates rather than numbers of pairs because the number of nest-boxes per patch varied between years. Population trend was calculated for each species separately.

Because rollers arrive at breeding areas later than kestrels, we considered two different roller occupation rates: one accounting for all nest-boxes at the beginning of the breeding season and one accounting for nest-boxes not occupied by kestrels only. This allowed us to compare results that did or did not account for the competition for nest-boxes.

Data analyses

To study habitat patchiness and predictability, we used PRS as a measure of patch quality. Patchiness was analyzed by testing whether the average reproductive success of pairs varied among patches and/or years. We used generalized linear mixed models (GLMMs; Littell et al., 1996) to analyze patch and year effects, as random factors, on the success versus failure of each species, and we used two-way ANOVA analyze the effects of patch and year, as random variables, on the success of successful nests of each species. Predictability was analyzed by using PRS of each species in $t+1$ as dependent variables and year, and PRS in t of the same species as independent effects (ANCOVA, GLM SAS procedure [SAS Institute, 1999]). For rollers we also analyzed predictability for a two-year time lag by using PRS in $t+2$ as the dependent variable and PRS in t and year as the independent variable.

The hypothesis predicts that patches that experienced the highest reproductive success should show the highest rate of increase the following year. Thus, predictions of this hypothesis are in terms of within-year ranks (rather than in absolute value) of PRS and population trends. Because of among-year global variations, the absolute value of the PRS for a given patch may not fully reveal the value of that patch relative to other patches. For instance, a given absolute value of PRS might be among the best in years of bad overall conditions but among the worst in years of very good global conditions. Thus, as in Brown et al. (2000), we ranked the PRS and population-trend effects within years. Analyses were performed on these ranks or when the year was included as a factor in the model on the absolute values. This is because the heterospecific habitat copying hypothesis predicts that to maximize fitness, animals should recruit in the currently best patches and should desert from the currently worst patches.

We analyzed nest-box occupation probability as a function of measures of PRS. We also analyzed nest-box reoccupation probability as a function of PRSs, as well as the reproductive success in that nest-box the first year. In these analyses, observations (nests) are not independent because several nests were included in the same patch. To account for this non-independence we introduced the patch as a random effect in these analyses.

We used the Univariate SAS procedure (SAS Institute, 1999) to test for the normality of residuals of the ANOVA and linear

Table 1
Environmental patchiness

Dependent variable		Test	P	df
Kestrel failure or success (N = 340)	Year	$Z = 0.98$	.16	
	Patch	$Z = 1.76$	.04	
	Year*Patch	$Z = 1.02$	.15	
Kestrel production of young (N = 142)	Year	$F = 1.76$	.19	3
	Patch	$F = 0.52$	.94	30
	Year*Patch	$F = 2.36$	.009	13
Roller failure or success (N = 600)	Year	$Z = 0.12$	.45	
	Patch	$Z = 0.88$	.19	
	Year*Patch	$Z = 0.52$	.30	
Roller production of young (N = 469)	**Year**	$F = 5.74$	.0007	3
	Patch	$F = 1.54$	.02	41
	Year*Patch	$F = 0.72$	.88	34

Nest reproductive success of each species, measured as a binary variable (failure or success) or as the number of young fledged per successful nest, according to the year and patch, both as random factors. Generalized linear mixed models were used to analyze the success as a binary variable (SAS GLIMMIX macro) and two-way ANOVA was used to analyze the success of successful nests (SAS Proc MIXED). The analyses started with the full model. Significant effects are in bold.

Table 2
Environmental predictability for one-year time lags

Dependent variables	Independent effects	Slope (± SE)	R^2
PRSk(*t*+1) (N = 24)	PRSk(*t*): $F_{1,19} = 0.19$, $p = .67$	0.31 ± 0.28	.25
	Year: $F_{1,19} = 3.30$, $p = .09$		.25
	PRSk(*t*)*Year: $F_{1,19} = 5.02$, $p = .037$		**.25**
PRSr(*t*+1) (N = 37)	PRSr(*t*): $F_{1,33} = 1.43$, $p = .24$	0.08 ± 0.14	.24
	Year: $F_{2,74} = 3.51$, $p = .035$		**.09**
	PRSr(*t*)*Year: $F_{2,31} = 0.23$, $p = .80$		.25

Generalized linear models with the species specific PRS in year *t*+1 (PRSr[*t*+1] for roller, PRSk[*t*+1] for kestrel) as dependent variables, and PRSr(*t*), PRSk(*t*), and year as independent effects. Model selection started from the complete model. Main effects in the final model are shown with their slopes (± SE). Results obtained with the absolute values of PRS. Significant effects are in bold.

regression models. We used multiple regression analyses for continuous dependent variables (population trend, GLM SAS procedure [SAS Institute, 1999]) and GLMMs for binary dependent variables, with some independent effects as random factors (nest occupation and reoccupation probability, SAS macro GLIMMIX [SAS Institute, 1999]). We checked the fit of logistic regression models with likelihood-ratio goodness-of-fit tests. Starting models contained the main effects plus all possible interactions unless otherwise stated. Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance, starting with the highest-order interactions down to the main effects.

