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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Receivers matter: the meaning of alarm calls and competition for nest sites in a bird community

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Abstract

Animal communities may constitute information networks where individuals gain information on predation risk by eavesdropping on alarm calls of other species. However, communities include species in different trophic levels, and it is not yet known how the trophic level of the receiver influences the informative value of a call. Furthermore, no empirical study has yet tested how increased competition may influence the value of alarm calls for distinct receivers. Here, we identify the importance of alarm calls emitted by a small owl, the little owl (*Athene noctua*), on the structure of a cavity-nesting bird community including mesopredators and primary prey under variable levels of competition for nest holes. Competitors sharing top predators with the callers and prey of the callers interpreted alarm and non-alarm calls differently. Competitors chose preferentially alarm and non-alarm patches over control patches to breed, while prey selected alarm patches. In contrast, competition for nest sites affected habitat selection of prey species more than that of competitors of the callers. This study provides support for a changing value of alarm calls and competition for nest sites for distinct receivers related to niche overlapping among callers and eavesdroppers, therefore, calling attention to possible cascading effects by the use of information in natural communities.

Keywords Animal communities · Information networks · Interspecific competition · Predation risk · Receivers

Introduction

Many prey species emit alarm calls when encountering a predator (Caro 2005). Individuals producing alarm calls may obtain benefits recruiting conspecifics for mobbing defence (Curio et al. 1978), warning relatives and/or mates who increase their chances to escape (Weary and Kramer 1995), also warning the predator that it has been detected (Hasson 1991), and attracting predators of the predator (Curio et al. 1978). In addition, alarm calls may inform about predation risk to non-related conspecific and heterospecific prey threatened by the same predator (Caro 2005; Magrath et al. 2015). Hence, alarm calls emitted by one species may warn all potential prey of a given predator within the community (e.g. Templeton and Greene 2007; Vitousek et al. 2007; Parejo et al. 2012).

In food webs, top predators often feed at more than one trophic level. Top predators may feed on primary prey (i.e. herbivore or granivore prey), but also, as part of intraguild predation, they may feed on mesopredators, which are the usual predators of primary prey. Killing of mesopredators by top predators is sometimes important enough to impact demography of mesopredator populations (Ritchie and Johnson 2009). Therefore, mesopredators would mainly benefit by detecting top predators, and, meanwhile, primary prey would get more advantages by detecting mesopredators than top predators because the formers are more of a threat. Evidence suggests that prey can recognize their predators' vocalizations to assess predation risk (Blumstein et al. 2008; Emmering and Schmidt 2011; Zanette et al. 2011; Cure et al. 2013; Schmidt and Belinsky 2013), and that this capability may be an important part of the top-down mechanisms

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mediating food web dynamics (Schmitz et al. 2000). In the landscape of fear, with peaks and valleys of predation risk (Laundré et al. 2001), mesopredators should avoid sites where top predators emit any vocalizations and sites where individuals from species sharing predators indicate high-predation risk by means of alarm calls. This is based on the fact that empirical studies in bird communities have shown that individuals at high risk of predation may change their distribution, shifting to safer places (Suhonen 1993; Cresswell 2008). Primary prey, on the other hand, could avoid sites where their predators occur and, hence, avoid sites where the mesopredators produce any vocalizations. Alternatively, primary prey could distinguish between sites where the mesopredator gives different type of vocalizations (alarm and non-alarm calls). Non-alarm calls are variable sounds made by many social animals, which differ from alarm calls in that they are not designed to communicate specific information about predators. Therefore, primary prey could prefer areas where mesopredators give alarm calls, because this would indicate that their predator is stressed, compared to sites where mesopredators emit non-alarm calls, because this would only indicate the occurrence of predators in the area. This idea is based on the "enemy of my enemy is my friend" rule proposed by Sabellis et al. (2001). The last hypothesis assumes that predators in risky situations would be ineffective, which is supported by evidence showing that animals would be unable to simultaneously allocate attention to important tasks such as the detection of predators and effective foraging (Metcalfe et al. 1987; Dukas and Kamil 2000; Dukas 2002). The two proposed hypotheses predict, hence, that alarm calls are differently decoded depending on the trophic level in which the receiver is included. As far as we are aware, however, nobody has yet investigated whether prey species may eavesdrop specifically on different calls of their predators to evaluate its presence, abundance and/or stress when choosing breeding habitats.

Individuals constrained by the same factors, from the same or different species, may be useful to each other because they are likely to provide profitable information on shared limiting factors (Parejo et al. 2005; Seppänen et al. 2007). However, the value of social information encoded in calls for receivers within food webs may change according to the intensity of competition between receivers and callers, as happens with other sources of social information (Seppänen et al. 2007; Parejo and Avilés 2016). For instance, resident titmice *Parus* spp. usually provides migratory flycatchers *Ficedula* spp. with information on breeding habitat quality that residents evaluate throughout the year (Forsman et al. 2002). However, this only happens when tit densities are between low and moderate levels. At higher tit densities, information from tits becomes ineffective because both flycatchers and tits suffer the costs of the increased competition for resources (Forsman et al. 2008). A number of studies have analyzed the effects of competition on social information use at the intraspecific level (e.g. Doligez et al. 1999; Szymkowiak et al. 2016). But no empirical study has yet tested how changes in the level of competition may influence the value of alarm calls, as a particular type of social information, for distinct receivers in natural communities. For example, increased community density, likely to increase competition, in the face of predation risk might have positive effects either through a dilution effect or through an increase in the probability of spotting predators but also might have some costs when predators respond functionally to prey distribution (Schmidt and Whelan 1999; Szymkowiak and Kuczynski 2015). Therefore, costs and benefits of clustered breeding, and hence of increased competition, emerging from social information use may affect the value of this information, and change the result of the interaction.

