



Mobbing behaviour varies according to predator dangerousness and occurrence



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Animals possess various antipredator behaviours to reduce their risk of predation. Whereas most prey make considerable effort to avoid their predators, sometimes individuals approach and mob predators as a group. Among the types of predators that elicit mobbing, raptors such as hawks and owls are one of the more consistent targets. We conducted playback experiments to investigate the strength of mobbing behaviour according to the perceived risk associated with either predator dangerousness or local predation pressure. We first determined whether mobbing is specific to dangerous predators or more broadly directed at predatory species. We experimentally investigated whether prey can discriminate the level of dangerousness of two owl species. Our results indicate that prey adjusted the strength of their mobbing behaviour according to the perceived risk: passerine birds mobbed the Eurasian pygmy owl, *Glaucidium passerinum* (i.e. a dangerous predator) but not the boreal owl, *Aegolius funereus* (i.e. a far less dangerous species). Second, we compared mobbing behaviour in similar habitats differing in predation pressure (with or without pygmy owls). Working on identical bird communities, we revealed that mobbing varied in relation to the local presence of the predator. Where the pygmy owl was absent, calls of this dangerous predator failed to elicit mobbing among passerine birds although they responded strongly to a playback of a mobbing chorus. This study provides experimental evidence that intense predation increases the expression of cooperative mobbing in passerine birds.

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Typically, once a predator has been detected, prey move away while emitting alarm signals. When hearing alarm calls, animals either flee to hide or remain motionless. More surprisingly, in some situations, prey do not flee but mob predators. Mobbing is defined as movements of prey towards the predator involving both attacks with stereotyped behaviours and easily localizable calls that quickly draw a crowd of both conspecific and heterospecific prey against the predator (Curio, 1978; Hartley, 1950; Hurd, 1996; Randler & Vollmer, 2013). The principal benefit of mobbing is to cooperatively chase the predator away ('move-on hypothesis', Curio, 1978; Pettifor, 1990; Flasskamp, 1994; Pavey & Smyth, 1998) although such strategy is not without risk (Curio & Regelman, 1986; Dugatkin & Godin, 1992; Sordahl, 1990).

Even though mobbing is not uncommon among vertebrates, how predation risk drives the expression of this behaviour is still poorly understood. Most studies have suggested that animals adjust the strength of their mobbing behaviour according to the perceived risk associated with either predator dangerousness or local predation pressure (Graw & Manser, 2007; Kaplan, Johnson,

Koboroff, & Rogers, 2009; Kobayashi, 1987; Koboroff, 2004; Koboroff, Kaplan, & Rogers, 2013). Predator dangerousness, i.e. the rate at which predators kill prey, can greatly vary between predator species, while predatory pressure mostly depends on the abundance of a local predator species. Although mobbing is thought to correlate positively with predator dangerousness, studies on mobbing have only compared prey responses to predators and nonpredatory species (Kobayashi, 1987; Koboroff, 2004; Lind, Jöngren, Nilsson, Schönberg Alm, & Strandmark, 2005). For example, Lind et al. (2005) has experimentally shown that great tits, *Parus major*, do not mob the European robin, *Erithacus rubecula*, i.e. a nonpredatory species, but approach and mob Eurasian pygmy owls, *Glaucidium passerinum*, a predator that is particularly dangerous for great tits. However, inoffensive species such as the European robin can be easily discriminated acoustically from predatory species. Hence, it is still unclear whether mobbing is specific to dangerous predators or more broadly directed at predatory species whatever their dangerousness. It is thus important to investigate the accuracy of prey discrimination facing predatory species of different dangerousness levels (see for instance Griesser, 2009 working at an intraspecific level on the Siberian jay, *Perisoreus infaustus*). Many studies have emphasized that local predation pressure is an excellent predictor of the strength of mobbing

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responses, with birds exhibiting stronger mobbing responses in locations where predators are common and weaker responses where predators are rare (Sandoval & Wilson, 2012; Tilgar & Moks, 2015). This is in agreement with the study of Reudink, Nocera, and Curry (2007) suggesting that birds mob only predatory species they have previously experienced. Interestingly, studies also indicate that prey respond to mobbing calls even in areas where their natural predator is absent (Johnson, McNaughton, Shelley, & Blumstein, 2004; Randler, 2012) suggesting that the convergent features themselves would facilitate interspecific communication (Marler, 1955, 1957). Nevertheless, it is worth noting that comparing behavioural responses between different localities should be interpreted with caution. For instance, prey communities may vary greatly between localities which can make comparisons irrelevant. This can be particularly problematic if the prey species richness or the relative abundance of the most commonly preyed on species vary according to predator occurrence. Unfortunately, to our knowledge, previous studies did not control for such variations in prey communities between the compared sites.