RESULTS

Numbers of patches varied from 12 to 43 from 1988 to 1991. They were distributed over a total of 142.5 km of power lines. Patch size (i.e., length) varied from 0.6 to 8.9 km. The mean number of boxes per patch differed among years (one-way ANOVA: $F_{3,121} = 4.07$, $p = .009$), the minimum and maximum values corresponding to 1988 and 1990–91, respectively (mean number of boxes ± SD: 1988, 12.2 ± 6.8; 1989, 20.8 ± 12.6; 1990, 30.9 ± 22.7; 1991, 30.5 ± 22.5). Nest-box occupancy rate per patch differed among years (one-way ANOVA: $F_{3,121} = 4.27$, $p = .007$), increasing from 1988 to 1991 (mean boxes occupancy rate ± SD: 1988, 29.1 ± 16.6; 1989, 41.3 ± 18.1; 1990, 43.9 ± 21.0; 1991, 50.4 ± 18.0; see Appendix), demonstrating that nest-box availability diminished over the study period despite its increase in number. This implied that new nest-boxes were occupied every year. Therefore, nest-box occupancy, as well as reoccupancy, was to be accounted for. The mean number of breeding pairs per patch and year was similar for the two species, although a little higher for rollers (mean number of nests ± SD: rollers, 7.26 ± 5.62, $N = 81$ patches; kestrels, 6.47 ± 7.27, $N = 81$ patches; see Appendix). Some kestrel nests could not be monitored up to the end of the breeding season, hence the smaller sample size for kestrels than for rollers. The proportion of kestrel nests with missing information about breeding success did not differ across patches (two-way ANOVA: patch effect, $F_{3,37} = 1.57$, $p = .21$; year effect, $F_{41,37} = 0.79$, $p = .77$), suggesting that no strong bias could result from such missing information.

Environmental patchiness

Kestrel reproductive success (measured as failure versus success) varied among patches. Furthermore, the interaction between the year and patch effects significantly affected the success of successful kestrel nests (Table 1), indicating that the relative quality of the patches varied over years.

Roller reproductive success (measured as failure versus success) was not significantly related to year and patch effects, either as main effects or in interaction. However, the year and patch effects significantly affected the success of successful nests in this species (Table 1), indicating the existence of some patchiness in that species.

Thus, although for both species there were no differences among patches and or years in the probability of fledging at least one chick, there were significant differences among years and patches in the final productivity of successful breeders, which is a prerequisite for habitat choice.

Environmental predictability

The effect on kestrel PRS (PRSk[*t*+1]) of the interaction between PRSk(*t*) and year was significant (Table 2); the relationship between PRSk(*t*+1) and PRSk(*t*) was always positive but yearly slopes differed. Furthermore, pooling years, the global effect of PRSk(*t*) on PRSk(*t*+1) was positive (slope = 0.31). In rollers (PRSr[*t*+1]) was not correlated to PRSr(*t*), neither as a main effect nor in interaction with the year effect. However, PRSr(*t*+1) varied in relation to years (Table 2). Neither PRSr(*t*) nor year was related to PRSr(*t*+2) (ANCOVA model: interaction term, $F_{1,13} = 1.29$, $p = .28$; PRSr(*t*) effect, $F_{1,14} = 0.02$, $p = .89$; year effect, $F_{1,48} = 0.90$, $p = .35$). There was a significant and positive relationship between PRSk and PRSr in a given year t (Pearson correlation: $r = .35$, $N = 38$, $p = .03$).

Nest-box occupation probability

Nest-box occupation in a given year influenced the probability of reoccupation in the subsequent year (logistic regression model: $\chi^2_1 = 165.65$, $p < .0001$; mean occupation probability ± SE: 0.75 ± 0.43 [$n = 577$] for formerly occupied nests versus 0.40 ± 0.49 [$N = 743$] for formerly unoccupied nests).