Here, we aim to identify the value of alarm calls emitted by a mesopredator for the organization of receivers from different trophic levels in a community of hole-nesting birds (Fig. 1a) under variable competitive pressure. This community includes within one trophic level the resident little owl (*Athene noctua*), which is the call emitter, and two migratory species, the scops owls (*Otus scops*) and the European roller (*Coracias garrulus*). Also, the community includes three resident passerines preyed upon species of the higher trophic level: great tits (*Parus major*), spotless starlings (*Sturnus unicolor*) and rock sparrows (*Petronia petronia*). Little owls emit conspicuous alarms calls used in habitat selection by conspecifics and scops owls (Parejo et al. 2012). Scops owls and European rollers compete for hole-nesting sites with little owls, while all share potential predators, for example, in larger owls (Parejo et al. 2012). Finally, the three passerine species also compete for breeding cavities with rollers, and little and scops owls, and are common prey of these two latter species (e.g. Obuch and Kristin 2004; Marchesi and Sergio 2005; Tome et al. 2008; Parejo et al. unpublished data) (Fig. 1a).

In a crossed design (Fig. 1b), we manipulated social information on a threat at the patch scale by broadcasting calls of little owls indicating different levels of danger. In addition, we modified availability of holes at the patch scale to manipulate competition for nest sites. Populations of non-excavator vertebrates, as secondary hole nesting birds, are limited by the availability of existing cavities (Newton 1998; Aitken and Martin 2007); hence, by modifying availability of holes during the choice of nest sites, competition for nest sites is likely to be changed. Then, we analyzed the effects of these two factors on the structure of this cavity-nesting bird community in which all the species compete for nest sites but where some species share predators with the little owl and others are their prey. Therefore, response to the experimental manipulation was measured separately for species within the same trophic level of little