In this study, we conducted a series of playback experiments to determine whether passerine mobbing behaviour depends on local predation risk. First, we studied birds' responses to two morphologically similar owl species to evaluate whether mobbing is specific to predator dangerousness. We used passerine responses to the Eurasian pygmy owl (hereafter pygmy owl), a predator specialized in passerine birds which constitutes an ideal model species for studying mobbing behaviour (Kellomäki, 1977; Kullberg, 1995; Muller & Riols, 2013; Solheim, 1984; Sotnar, Pacenovsky, & Obuch, 2015). We also used the boreal owl, *Aegolius funereus*, a less dangerous species as indicated by the low prevalence of birds in its diet (Korpimäki, 1986). We predicted that passerines should respond more strongly to the pygmy owl than to the boreal owl. Second, we tested mobbing in two forest patches, one with and one without pygmy owls, in the same mountain range and with identical bird communities, to compare mobbing behaviour with different predation pressures. We predicted that birds would not mob in response to predator vocalizations where the predator was absent, because owl calls are not associated with predation. However, it was important to control for the possibility that the absence of response was due to a loss of mobbing ability; hence, in both forest patches (with or without pygmy owls), we tested whether birds responded to the playback of a mobbing chorus.

METHODS

Site and Species Studied

The study was conducted in mixed deciduous-coniferous forests in the Jura mountains (Ain, France) in two study areas. The first is located near Oyonnax (46°15'N, 5°39'E, mean altitude 850 m) where the Eurasian pygmy owl, a dangerous predator of passerine birds, and the boreal owl, a less dangerous predator of passerine birds, are both common. The second study area, in which owls are absent, is located 40 km away from the first (45°57'N, 5°20'E, mean altitude 260 m). Four listening sessions were performed at each site to control for owl occurrence using site occupancy models (Appendix 1). While owls were detected in each site of the first area ($N = 20$), none was detected in the second area ($N = 15$), confirming previous information (Lengagne & Bulliffon, 2014) and making the two sampled areas (hereafter referred as area with owls versus area without owls) highly relevant to investigate the influence of owl predation exposure on mobbing. The distance between the different sites was at least 500 m to avoid a responding individual contributing more than once to the analyses. At each of the 35 sites, bird species diversity was surveyed through a 20 min acoustic

census of about 100 m radius around the observer. A census was performed before any experiment (Blondel, Ferry, & Frochot, 1970). In total, 32 passerine species were identified in the area where pygmy owls were present and 22 where pygmy owls were absent. In all cases, we focused on the eight bird species that were most commonly preyed on by pygmy owls (Muller & Riols, 2013): common chaffinch, *Fringilla coelebs*, coal tit, *Periparus ater*, European crested tit, *Lophophanes cristatus*, great tit, blue tit, *Cyanistes caeruleus*, goldcrest, *Regulus regulus*, common firecrest, *Regulus ignicapilla*, and European robin. This passerine community did not vary significantly between the two study areas (see Appendix 2, Fig. A1).

Experimental Design

Data were collected during playback experiments conducted between May and July 2014 (experiment 1) and between September and November 2014 (experiment 2).

Response specificity (experiment 1) was tested in different sites of the area with owls ($N = 20$). For this purpose, we applied a crossover design: at each site, the bird community was offered a broadcast sequence of the following three experimental stimuli, pygmy owl calls, mobbing chorus and boreal owl calls. This study design is particularly convenient for minimizing the error variance resulting from the subject effect (i.e. the bird community present at the site), since the relative effect of stimuli can be assessed within each bird community (Jones & Kenward, 2003). A latency period of 5 min was systematically observed between each experimental test (see test procedure for the complete description) in order to avoid carryover effects (i.e. residual effects of the experimental stimuli tested during the previous period on the next one). The sequence order of the three playback stimuli was also alternated between sites to avoid any bias that could result from the sequence order.