Table 3

Factors influencing the probability of an occupied nest-box in year *t* being reoccupied in the following year

Independent effects	Reoccupation by kestrel in year t+1	Reoccupation by roller in year t+1
NS	**$F_{1,403}$ = 4.75, p = .03**[a]	$F_{1,397}$ = 0.01, p = .90
PRSr	$F_{1,402}$ = 0.95, p = .33	$F_{1,397}$ = 0.38, p = .54
PRSk	**$F_{1,403}$ = 9.34, p = .002**	$F_{1,397}$ = 0.51, p = .47
SP	**$F_{1,403}$ = 21.31, p < .0001**	$F_{1,397}$ = 3.37, p = .07
PRSr*NS	$F_{1,397}$ = 0.09, p = .77	$F_{1,397}$ = 0.01, p = .91
PRSk*NS	$F_{1,401}$ = 1.36, p = .24	$F_{1,397}$ = 0.40, p = .53
SP*NS	$F_{1,398}$ = 0.17, p = .68	$F_{1,397}$ = 6.32, p = .01
PRSr*PRSk	$F_{1,399}$ = 0.60, p = .44	$F_{1,397}$ = 0.15, p = .69
PRSr*SP	$F_{1,400}$ = 1.53, p = .22	$F_{1,397}$ = 2.65, p = .10
PRSk*SP	$F_{1,396}$ = 0.04, p = .84	$F_{1,397}$ = 4.30, p = .04
PRSr*PRSk*SP	$F_{2,395}$ = 1.44, p = .24	**$F_{1,397}$ = 4.54, p = .03**[b]
PRSr*NS*SP	$F_{1,392}$ = 0.19, p = .66	$F_{1,394}$ = 0.00, p = .98
PRSr*PRSk*NS	$F_{1,394}$ = 0.48, p = .49	$F_{1,396}$ = 0.82, p = .37
PRSk*NS*SP	$F_{1,393}$ = 0.26, p = .61	$F_{1,395}$ = 0.30, p = .58
PRSr*PRSk*NS*SP	$F_{1,391}$ = 1.19, p = .28	$F_{1,393}$ = 0.45, p = .50
Year	$F_{2,389}$ = 1.44, p = .24	$F_{2,391}$ = 0.60, p = .55
Patch	Z = 1.45, p = .07	Z = 1.29, p = .10

[a] Figure 1 illustrates the corresponding effect.

[b] Figure 2 illustrates the corresponding effect.

NS: nest success of the focal nest-box (success versus failure) in year *t*. PRS: patch reproductive success for rollers (r) and kestrels (k) in year *t*. SP: species occupying the nest-box in year *t*. Generalized linear mixed models (SAS GLIMMIX macro) with the probability of a nest to be reoccupied in year *t*+1 as dependent variable and focal nest success in year *t* as well as the species specific PRS in year *t*, the species occupying the nest-box in that year and year as fixed effects, and the patch as a random factor. All the analyses took into account the interactions among all independent effects except for the year. Significant effects are in bold.

Occupancy of previously unoccupied nest-boxes

Kestrel occupation probability of previously unoccupied nest-boxes was only related to PRSk(t) (GLMM: retained PRSk(t) effect, χ^2_1 = 6.36, p = .012, slope = 0.26; patch effect, Z = 1.49, p = 0.07). Nest-boxes in patches where kestrels bred successfully in year *t* were more likely to be occupied in year *t*+1 by kestrels. In rollers, the occupation probability in year *t*+1 of unoccupied nest-boxes in year *t* was only influenced by the patch as a random effect (GLMM: patch effect, Z = 1.83, p = .03), indicating that roller occupation probabilities across years in each patch were not independent.

Occupancy of previously occupied nest-boxes

Reoccupation by kestrels. Formerly successful boxes were more likely to be occupied in *t*+1 by a kestrel pair than unsuccessful ones (Table 3 and Figure 1). This reoccupation probability was, however, related to the species occupying the box the first year (Table 3). Boxes formerly occupied by a kestrel pair were twice as likely to be occupied by a kestrel than those occupied by a roller pair (mean occupation probability ± SE: 0.23 ± 0.02 [N = 304] for roller boxes versus 0.49 ± 0.03 [N = 273] for kestrel boxes). Furthermore, the occupation probability by a kestrel in *t*+1 of a box occupied in *t* was positively related to PRSk(t) (Table 3, slope = 0.27).

The reoccupation probability of successful nests by kestrels was positively related to PRSk(t) (GLMM: $F_{1,331}$= 8.93, p = .003, slope= 0.29), but this effect depended on the species occupying the nest in the first year (GLMM: $F_{1,331}$= 16.28, p < .0001), with former kestrel boxes being twice as likely to be reoccupied by a kestrel than roller boxes (mean occupation probability ± SE: 0.25 ± 0.03 [N = 235] for roller nests versus 0.53 ± 0.03 [N = 230] for kestrel nests). In this model the patch effect was not significant (Z = 1.50, p = .07).