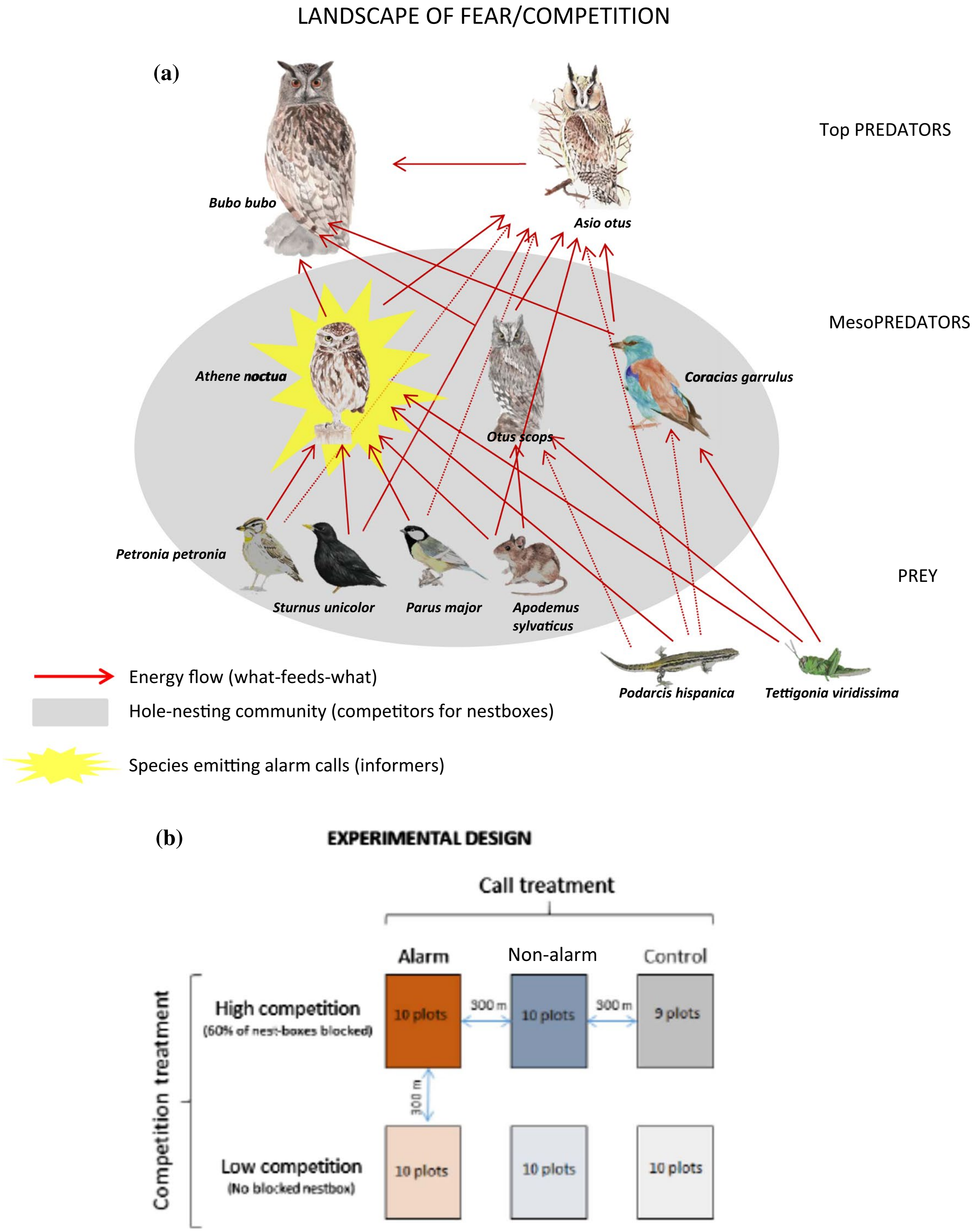

Fig. 1 **a** Simplification of the food web in which the studied hole nesting bird community is included. The little owl (*Athene noctua*), that is the species emitting alarm calls, is marked in yellow. European rollers (*Coracias garrulus*), little and scops owls (*Otus scops*) compete for hole-nesting sites and share potential predators for example in larger owls (Parejo et al. 2012). Great tits (*Parus major*), spotless starlings (*Sturnus unicolor*) and rock sparrows (*Petronia petronia*) also compete for breeding cavities with rollers and little and scops owls, and are common prey of the two latter species (e.g. Obuch and Kristin 2004; Marchesi and Sergio 2005; Tome et al. 2008; Parejo et al. unpublished data). Arrows of different width indicates the importance of each species in the diet of the predators. Illustrations were made by ME. **b** Schematization of the experimental crossed design. One of the groups of six plots in which all the treatments were applied is represented (colour figure online)

owls (little owl's guild hereafter) and prey species of the little owl. Distinguishing the relative impacts of predation risk and competition for nesting sites on the spatial settlement of small predators is important to lower trophic levels because the spatial distribution of prey will be strongly determined by the distribution of predators (Morosinotto et al. 2017). We predicted first that species from the little owl's guild deciphered little owls' alarm calls as a measure of predation threat by top predators, whereas prey of the little owl could interpret them either as a measure of predator presence and/or abundance, or as a measure of their predator's stress. Second, we predicted that the value of information encoded by little owls' calls changed with the level of competition for nest holes and the competitive ability of each guild.

Materials and methods

Study system

The study was conducted during the 2013–2014 breeding seasons (April–July) in southeastern Spain (37°18′N, 3°11′W). In the study area, the cavity-nesting bird community, including little and scops owls, rollers, great tits, spotless starlings and rock sparrows, use as breeding sites 346 cork-oak nest-boxes held in trees that have been used by these species for years (Parejo and Avilés 2011; Parejo et al. 2012); that is, birds from the cavity-nesting community may have previous knowledge of these nest-boxes because no nest-box was added during the study years. All used nest-boxes had a base and roof surface of 24 × 24 cm, a height of 40 cm and an opening 6 cm in diameter, which is wide enough to allow easy nesting of all the studied species. The area is a homogeneous holm oak (*Quercus ilex*) wooded landscape where natural holes are scarce, and when present they are so small that are unsuitable for most of these hole-nesting species (Parejo et al. unpublished data).

Little owls are resident birds in the study area and, hence, are likely to have more precise information on breeding habitat quality than the other two medium-size migrant species, scops owls and rollers, as has been shown in other communities (Monkkönen et al. 1990). Indeed, experimental work has shown that little owls' vocalizations encode valuable information affecting settlement decisions for conspecifics, and heterospecific migrants (Parejo et al. 2012). Furthermore, the other three species breeding in the community (great tits, spotless starlings and rock sparrows) are more or less commonly preyed by the little owl. Therefore, the little owl is a suitable informer of all the species from the different trophic levels in this bird community.