The goal of experiment 2 was to test whether mobbing behaviour of passerine birds varied in relation to predator presence. For this purpose, we selected 15 sites in the area without owls and 15 of the 20 sites in the area with owls that were previously used in experiment 1. Experimental tests were performed as in the first experiment except that the broadcast sequence included only two experimental stimuli: the pygmy owl calls and the mobbing chorus.

Test Procedure

Two observers with binoculars were positioned opposite each other at vantage points at least 10 m from the playback (i.e. focal zone) and collected data for 13 min (duration of a test). During the first 5 min we identified and counted all the birds present in the focal zone close to the loudspeaker; these observed birds were excluded from counts in subsequent analyses. Such observations were rare (2.2% of total observed birds). Then, during the 3 min playback, we quantified the birds' response using the number of species observed within a 10 m radius of the loudspeaker. After the playback, observers waited for 5 min before beginning the next test.

Experimental Stimuli

We broadcast playbacks via an amplified loudspeaker (SMC8060, Beyma) connected to a digital playback device (WAV player). Playbacks were restricted to 0600–1200 hours, which corresponds to a period of high activity in birds. To avoid pseudoreplication, we first tested whether prey response was specific to a particular soundtrack or generalizable to various soundtracks of the same species. For both owl species, we downloaded from online databases of avian sounds (<http://www.xeno-canto.org>) two soundtracks recorded in two populations located on both sides of the species' range in order to encompass the call variation range that a local prey community

could experience. Both the call variability within each soundtrack and the call variation between pairs of soundtracks were controlled a posteriori (results not shown). Results showed that passerine responses (i.e. number of species observed) to pygmy owl calls recorded in Switzerland or Sweden were the same whatever the soundtrack used (permutation test: $t = -1.48$, $N = 12$, $P = 0.20$). In addition, the proportion of species that responded to boreal owl calls recorded in Denmark or France was close to zero ($N = 12$ sites). Hence our results were not due to a particular soundtrack (no pseudoreplication). Although it was easy to ensure that pygmy owl or boreal owl soundtracks had the same 'predator value' for passerines, the mobbing chorus recorded in the field may have differed in ways (intensity, species composition) difficult for a human observer to measure. To avoid this problem, we built a soundtrack corresponding to a mixture of four different bird species. Building an artificial manipulated stimulus ensured that we avoided any pseudoreplication problem and that passerine birds would all be tested with the same threat. We used multispecies bouts of mobbing chorus (common chaffinch, coal tit, European crested tit and great tit) recorded in response to a pygmy owl song with a Fostex FR2LE digital recorder connected to a Sennheiser ME62-K6 microphone.

Statistical Analysis

All analyses were done using the SAS 9.3 software (SAS Institute Inc., Cary, NC, U.S.A.). To investigate the relative effect of predator dangerousness and mobbing chorus (experiment 1), we tested whether the proportion of mobbing species varied within each site according to the experimental stimuli sequentially presented (i.e. pygmy owl call, boreal owl call and mobbing chorus). These analyses were performed using a log linear mixed model (LLMM, Procedure GLIMMIX, SAS Institute Inc.). More specifically, we modelled the proportion of mobbing species using the number of responding species as the dependent variable with a Poisson distribution for the error term specification and the number of bird species inventoried at the experimental location (i.e. site) as the offset covariate. The experimental stimulus was introduced as an explanatory factor in the fixed part of the model. Since our experiment was designed to assess the relative effect of the three stimuli within the bird community located at each site, we treated the site as a random effect. To check for a possible carryover effect, the presentation order of the experimental stimuli (i.e. three modalities: first, second or third) and the sequence order of the three stimuli (i.e. six combination orders) were also included as factors in the fixed part of the model. The significance of each explanatory term was tested using a nonsequential F test and the Kenward–Roger method was used to estimate the degrees of freedom. Nonsignificant terms were then removed to obtain the final model. Proportions of mobbing species were then compared between the experimental stimuli using the contrast method. We used a similar approach to investigate whether the local occurrence of the predator had any effect on the proportion of species responding either to the predator stimuli or to a mobbing chorus. As above, sites were introduced in the model as a random effect. The experimental stimulus (i.e. pygmy owl call versus mobbing chorus), the study area (with versus without predator) and their interactive effect were introduced as explanatory terms in the fixed part of the model.