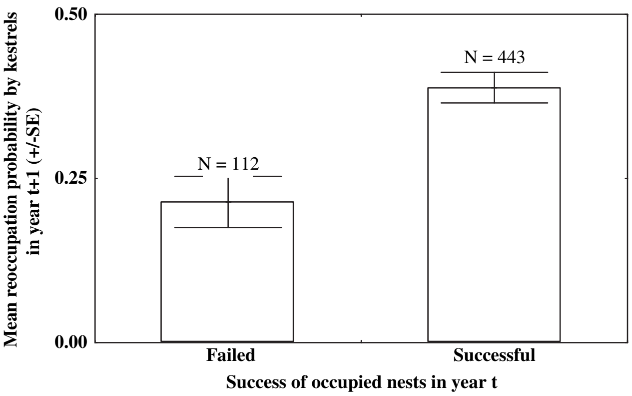

Figure 1
The probability (mean ± SE) that a nest is occupied by a kestrel in the following year as a function of the nest success (failure versus success) in the first year. Successful nests are more likely to be reoccupied in the subsequent year. Sample sizes are shown above bars (see Table 3 for significance).

Reoccupation by rollers. The roller reoccupation probability in year *t*+1 of previously occupied nests in year *t* was related to the interaction between the species occupying the box the first year and both PRSr(t) and PRSk(t) (Table 3). Therefore, reoccupancy of nest-boxes by rollers depended on the species nesting there in the previous year; the roller reoccupation probability of a previously occupied nest-box was lower when the species occupying the nest used to be a kestrel than when it was a roller (see Figure 2a,b). We thus tested the relationship for each species separately. Kestrel boxes from patches with low PRSs, as well as kestrel boxes from patches with high PRSk and high PRSr, in year *t*, had low roller reoccupation probability in year *t*+1 (Figure 2a). Kestrel boxes from patches with either high PRSk or high PRSr had a high roller reoccupation probability (Figure 2a). In contrast, roller nests from patches with both high PRSr and high PRSk in year *t* were the most likely to be reoccupied by a roller in year *t*+1; in addition, nests from patches with both low PRSr and low PRSk in *t* were more likely to be reoccupied than nest-boxes from patches with just one high PRS (Figure 2b).

The reoccupancy probability of successful nests in year *t* by a roller was only related to the species occupying it in year *t* (GLMM: $F_{1,433}$ = 26.89, p < .0001, and Z = 1.54, p = .06 for the effect of patch as a random factor), with roller nests more reoccupied than kestrel ones.

Population trends

In kestrels, within-year ranks in population trends were positively related to within-year ranks in PRSk (Table 4). The within-year ranks in roller population trends were not related to within-year ranks in PRSr or PRSk when considering all nest-boxes as available for rollers (Table 4). However, within-year ranks in roller population trends were positively related to within-year ranks in PRSk when only considering the nest-boxes left unoccupied by kestrels before rollers' arrival (Table 4).

DISCUSSION

Assumptions

For both kestrels and rollers the environment appeared somewhat patchy (Table 1). Thus, patch selection may be

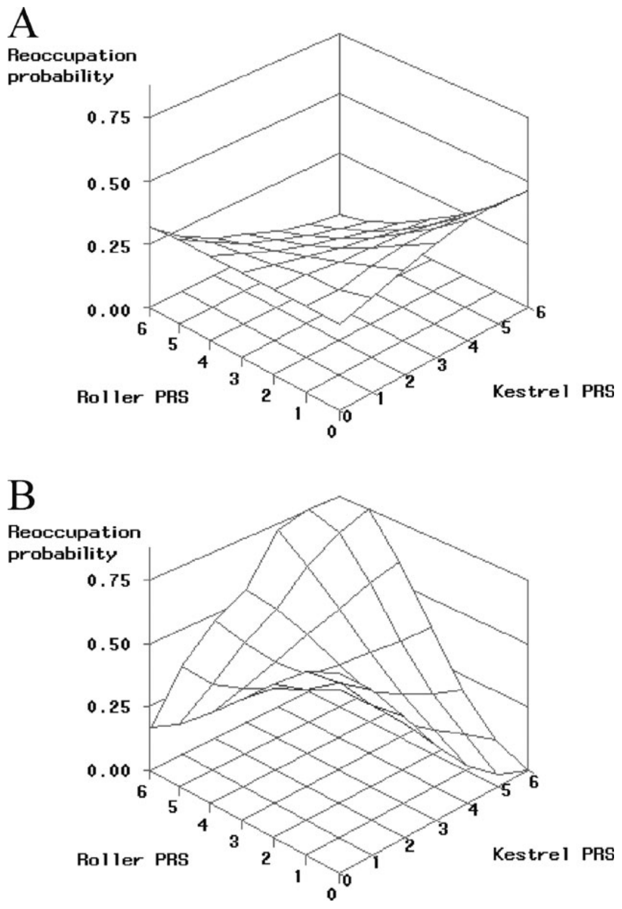

Figure 2
Effects of kestrel public information (kestral PRS: mean number of fledglings per kestrel nest in a patch) and roller public information (roller PRS: mean number of fledglings per roller nest in a patch) on roller nest-box reoccupation probability for (a) nests formerly occupied by kestrels and (b) nests formerly occupied by rollers. Reoccupation probabilities are the values predicted by the selected logistic regression (see Table 3 for significance).