Experimental design

In 2014, nest-boxes were assigned by proximity to patches, each one containing on average 5.86 nest-boxes (range 4–11, $n = 346$ nest-boxes in 59 patches). Patches were at least 300 m apart of each other and nest-boxes within each patch were separated by 50–100 m of each other. As the experiment produced six different kinds of patches (Fig. 1b), we spatially assembled patches into groups of six to avoid spatial influence, and hence of habitat quality, on treatments. Within each group of six patches, three duplets of two spatially paired patches were established and randomly assigned to one of the three following treatments: (a) "Alarm" ($N = 20$ patches), in which we simulated alarmed little owls by broadcasting their alarm calls; (b) "Non-alarm" ($N = 20$ patches), in which we simulated the presence of non-stressed little owls by broadcasting non-alarm calls; and, (c) "Control" ($N = 19$ patches), in which no playback was broadcasted but visits were as frequent as to alarm and non-alarm patches. In addition, competition for holes to breed was increased during the experimental time, which is the period in which nest-site selection of every species is more likely to occur. This was done by blocking the first day of the experiment the entrance of the 60% of nest-boxes (High-competition treatment) in one of the two patches of each duplet ($N = 29$ patches), while competition was not manipulated at all in the other patch of each duplet (low-competition treatment) ($N = 30$ patches) (Fig. 1b). After 15 days, the blocking was removed and, thus, all nest-boxes were available to birds. Each group of six patches included two alarm, two non-alarm and two control patches, each of which one patch was assigned to the high competition and the other to the low-competition treatment (Fig. 1b). Despite the blocking of nest-boxes, in all patches some nest-boxes remained empty through the season (see occupation rates of patches within each treatment in Table 1), which minimizes the possibility that responses to the manipulation were due to the lack of nest-boxes and not to changes in the intensity of competition during nest-site choice. Furthermore, we acknowledge that the high-competition treatment might actually represent low competition for individual birds after settlement, whenever this treatment triggers low occupation. However, this treatment clearly causes high competition during nest-site choice, which is the effect we looked for as we aimed to measure the response of birds to treatments in terms of distribution, that is, when choosing a place to breed.

Due to the limited number of patches we could define within the study area, we chose to establish a silent control treatment instead of a noise control treatment (as in Betts et al. 2008; Szymkowiak et al. 2016). As we had two noise treatments, we consider that responses to playbacks, which we expected to be different according to previous results in the same study system (Parejo et al. 2012), were not likely

Table 1 Proportion of occupied patches and average occupation rates for each group of species (little owl's guild and prey species of the little owl) in the different treatments

Treatments		Variables				
Call	Competition	Occupied patches by species of the little owl's guild/no. of patches	Occupied patches by prey species of the little owl/no. of patches	Occupied patches by all species of the community/no. of patches	Mean occupation rates of patches occupied by species of the little owl's guild	Mean occupation rates of patches occupied by prey species of the little owl's guild
Alarm	LC	6/10	4/10	1/10	0.22	0.40
Non-alarm	LC	5/10	5/10	2/10	0.28	0.26
Control	LC	3/10	4/10	0/10	0.23	0.18
Alarm	HC	7/10	4/10	2/10	0.24	0.26
Non-alarm	HC	6/10	1/10	1/10	0.32	0.25
Control	HC	2/9	1/9	1/9	0.14	0.20

Competition treatment: *LC* low competition, *HC* high competition

to be due to attraction to a novel sound. Moreover, the use of vocalizations of a presumably neutral bird species in a noise control treatment could cause unexpected reactions in receivers because these vocalizations might be conceived as non-neutral and, hence, being attractive or aversive for receivers.

Call and competition treatments were applied during 15 days, from 21 April to 5 May (as in Parejo et al. 2012). The duration and dates of the treatments comprised the time in which most breeding birds in the community are evaluating territories, and, thus, performed manipulations are expected to influence breeding patch selection (Parejo and Avilés 2011; Parejo et al. 2012).

Little owl calls were extracted from Llimosa et al. (1990). They were broadcasted during 2 h just before dusk, to be sure that diurnal birds as rollers and passerine species were still active, on alternative days at the core of patches using portable amplified speakers connected to digital takeMS audio players (model deseo) (as in Parejo et al. 2012). Three non-alarm and three alarm calls from different individuals were used to generate two distinct 1.5–3 min of uncompressed audio files with the recordings of the various calls. These two files were randomly mixed with periods of silence from 3 to 8 min and then randomly broadcasted to reduce pseudoreplication (Parejo et al. 2012). Little owl calls and silent periods were recorded in separate tracks so that the exact sequence of calls and silences was randomly decided by selecting the random playback mode. The randomized presentation of the three calling bouts of each type in combination with the silence tracks during the 2 h of broadcasting produces a unique assortment of calls for each day of treatment and patch (see for similar approaches Eggers et al. 2006; Schmidt 2006; Parejo et al. 2012). We chose to use the highest quality available little owl calling bouts instead of own recordings of local little owls to avoid data biases resulting from discrimination of familiar calls in our experiment (Hardouin et al. 2006). Average broadcasting volume was 89.1 (+ 1.1) dB measured 1 m away from the speaker, which closely resembles by ear to the natural production of real little owl calls.

Two days before the start of the experiment, all nest-boxes were visited to be sure that no bird was already breeding. At that moment, we only found seven occupied nest-boxes which were removed from our analyses, which were finally performed on 339 nest-boxes. Patches were visited weekly from 21 April to the end of June to register occupation (assuming a nest-box was occupied when at least one egg was laid in it), breeding species, laying dates and reproductive parameters.