Ethical Note

Although our playbacks experiments changed the behaviour of the targeted birds, we do not feel that these experiments were stressful. Indeed, birds recovered normal activity and were not present near the loudspeaker 5 min after our experiments. All behavioural observations performed during this study complied with the legal requirements in France and followed the ASAB/ABS

Guidelines for the Use of Animals in Research. The study was approved by the DREAL supervisor and permit no. 69266347 of the Direction des Services Vétérinaires.

RESULTS

Mobbing Response and Predator Dangerousness (experiment 1)

There was no significant carryover effect in bird responses (LLMM: treatment position: $F_{2,35.5} = 0.16$, $P = 0.85$; sequence: $F_{5,21.76} = 0.82$, $P = 0.55$). In addition, there was no variation in mobbing according to the presentation order between pygmy owl and mobbing chorus playbacks ($t = 1.94$, $P = 0.12$). The playback type (call of pygmy owl, call of mobbing chorus and call of boreal owl) had a significant effect on bird responses (LLMM: $F_{2,39.83} = 10.51$, $P = 0.0002$; Fig. 1). Indeed, bird species mobbed the pygmy owl more intensely than the boreal owl ($F_{1,45.6} = 20.92$, $P < 0.0001$). Bird species also responded more to mobbing chorus playback than to boreal owl playback ($F_{1,45.29} = 19.61$, $P < 0.0001$), the latter response being close to zero (0.013). In addition, mobbing did not differ between pygmy owl and mobbing chorus playbacks (proportion of species = 0.229 for pygmy owl, 0.249 for mobbing chorus; $F_{1,34.54} = 0.15$, $P = 0.70$). The average number of bird species detected in the test was 2.30 ± 1.30 (corresponding to 5.1 ± 3.67 individuals) during pygmy owl playback and 2.25 ± 0.97 (corresponding to 4.8 ± 2.88 individuals) during mobbing chorus playback.

Mobbing Response and Predation Pressure (experiment 2)

Bird species response was significantly affected by the interaction between the type of stimulus that was broadcast and the presence of the pygmy owl (LLMM: $F_{1,45.88} = 32.48$, $P < 0.0001$; Fig. 2). Species observed in the area where the pygmy owl was present were 12.8 times more likely to respond to a pygmy owl call than species observed in the area where the pygmy owl was absent (contrast test: $F_{1,55.79} = 32.54$, $P < 0.0001$). However, we found that the proportion of species responding to a mobbing chorus did not differ significantly between the two study areas (contrast test: $F_{1,55.79} = 0.37$, $P = 0.21$).

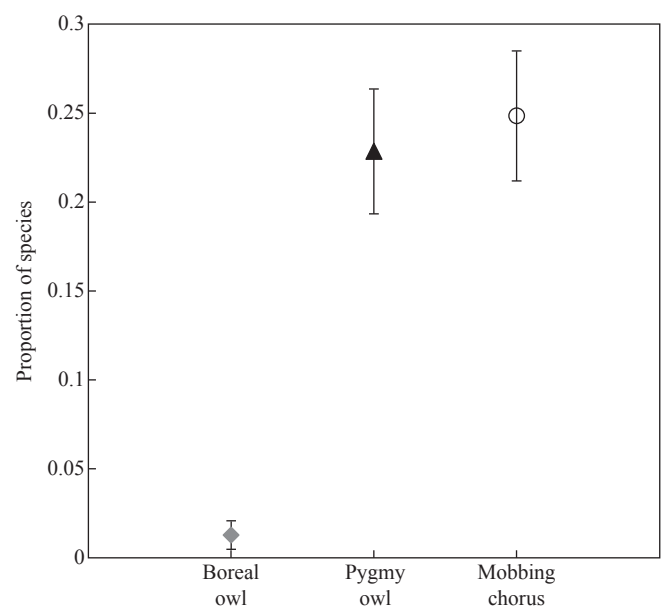


Figure 1. Proportion of species responding to the presentations of a boreal owl (grey diamond), a pygmy owl (black triangle) and mobbing chorus (white circle) calls at sites where owls were present ($N = 20$ sites). Error bars represent SEs.