Table 4
Factors predicting the species specific population trend (PTsp) in a patch in two consecutive years

Independent effects	Population trend		
	Rollers 1 (PTr_1)	Rollers 2 (PTr_2)	Kestrels (PTk)
PRSk	$F_{1,36} = 3.02$, $p = .09$	$\mathbf{F_{1,36} = 11.71}$, $\mathbf{p = .0016}$, $\mathbf{R^2 = .24}$, **slope = 0.80**	$\mathbf{F_{1,36} = 11.36}$, $\mathbf{p = .0018}$, $\mathbf{R^2 = .24}$, **slope = 0.64**
PRSr	$F_{1,35} = 0.00$, $p = .97$	$F_{1,35} = 1.02$, $p = .32$	$F_{1,35} = 0.35$, $p = .55$

Population trend for each species in each patch was calculated as the difference between the patch percentages of nest-boxes occupied by either of the species between successive years. For the rollers two different population trends were used, one considering that all nest-boxes in each patch were available for that species (PTr_1) and another considering that the later arrival of rollers makes them unable to select nest-boxes already occupied by kestrels (PTr_2). Independent effects are roller and kestrel patch reproductive success (PRSr and PRSk). We used within-year ranks for all variables (see Methods). Main effects in the final model are shown with their slopes and R^2. Significant effects are in bold.

valuable. The measure of environment quality also showed some level of predictability in kestrels but not in rollers (Table 2). The latter result may be because the environment of rollers is actually unpredictable, or because the predictability of its measure, PRS, is difficult to detect because of competition with kestrels over nest sites. The former explanation seems unlikely because rollers and kestrels share similar food in the study area (Avilés et al., 1999, 2000; Avilés and Parejo, 2002), implying that this component of their environment should show similar levels of predictability.

Results supporting the heterospecific habitat copying hypothesis

We found two convincing pieces of evidence for the use of heterospecific public information in our kestrel-roller system: (1) the increase in reoccupancy by kestrels of nest-boxes previously occupied by rollers with increasing nest success (Tables 3 and 5, Figure 1), and (2) the increase in roller breeding population with increasing local kestrel success (Tables 4 and 5). Reoccupation of boxes by rollers may also provide some support of this hypothesis.

Regarding the first of those results, more successful nests in year *t* were more likely to be reoccupied by kestrels in year $t+1$, regardless of the former occupying species. In boxes occupied by kestrels three mechanisms others than heterospecific habitat copying may explain the observed pattern: (1) higher nest site fidelity in successful breeders would lead to higher reoccupation probability; (2) natal philopatry to the birth nest may naturally increase reoccupation probability through the recruitment of locally born juveniles; and (3) intraspecific habitat copying may explain the higher probability of reoccupation because high PRS attracts more non-locally born potential recruits. However, in nest-boxes formerly occupied by rollers, the increased reoccupation by kestrels following high local success can be explained by none of those mechanisms alone or in combination. Thus, heterospecific habitat copying is likely to be involved (Table 5); kestrels seem to rely on former rollers' performance to choose a nest-box.

Similarly, rollers were more likely to use patches with successful kestrels the previous year. This result was detected only after discounting nest-boxes already occupied by kestrels. The difference between our two estimates of population trends in the roller underlines the likely importance of competition in that species; despite their late arrival, rollers tend to occupy patches with high PRSk. This could reflect the tendency of rollers to cue on kestrel density when arriving from migration, but this is unlikely because we did not find a significant positive relationship between PRSk and kestrel breeding density (correlation between the kestrels PRS and density measured as the proportion of nest-boxes occupied by kestrels: $r = .19$, $p = .24$, $N = 38$). Hence, heterospecific habitat copying appears to be the most likely mechanism to explain the positive effect of PRSk on subsequent roller population trends (Table 5).