The responses of species from the little owl guild and prey species of the little owl to the experimental manipulation were measured using three variables estimating breeding habitat preference: (1) the occupation of a patch by each group of species, i.e. whether a patch is occupied or not at least by one breeding pair of the corresponding group. Preferred habitats should be more likely occupied. (2) For occupied patches, the specific rate of occupation of a patch by each group of species, i.e. the proportion of nest-boxes occupied by individuals of a group per patch. Preferred habitats should be more occupied (Fretwell 1972). Finally, as preferred patches should be more prone to be reoccupied, we used data from 2013, as a pre-treatment year, on nest-box occupation by the different species of each group to analyze: (3) the re-occupation of patches already used in 2013 by individuals of a group of species, i.e. whether an occupied patch in 2013 by individuals of a group of species is reoccupied or not in 2014, that is the treatment year. During the 2013 breeding season, the pre-treatment year, nest-boxes were monitored following the same field protocol as in 2014. In 2013, 41 out of 59 studied patches were occupied by at least one of the target species, 32 patches by species of the little owl's guild and 20 by prey species of the little owl. Therefore, these patches are the sample for analyzing this last variable.

Statistical analyses

Analyses were performed using SAS v.9.4 statistical software (SAS 2002–2008 Institute, Cary, NC, USA).

Generalized linear models (Genmod procedure in SAS), with binomial error structure and link function logit, were performed to analyze the effect of the treatments of both little owls' calls (alarm calls, non-alarm calls and control) and competition (high and low competition) on: (1) patch occupation by the different groups of species during the experimental year; and, (2) patch re-occupation in 2014 of patches already occupied in 2013 by the different groups of species.

With the aim to test whether the experiment affected occupation rate of patches by the two groups of species, we ran General linear models (GLM procedure in SAS), with Gaussian error structure and link function identity, in which patch occupation rate (arcsine transformed) was the dependent variable and the call treatment and the competition treatment were explanatory factors.

In all statistical models, the number of nest-boxes per patch was introduced as a covariate to control for the fact that the number of nest-boxes varied among patches and, thus, the actual level of competition. For each statistical model, we provide a measure of its goodness-of-fit (Pearson χ^2 for the logistic models and R^2 for regression models). Pairwise differences in significant models were checked by comparisons of least-squared means of each treatment.

Results

In 2014, in 41 out of the 59 studied patches we reported nesting at least one of the species of interest (23% of nest-boxes being occupied). Species of the little owl's guild occupied 29 patches, while prey species of the little owl occupied 19 patches. The rate of occupied patches and occupation rate of occupied patches by species of each group in the experimental treatments are shown in Table 1.

Little owl's guild

Occupation of patches by individuals belonging to the little owl's guild was influenced by the call treatment (Table 2), so that individuals occupied more frequently patches in which calls were broadcast (i.e. alarm and non-alarm calls' patches) than control patches (post hoc comparisons: alarm versus control patches: $z=-2.39$, $P=0.017$; non-alarm versus control patches: $z=-1.90$, $P=0.047$; alarm versus non-alarm patches: $z=-0.40$, $P=0.69$) (Fig. 2a).

In occupied patches, the occupation rate by species within the little owl's guild was not affected by the call or competition treatments (Table 2).

On the other hand, the call treatment affected the reoccupation of patches previously occupied by owls and rollers in 2013 but in interaction with the competition treatment (Table 2). Thereby, in 2014, patches where little owl non-alarm or alarm calls were broadcasted (informed patches hereafter) were more likely to be reoccupied than control patches when competition was low (call treatment effect for the low-competition treatment: $\chi^2_2=4.95$, $P=0.084$) and high (call treatment effect for the high-competition treatment: $\chi^2_2=5.75$, $P=0.056$) (Fig. 2b). However, the effect of the competition treatment was only shown in alarm patches (competition treatment effect for the alarm treatment: $\chi^2_1=3.68$, $P=0.055$) so that they tended to be more reoccupied when competition was low (Fig. 2b). In non-alarm and control patches, the effect of the competition treatment was farther from significance (competition treatment effect for the non-alarm treatment: $\chi^2_1=2.68$, $P=0.102$; competition treatment effect for the control treatment: $\chi^2_1=0.07$, p = 0.787). No other explanatory factor had an effect on any of the response variables of the little owl guild (Table 2).

Table 2 Sources of variation in the response variables of the little owl guild to the little owls' calls and competition treatments

Parameter	Patch occupation ($N=59$ plots) Pearson $\chi^2_{52}=58.99$, $P>0.1$			Patch occupation rate ($N=29$ plots) $R^2=0.37$			Patch re-occupation ($N=32$ plots) Pearson $\chi^2_{25}=22.96$, $P>0.1$		
	χ^2	df	P	F	df	P	χ^2	df	P
Call treatment	7.06	2	0.029	1.62	2, 22	0.220	8.78	2	0.012
Competition treatment	0.03	1	0.855	0.08	1, 22	0.775	0.00	1	0.989
Call x competition treatment	0.65	2	0.723	0.79	2, 22	0.467	6.41	2	0.040
Number of nest-boxes	0.72	1	0.397	4.13	1, 22	0.054	0.05	1	0.817

Results of: (1) Generalized linear models investigating patch occupation in 2014 (the year of the experiment) and patch re-occupation in 2014 of patches already occupied in 2013 in relation to calls and competition treatments; and (2) General linear model in which patch occupation rate was the dependent variable and the call and the competition treatments, together with its interaction, were explanatory fixed factors. For each whole model, sample size and Pearson χ^2 (for logistic regression models) or R^2 (for lineal regression models) values are shown as measures of their relevance. Note that a non-significant Pearson χ^2 is indicative of no evidence of lack of fit of the model