DISCUSSION

In the present study, we tested the effects of pygmy owl predation on the mobbing behaviour of passerine birds. We showed experimentally that bird responses varied with predation risk (predator dangerousness and presence) and that prey responded to a mobbing chorus even in areas in which these predators were absent.

Several studies have shown that prey respond to predators by adopting behaviours specific to the perceived risk (Graw & Manser, 2007; Kaplan et al., 2009; Kobayashi, 1987; Koboroff, 2004; Koboroff et al., 2013; Lind et al., 2005). However, most of these studies have opposed predator species and inoffensive species such as quails, *Coturnix* sp., tortoises, *Pseudemys scripta*, or parrots, *Platycercus eximius*. In the present study, we have shown that birds responded selectively to the presentation of predator calls according to predator dangerousness: passerine birds mobbed the pygmy owl (i.e. a dangerous predator) but not the boreal owl (i.e. a far less dangerous species). Although we used only two distinct soundtracks per species, it is unlikely that our results are confounded by pseudoreplication because the birds' response did not differ between soundtracks even though these differed substantially. Our results therefore indicate that prey adjusted the strength of their mobbing behaviour according to the perceived risk. The low predatory risk associated with the boreal owl is probably related to its hunting strategy. Indeed, while pygmy owls are diurnal (Cramp, 1985; Mikkola, 1983) and have flexible hunting strategies, boreal owls are nocturnal with a single hunting strategy. Hence, it is not surprising that passerine birds display a differential mobbing response according to owl species. Our results are also congruent with the field study of Morosinotto, Thomson, and Korpimäki (2009) showing that pied flycatchers, *Ficedula hypoleuca*, strongly avoid the territories of pygmy owls but not those of boreal owls for settling. If it is now clear that bird mobbing varies with predator dangerousness, which level of dangerousness is required to elicit mobbing in the prey community remains unclear. In our study, birds did not respond to the boreal owl while the proportion of passerines in the diet of this predator estimated near our study area is about 0.3 (Henrioux, 2014a; versus 0.58 in the pygmy owl diet; Henrioux, 2014b). Although comparisons

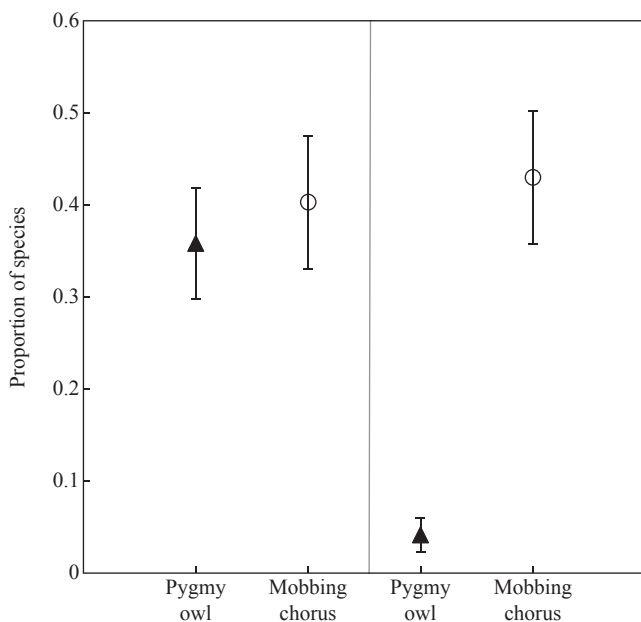


Figure 2. Proportion of species responding to the presentations of a pygmy owl (black triangle) and a mobbing chorus (white circle) calls at sites where the pygmy owl was present (on the left side, $N = 15$ sites) and sites where the pygmy owl was absent (on the right side, $N = 15$ sites). Error bars represent SEs.

between studied models should be interpreted with caution, Kaplan et al. (2009) found that birds mob the monitor lizard, *Varanus varius*, while these birds constitute only 0.14–0.16 of the predator's diet. It therefore seems likely that the threshold value of 'dangerousness' above which mobbing is elicited is relatively low. Similarly, one should also expect some variation in mobbing across the prey community, since the relative risk of predation may vary between prey species. For instance, field studies conducted on commonly preyed on bird species have found a relationship between how often a species mobs predators and how often predators prey upon this species (Courter & Ritchison, 2012; Gehlbach, 1994). Investigating more precisely the correlation between the relative prevalence of a species in a predator's diet and its relative involvement in mobbing could thus be particularly insightful.