The significant interaction between the species formerly occupying a box and both PRSs on roller reoccupancy probability provides further support for the use of information from kestrels by rollers. Globally, rollers were more likely to reoccupy nests previously used by rollers than by kestrels (compare Figure 2a,b). This is probably due to breeding site fidelity. Patterns of reoccupation by rollers were of opposite shapes when formerly occupied by a kestrel or a roller (Figure 2). It is difficult to make specific predictions for roller reoccupation probability if we assume the use of heterospecific

Table 5
Summary of the results obtained for both species and possible mechanisms involved

Occupancy in year t	Species occupying in $t+1$	Significant factors	Relationship	Possible mechanisms
Empty	Kestrel	PRSk(t)	Positive	Patch natal philopatry Breeding patch fidelity Conspecific attraction Conspecific habitat copying
	Roller	None	—	Competition?
Occupied	Kestrel (all nests)	Nest success(t)	Successful nests more reoccupied	Nest natal philopatry or breeding site fidelity if formerly occupied by kestrels Con- and heterospecific habitat copying
		Species(t)	Kestrel nests more reoccupied	Nest natal philopatry Breeding site fidelity
		PRSk(t)	Positive	Patch natal philopatry Breeding patch fidelity Conspecific attraction Conspecific habitat copying
	Kestrel (successful nests)	Species(t)	Kestrel nests more reoccupied	Nest natal philopatry Breeding nest fidelity
		PRSk(t)	Positive	Patch natal philopatry Breeding patch fidelity Conspecific attraction Conspecific habitat copying
	Roller (all nests)	(Species*PRSk*PRSr)(t)	See Figure 2	Competition + con- and heterospecific habitat copying?
	Roller (successful nests)	Species (t)	Roller nests more reoccupied	Nest natal philopatry Breeding nest fidelity

Species Population Trend	Factors affecting	Relationship	Possible mechanisms
Kestrels	PRSk(t)	Positive	Natal philopatry Conspecific attraction Conspecific habitat copying
Rollers (considering all nests)	None	—	Competition
Rollers (considering only nests not taken by kestrels)	PRSk(t)	Positive	Heterospecific attraction Heterospecific habitat copying

PRS: patch reproductive success for rollers (r) and kestrels (k) in year t. Only significant results are shown.

public information by this species and that kestrels are dominant over rollers for nest-box occupation. This is because several potential mechanisms may be interacting with heterospecific habitat copying (e.g., nest site and patch fidelity, within-species habitat copying as well as natal philopatry coupled with habitat predictability over several years).

In former kestrel boxes, we may, however, tentatively expect rollers to be unable to occupy highly attractive boxes (i.e., situated in patches with high PRSr and PRSk), both because of nest-site fidelity of successful kestrels and because of their situation in high quality patches as revealed by high PRSs (conspecific habitat copying in kestrels). Similarly, rollers are expected to avoid unattractive boxes (i.e., in patches with low PRSr and PRSk). These two expectations combined may lead to observing the highest occupation probability in intermediate situations (i.e., with one high and one low PRS). This corresponds to the observed pattern (Figure 2a). In former roller boxes, the situation is made more complex by the potential effect of high breeding site fidelity in successful individuals and the cost of acquiring a new nest-box. Natal philopatry at the scale of the nest site is unlikely to be involved because rollers first breed at age two and PRSr does not appear significantly autocorrelated over successive years. However, assuming that formerly successful rollers (i.e., high quality individuals) are capable of reoccupying their former box in spite of high competition with kestrels, we may speculate that nest site fidelity tends to increase reoccupation probability in attractive boxes, which is what we observe (compare reoccupation probabilities for high PRSr and PRSk between Figures 2a,b). Similarly, the lower costs of reoccupying the same box may lead rollers to reoccupy the same box more often in patches with both low PRSr and PRSk (which are avoided by kestrels). However, all these interpretations are speculative and made a posteriori in attempt to explain the observed patterns.

Alternative hypotheses

All the other results may be explained by mechanisms other than heterospecific habitat copying (Table 5).

Natal philopatry

Many results for kestrels could be explained by natal philopatry to the nest or patch (Table 5). Because kestrels begin to breed when one-year old, the positive relationships between the occupancy and reoccupancy probabilities in year $t+1$ and PRSk in t could result from the return to the natal area of offspring born in year t. The same reasoning holds for the positive effect of kestrel nest success in year t on the probability of reoccupation by kestrels in year $t+1$, as well as the higher reoccupancy probability by kestrels of former kestrel nest-boxes and the increase in kestrel population in patches with increasing PRSk (Table 5). However, natal philopatry cannot explain the effect of nest success on the probability of occupation of former roller nest-boxes by kestrels, once PRSk has been accounted for. Kestrel patch natal philopatry seems to be low (Village [1990] reports 5% philopatry to the natal patch in another population), and natal philopatry to the nest is expected to be even lower. However, because our kestrels were unmarked we could not assess the real level of philopatry in the study population.

In rollers, philopatry alone cannot explain our results because they first breed when older than one year and environmental quality (as assessed through PRS) does not appear predictable in time.