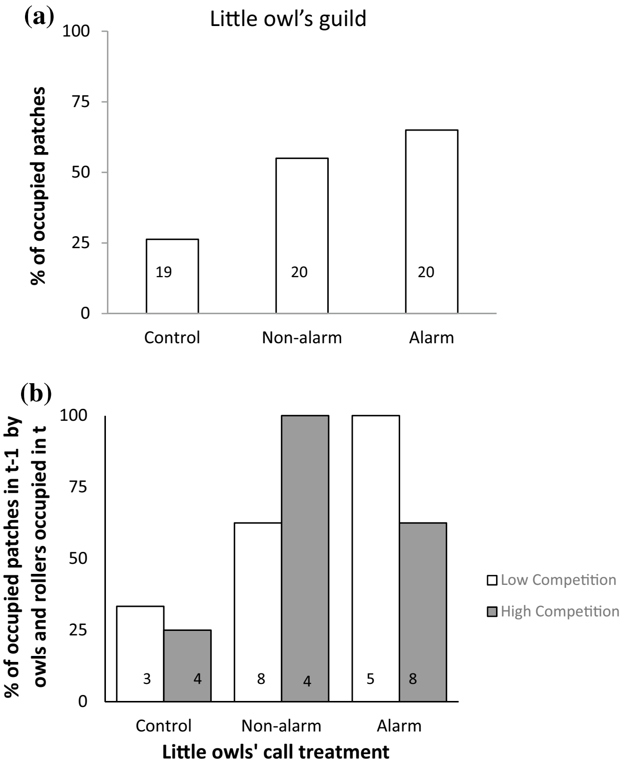

Fig. 2 Effects of the call and competition treatments on organization of species within the little owl's guild. **a** Percentage of patches occupied by at least one breeding pair of the little owl's guild in each call treatment. **b** Percentage of patches already used by individuals of the little owl's guild in 2013 which were reoccupied in 2014 (the year of the experiment) in each treatment. The number of patches per treatment is shown in bars

Prey species of the little owl

Occupation of patches by prey species of the little owl was not influenced by the call treatment, but was influenced, although only marginally, by competition for nest sites (Table 3). Prey species mainly settled down in patches with relaxed competition (Fig. 3a).

In occupied patches, the occupation rate by prey species was unaffected by call and competition treatments (Table 3).

Reoccupation of occupied patches in 2013 by prey species was determined by the call treatment in 2014 (Table 3), so that patches where alarm calls were broadcasted in 2014 were preferentially reoccupied by individuals of these species (post hoc comparison: alarm versus non-alarm patches: $z = -1.99$, $P = 0.049$; the other two pairwise comparisons: $P > 0.10$) (Fig. 3b).

Discussion

The value of alarm calls

We found support for the idea that the informative value of alarm calls emitted by a bird species differs for species in different trophic levels in a food web. For species included in the same guild of the little owl, calls were very important, regardless of the level of competition. Thereby, informed patches were the preferred ones by competitors (Fig. 2a, b). Meanwhile, prey species of the little owl appeared to rely on calls of little owls as indicators of predators' stress to reoccupy patches already used in the precedent year because they preferentially re-settled down in patches where little owls were alarmed (Fig. 3b). Hence, these results would provide support for the idea that information on predation risk encoded in alarm calls can be a driver of the structure of bird communities, through its effects on both individuals of the trophic guild of callers, i.e. competitors, and their prey.

There are many pieces of evidence showing that eavesdroppers get benefits using information from alarm calls emitted by heterospecifics. In the short time, the benefits

Table 3 Sources of variation in the response variables of prey species of the little owl to the little owls' calls and competition treatments

Parameter	Patch occupation ($N = 59$ plots) Pearson $\chi^2_{52} = 53.50$, $P > 0.1$			Patch occupation rate ($N = 19$ plots) $R^2 = 0.17$			Patch re-occupation ($N = 20$ plots) Pearson $\chi^2_{13} = 13.99$, $P >= 0.1$		
	χ^2	df	P	F	df	P	χ^2	df	P
Call treatment	2.21	2	0.330	0.49	2, 12	0.622	6.77	2	0.034
Competition treatment	3.78	1	0.052	0.22	1, 12	0.644	0.00	1	0.998
Call x competition treatment	2.02	2	0.365	0.21	2, 12	0.815	2.22	2	0.329
Number of nest-boxes	3.84	1	0.050	0.24	1, 12	0.631	1.66	1	0.198

Results of: (1) Generalized linear models investigating patch occupation in 2014 (the year of the experiment) and patch re-occupation in 2014 of patches already occupied in 2013 in relation to calls and competition treatments; and (2) General linear model in which patch occupation rate was the dependent variable and the call and the competition treatments and its interaction were explanatory fixed factors. For each whole model, sample size and Pearson χ^2 (for logistic regression models) or R^2 (for lineal regression models) values are shown as measures of their relevance. Note that a non-significant Pearson χ^2 is indicative of no evidence of lack of fit of the model