Our results also reveal that mobbing varied in relation to the local presence of the predator. In the locations where the pygmy owl was absent, calls of this dangerous predator failed to elicit mobbing among passerine birds. This result is in agreement with Reudink et al. (2007). In their study, tropical birds living in environments devoid of predators often expressed inappropriate antipredator behaviours. Moreover, recent studies have experimentally shown that local predation pressure can predict the strength of mobbing responses in birds: individuals exhibit a stronger mobbing response when local predation pressure is high (Krams et al., 2010; Sandoval & Wilson, 2012; Tilgar & Moks, 2015). However, these authors did not take into account the number of species present before tests began. We did this in our study, so were able to control for available prey and predators. The predatory response where the pygmy owl is a common predator is linked either to a selection process (local adaptation) or to a learning process. In the first case, only one recent study, in Alpine swifts, *Apus melba*, has shown that antipredator behaviour is heritable (Bize, Diaz, & Lindström, 2012). In many situations, it is most probable that offspring may learn to adjust their behaviour and to express a mobbing response by observing their conspecifics' mobbing behaviour (Curio, 1978; Francis, Hailman, & Woolfenden, 1989; Graw & Manser, 2007). For example, in an experimental study, Campbell and Snowdon (2009) showed that captive-reared cottontop tamarins, *Saguinus oedipus*, do not innately recognize predators and a demonstrator seems to be necessary to acquire predator recognition. Hence, the fine-tuning of this behaviour probably depends on experience. In our case, we cannot determine whether bird mobbing behaviour observed in areas with pygmy owls results from an innate or a learned process. Experiments involving passerine eggs transferred from areas where pygmy owls are present to areas without owls would answer this question.

As predicted, prey responded to a mobbing chorus whether or not pygmy owls were present in the area, a result that is in agreement with previous studies on other predators known to elicit mobbing (Johnson et al., 2004; Randler, 2012). The most likely explanation for the similar response to a mobbing chorus regardless of whether the studied predator species is present is that numerous predator species are known to elicit mobbing behaviour (Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Curio, Klump, & Regelmann, 1983). Thus, in a multipredator environment, mobbing behaviours could be maintained even in the absence of a specific predator species. This is probably particularly true for avian prey given the ubiquity of opportunist nest predators. These predators can be expected to favour mobbing since they do not usually represent an immediate danger for the adults but are particularly dangerous for offspring. More surprisingly, our results have also shown that the strength of passerine response to a mobbing chorus was not significantly higher than that to the pygmy owl calls in the area where this predator was present. Indeed, a previous study has reported that the mobbing calls elicited a stronger response than that elicited by a specific dangerous predator, suggesting that mobbing calls give information not only on the

presence of the predator, but also on the response of other prey species perceiving the situation as threatening (Sandoval & Wilson, 2012). Previous studies have also suggested that mobbing calls contain information about the degree of threat that a predator represents (Billings, Greene, & Lucia Jensen, 2015; Graw & Manser, 2007; Griesser, 2009; Koberoff et al., 2013; Naguib et al., 1999; Suzuki, 2014; Templeton, Greene, & Davis, 2005). The difference in the method used to infer the strength of the response may well explain why our results differ from those reported in previous studies (Sandoval & Wilson, 2012). In particular, our measure of mobbing response is probably more conservative than that used by Sandoval and Wilson (2012), since we did not use the number of individuals attracted by the mobbing call but the proportion of responding species among species present at the experimental location.

Mixed-species avian mobbing is a widely recognized phenomenon. Mobbing calls can communicate the presence of a predator to heterospecifics as well as conspecifics (Forsman & Mönkkönen, 2001; Hetrick & Sieving, 2012; Hurd, 1996; Marler, 1957; Randler & Vollmer, 2013; Randler & Förchler, 2011; Sandoval & Wilson, 2012; Templeton & Greene, 2007; Zimmermann & Curio, 1988). Indeed, our soundtrack of the mobbing chorus with four species elicited a response not only from these four species but also from all the other species strongly preyed by the pygmy owl. In our study, the proportion of conspecific species (i.e. four species of the mobbing chorus playback) that responded to the mobbing choruses was 0.697 whereas the proportion of heterospecific species (i.e. four species not included in the mobbing chorus playback) was 0.375. However, responses to mobbing choruses vary greatly between heterospecific passerine species. For example, in our experiments, the goldcrest responded in 20 of 24 tests where it was present whereas the European robin responded in only two of 32 tests where it was present. Hence, we emphasize heterospecific communication and our results suggest that responses are asymmetrical across species. In future experiments we will investigate the underlying processes of the response to mobbing calls.