Breeding site fidelity

Most of our results on occupancy and reoccupancy probability may result from breeding nest or patch fidelity (Table 5). This is the case for the increase in kestrel occupancy and reoccupancy probabilities with increasing PRSk, the increase in kestrel reoccupancy probability with increasing kestrel nest success in the previous year, the higher kestrel reoccupancy probability of previous kestrel nests, and the higher roller reoccupancy probability of previous roller nests (Table 5). However, we obtained an increase in population size of kestrels with increased PRSk that could not be caused only by breeding site fidelity (Tables 4 and 5), since a population increase always involves immigration of new recruits. Thus, population increase refers to individuals that do not have previous experience in the area.

Conspecific and heterospecific attraction

The increase in the occupancy and reoccupancy probabilities by kestrels with increasing PRSk and also the higher growth rate of kestrel population in patches with high PRSk may result from conspecific attraction (Table 5). However, conspecific attraction may be involved if PRSk is positively linked to kestrel density, but we found no such relationship. Thus, conspecific attraction is unlikely in our system.

Individuals may also be attracted to heterospecifics. We found an increase in roller (migrants) population with increased PRSk (PRS of residents), which may suggest that rollers are attracted to kestrels. However, since PRSk and kestrel density were not related, heterospecific attraction is unlikely here.

Intraspecific habitat copying

Conspecific habitat copying may also explain several of our results for kestrels (Table 5). The increase in kestrel occupancy and reoccupancy probability with increased PRSk, the increase in kestrel reoccupancy probability with increased kestrel nesting success, and the increase in kestrel population with PRSk (Table 5) may all involve intraspecific habitat copying. However, we did not find any support for conspecific habitat copying in rollers. This may be because of the low predictability of environmental quality in rollers, or it may be a consequence of competition, which may weaken the effect of conspecific public information on patterns of nest reoccupancy by rollers. Indeed, when arriving from migration, rollers may not freely access formerly successful roller boxes because kestrels may have already occupied them.

Evaluation of each component of habitat quality

Animals may also assess all or several environmental components acting on reproductive success, and decide accordingly. Presumably, many of these components are likely to be correlated with some of the single cues proposed here. The only way to distinguish these alternatives is through manipulations of PRSk or PRSr.

The importance of competition

Finally, competition for nest-box acquisition between kestrels and rollers might explain some of the results in rollers, although the way in which competition is working is far from clear. Competition may explain the absence of a significant effect on roller occupancy patterns and roller population growth rate when considering that all nest-boxes were available for both species. Patterns in kestrels were more in agreement of the predictions of the conspecific or heterospecific habitat copying hypotheses. The two species probably do not use information in the same way, a difference that may be a consequence of competition.

However, nest-boxes did not seem to be a limiting factor in the area (maximum occupation percentage = 52.4%), but competition may arise well before saturation. Territoriality may strongly limit nest-box availability. In our system nest-boxes were 110 m apart. Roller territories have an average diameter of 200 m ($N = 30$) in the study area (Avilés and Costillo, 1998), implying that only one in two nest-boxes could be used. Kestrels' territories have a minimum diameter of 800 m in natural areas, but territory size may vary in response to many factors, such as variations in food availability (Village, 1990). Moreover, the similar breeding population size per patch for the two species suggests that territory size probably does not differ strongly in the two species. As a result, saturation may be reached when only one box in two is occupied, which seemed to be the case in the study population. Another possibility is that habitat heterogeneity may render some nest-boxes much less attractive than others, implying competition for the best boxes, in spite of the fact that some may remain empty.

In some bird species intraspecific competition seems to determine the way in which different phenotypes in the population use conspecific public information (collared flycatcher, Doligez et al., 1999; great cormorant, Schjørring et al., 2000). Therefore, if heterospecific habitat copying is a strategy used, interspecific competition might affect the use of heterospecific public information.

Conclusion

We propose the heterospecific habitat copying hypothesis, which is an extension of the habitat copying hypothesis: public information (i.e., the performance of others) from con- and heterospecifics may be used as a source of information about habitat suitability. We thus suggest that information extracted from fitness components of any other individuals sharing similar ecological requirements may be used to assess environmental suitability. Even competitors may thus provide valuable information about environmental conditions: the stronger the overlap in ecological needs among species, the stronger the competition but also the higher the value of heterospecific public information.

In spite of the fact that heterospecific copying is expected to be less effective than within-species copying, we provide a tentative correlative test of some of the assumptions and predictions of the heterospecific habitat copying hypothesis. Some results support heterospecific habitat copying in kestrels and rollers nesting in the same nest-boxes and feeding on similar prey in Extremadura, Spain. However, the impact of many potential alternative explanations, as well as the impact of competition, made such correlative results particularly difficult to interpret. The best way to overcome such difficulties would be by manipulating the reproductive success of one of the species (as in Doligez et al., 2002) and measuring the expected effect on the other species, to distinguish the importance of heterospecific habitat copying from other alternative mechanisms such as intraspecific habitat copying, competition, personal information, direct assessment of habitat, etc.