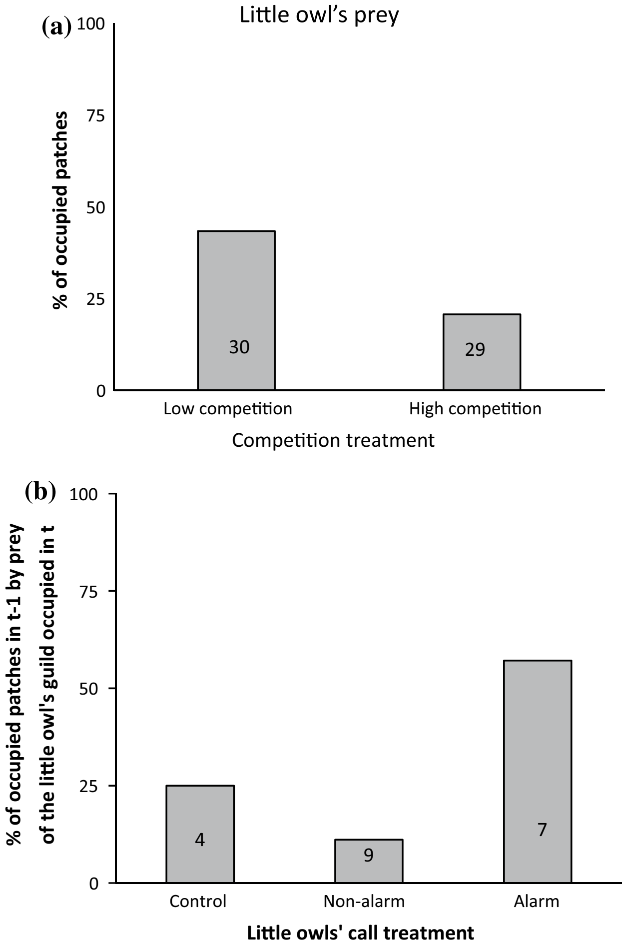

Fig. 3 Effects of the call and competition treatments on organization of little owl's prey species. **a** Percentage of patches occupied by at least one breeding pair of prey of the little owl's guild in each competition treatment. **b** Percentage of patches already used by prey of the little owl's guild in 2013 which were occupied in 2014 (the year of the experiment) in each call treatment. The number of patches per treatment is shown in bars

can come in the form of improved antipredatory responses (Seyfarth and Cheney 1990; Templeton and Greene 2007; Vitousek et al. 2007; Magrath and Bennett 2012). In the longer term, benefits can come by the choosing of safe habitats (Parejo et al. 2012) and by the enlargement of foraging niches (Ridley et al. 2014). Here, we have detected that species of the little owl's guild (little owls, scops owls and rollers) preferred to breed in patches where little owls' vocalizations were broadcasted, but they did not preferentially choose non-alarm patches. Little owls were expected to respond in this way, as previous experimental work in this community has shown that they were attracted to conspecifics even when they signal high local predation risk through alarm calls (Parejo et al. 2012). Regarding the diurnal roller, it could be argued that it does not distinguish between little owls' alarm and non-alarm calls. As top predators may be behaviourally flexible and adjust their activity rhythms to the rhythms of their prey (Penteriani et al. 2013), the alarm system of little owls against shared predators might be useless for a diurnal bird as the roller. Therefore, rollers could simply be attracted to little owls' calls as indicators of suitable places for competitors and, consequently, for them. However, rollers tended to choose non-alarm patches on their own (Supplementary Material Appendix 1, Fig. A1), indicating that they are able to decode little owls' calls and to choose the safer places. For scops owls, based on previous results in the area (Parejo et al. 2012), they should prefer the patches with lower predation risk indicated by little owls, however, here they seem to prefer alarm patches (Supplementary Material Appendix 1, Fig. A1). The difference between the two studies (Parejo et al. 2012) may reside on the fact that preference for breeding sites was differently measured. Indeed, in Parejo et al. (2012) preference was measured using the earliest laying date of scops owls per patch. Here, however, as we aimed to measure preference by individuals from different species of the same trophic level, the use of the earliest laying date as a proxy of preference is unsuitable due to species-specific phenologies. Therefore, while in the first study we measured the preference of the best individuals immediately after the performance of the experiment, here we analyze the preference of all scops owls through all the breeding period. The effect of the latter experiment could have been diluted after a time, which might lead to the found preference for alarm patches whenever later individuals choose patches with low-quality individuals to avoid competition.