In conclusion, we have shown that passerines responded to a mobbing chorus regardless of the presence of dangerous predators in the area, suggesting that it is a conserved trait. In this case, the removal of one predator should have limited effect on the persistence of the antipredator strategy because predation pressure is usually not due to a single species. On the other hand, the absence of passerine response to owls in the area where these predators were absent suggests that mobbing behaviour against owls is an experience-dependent and highly flexible trait. Future studies should explore the costs and benefits of mobbing at species level to assess to what extent this trait is flexible.

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APPENDIX 1. SITE OCCUPANCY MODEL (EURASIAN PYGMY OWL)

Model selection was based on Akaike's information criterion (AIC). The model including study area as covariate was considered best ($\Delta AIC = 29.26$) and showed that the occurrence of pygmy owls was 1 in areas where the pygmy owl was present and 0 in areas where the pygmy owl was absent.

APPENDIX 2. SPECIES RICHNESS IN AREAS WITH OR WITHOUT OWL

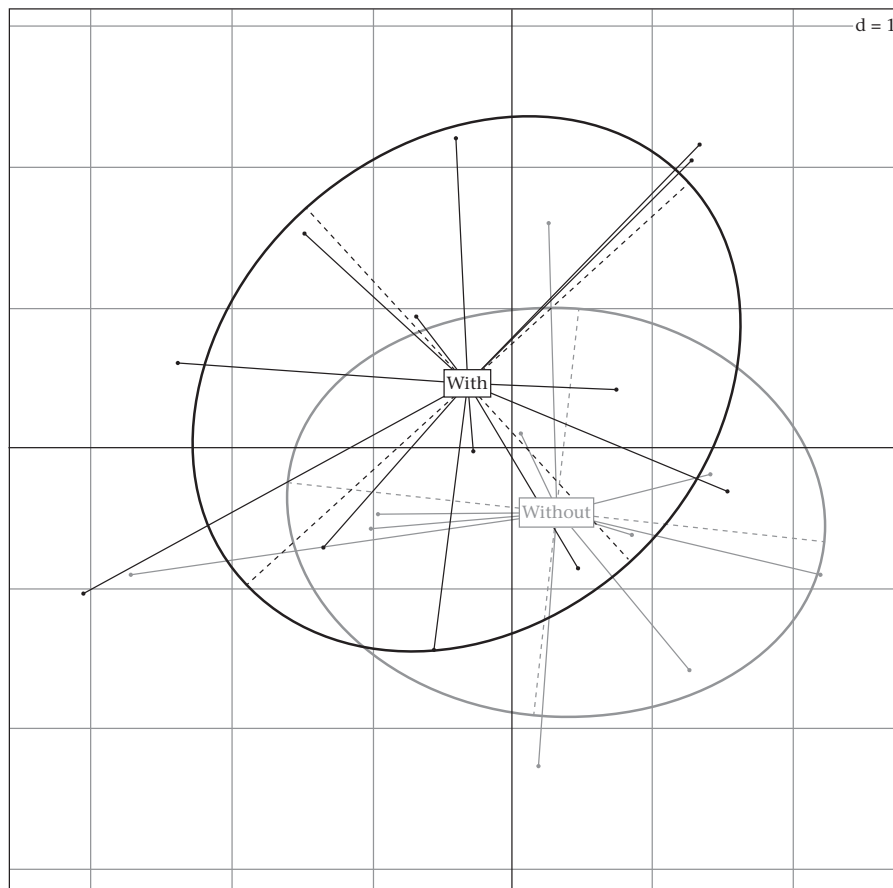


Figure A1. Schematic representation of factor correspondence analysis (FCA) of the bird species most frequently killed by Eurasian pygmy owls in areas with (black) and without (grey) owls (FCA1: 25.27%; FCA2: 21.45%).