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APPENDIX: RAW DATA

	Years											
	1988			1989			1990			1991		
Patches	Avail. boxes	Roller Occup (%)	Kestrel Occup (%)	Avail. Boxes	Roller Occup (%)	Kestrel Occup (%)	Avail. boxes	Roller Occup (%)	Kestrel Occup (%)	Avail. boxes	Roller Occup (%)	Kestrel Occup (%)
A	0	—	—	31	16.1	41.9	90	22.2	47.8	87	19.5	44.8
AA	0	—	—	8	25	25	8	37.5	25	7	57.1	28.6
AB	0	—	—	11	0	37.5	11	9.1	36.4	14	28.6	21.4
AC	14	0	7.1	14	0	35.7	14	21.4	50	14	28.6	42.9
AD	25	16	20	25	28	44	25	40	32	25	40	36
AE	10	20	40	10	10	50	10	10	30	10	10	30
AF	26	34.6	15.4	26	57.7	11.5	26	65.4	11.5	26	57.7	11.5
AG	8	12.5	12.5	37	29.7	8.1	28	32.1	10.7	28	39.3	10.7
AH	7	42.9	0	7	42.9	0	7	42.9	14.3	7	28.6	28.6
AI	8	12.5	0	16	25	0	16	25	18.7	16	31.2	12.5
AJ	0	—	—	0	—	—	38	13.2	7.9	38	18.4	5.3
AK	0	—	—	0	—	—	30	23.3	13.3	30	46.7	30
AL	0	—	—	0	—	—	28	7.1	14.3	26	19.2	19.2
AM	0	—	—	0	—	—	10	20	0	10	20	0
AN	0	—	—	52	7.7	9.6	52	9.6	23.1	51	13.7	17.7
AO	0	—	—	25	16	12	25	32	28	25	44	38
AP	0	—	—	0	—	—	31	12.9	6.4	25	24	20
AQ	0	—	—	0	—	—	43	7	4.3	43	20.9	13.9
AR	0	—	—	0	—	—	86	4.6	7	86	16.3	24.4
AS	0	—	—	0	—	—	61	0	16.4	60	11.7	21.7
AT	0	—	—	13	15.4	38.5	13	23.1	76.9	13	30.8	38.5
AU	8	37.5	0	8	37.5	12.5	8	50	0	8	25	0
AV	15	20	0	15	13.3	13.3	15	33.3	20	15	26.7	13.3
AX	0	—	—	0	—	—	58	10.3	20.7	58	29.3	20.7
AY	0	—	—	10	10	10	10	40	20	10	10	20
AZ	0	—	—	22	27.3	4.5	22	31.8	13.6	22	18.3	18.2
B	0	—	—	0	—	—	56	23.2	26.8	56	33.9	35.7
BA	0	—	—	0	—	—	21	4.8	9.5	21	19	19.1
BB	0	—	—	28	32.1	3.6	28	53.6	14.3	28	75	3.6
C	0	—	—	0	—	—	75	18.7	21.3	75	18.6	21.3
D	7	14.3	0	7	0	14.3	70	15.7	17.1	69	11.6	15.9
E	0	—	—	0	—	—	12	33.3	0	12	41.6	16.7
F	0	—	—	0	—	—	20	35	5	20	25	15
G	0	—	—	0	—	—	47	23.4	6.4	47	38.2	17
H	0	—	—	0	—	—	11	9.1	9.1	11	27.2	18.2
I	13	15.4	7.7	39	30.8	30.9	39	41	35.9	39	23.1	33.3
J	0	—	—	30	26.7	6.7	30	33.3	16.7	29	27.6	6.9
K	0	—	—	35	20	14.3	35	37.1	20	34	32.3	26.5
L	6	0	16.7	13	15.4	23.1	13	23.1	0	11	45.4	27.3
M	0	—	—	16	12.5	12.5	16	18.7	12.5	15	46.7	6.7
N	0	—	—	44	22.7	6.8	69	31.9	17.4	69	30.4	24.6
O	0	—	—	14	35.7	57.1	14	35.7	35.7	14	28.6	14.3
P	0	—	—	7	0	28.6	7	14.3	14.3	7	14.3	14.3
Means		11.2	8.6		12.2	20.1		27.3	16.9		29.2	20.6
Totals	147			563			1328			1311		

Number of available nest-boxes in the different patches and years and the occupation percentages by rollers and kestrels in them.

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