Regarding prey species, we only found a response to little owls' calls when we analyzed the reoccupation in the experimental year of occupied patches in $t-1$. This result means, first, that primary prey can distinguish between alarm and non-alarm calls of their predators and, second, that sites with stressed predators attract their prey. That is, predators surrounded by many enemies in a site may make the site attractive to prey because enemies of the enemies may be allies (Sabellis et al. 2001). This could be because predators under high risk of predation would be ineffective predators. Alarm calls as indicators of predation risk so far have largely been considered relevant only when produced in response to threats that endanger the eavesdropper (Templeton and Greene 2007; Magrath et al. 2009). However, alarm calls may have a different meaning for different receivers, as it is shown above. Here we show that alarm calls may be important to assess local predation risk only for species that share predators with the callers. This happens even when little owls and their prey species share several predators (Fig. 1). However, as prey species of little owls are mainly predated by species from the little owl guild, including the little owl (Obuch and Kristin 2004; Marchesi and Sergio 2005; Tome et al. 2008; own unpublished data), alarm calls of the predator might provide information about the stress of the predator. This may constitute an example of a top-down mechanism where the (simulated) occurrence of a top predator negatively affects the mesopredator and, in the end, favours the primary prey.

The importance of competition

For species of the little owl's guild, the competition treatment affected the responses to the call manipulation of individuals reoccupying previously used patches in 2013. At least 30% of captured individuals from the little owl's guild in 2014 were also breeding in the area in 2013. Therefore, many individuals occupying in 2014 previously occupied patches are probably familiar with the area. Results suggest that in informed environments, because they mainly chose informed patches, competition for nest sites with both conspecifics and heterospecifics may have some influence on the structure of the communities of this group of species. Indeed, within informed patches, birds likely to have already bred in the area the year before the experiment chose alarmed patches when availability of holes was high, but trended to choose non-alarm patches when hole availability was low. This pattern might be given by the choice each time of only one commodity by individuals with previous experience in the area. That is, animals might opt by either avoiding competition (through the choice of alarm patches with low competition) or by avoiding predation risk (through the choice of non-alarm patches but with higher competition) in relation to their individual condition or personality. Supporting this argument, animal behaviour is claimed to be determined by individual state on the one hand (Dingemanse and Wolf 2010), and, on the other hand, individual personality may affect risk-taking behaviour (e.g. Couchoux and Cresswell 2012). These results point out that information, more than competition for nest sites, influences decisions in this trophic level because competition only modulates responses in informed patches, which may be based on the size of these species because they are clearly stronger competitors than the smaller prey species. This seems to be the case at least under the competitive regime we have imposed with our experiment, which could in any case be not large enough to lead to the complete avoidance of competitors and hence to the discarding of call information (Parejo and Avilés 2016).

In contrast, prey species of the little owl tended to preferentially occupy patches with high availability of holes to breed, irrespective of the information they conveyed. Secondary hole nesting birds are highly limited by hole distribution and availability to breed (Newton 1998), which may strongly determine their breeding process. Therefore, prey species may be strongly constrained to get a breeding site. Moreover, this response may be because competition for nest sites also involves predation risk for prey because they compete for nest sites in many occasions with their predators (Fig. 1). When competitors are also potential predators, it may be difficult to predict the spatial distribution of competitors (Morosinotto et al. 2017). Therefore, in this case results are difficult to interpret and could have been different if we had used calls of a non-competing predator whose calls would only inform on predation risk to prey species and not on competitive pressure. The trend of individuals of this trophic level for areas with low competition leads, however, to these areas to show the highest densities of birds (Fig. 3a), indicating that the manipulation induced a preference. Furthermore, the fact that mean laying dates of the three prey species are within or just after the experimental time (rock sparrow: 7th of May, great tit: 1st of May and spotless starling: 5th of May), leads us to think that the described distribution is mainly a result of the competition manipulation itself.

Conclusion

In conclusion, this study provides a first empirical evidence of the idea that the value of alarm calls as determinants of the spatial distribution of eavesdropping species in different tropic levels may depend on the level of niche overlap among callers and receivers (Parejo and Avilés 2016). The importance of heterospecific alarm calls for susceptible species seems to be determined by the number of limiting factors shared by the callers and the receivers. Thereby, species sharing predators and nest sites with the callers seem to rely on any vocalization of their competitors to choose their breeding sites. Meanwhile, species sharing nest sites with the callers and being predated by callers and by others species as well, seem to respond, at least in familiar environments, to their alarm calls when choosing their nesting sites. That is to say, for prey species, alarm calls of their predators seem to inform on predators' stress. Therefore, the consequences of alarm calls on prey distribution should be explored in each particular system to shed light on our understating of cascading effects through the use of social information in natural communities, which may have profound implications in food web dynamics. On the other hand, and also contrary to our expectations, competition for nest sites seemed not to modify the value of alarm calls when they inform on important predators. However, competition seemed to be an important factor of species distribution within a community when information on predation risk was not so relevant since the top predators that endanger the callers are less dangerous for the prey than for the mesopredators. Finally, one recommendation derived from our findings is that studies on community structure should not ignore species that emit alarm calls. Since animal communities are ideal information networks where individuals can gain information on danger from many different species (Parejo et al. 2012), because alarm calls are widespread in animals, social information encoded in alarm calls may greatly influence community structure through interspecific eavesdropping.

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Author contribution statement DP and JMA designed the study. DP, JMA and MEG collected field data. DP carried out the statistical analyses and wrote a first version of the manuscript that was discussed, revised and approved for all the authors. MEG makes the drawings of Fig. 1.

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