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ARTICLE

Large-scale spatial pattern of bird responses to a potential predator suggests that predator-specific mobbing is a plastic trait

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Abstract

Mobbing is a prey antipredator behaviour aimed to reduce the risk of predation. The behaviour may be innate and/or learned. Evaluating this behaviour on a large spatial scale can help to explore the mechanisms behind it. Using a playback experiment, I investigated variation in antipredator behaviour in small passerines in response to vocalisation from a potential predator, Eurasian pygmy owl (*Glaucidium passerinum*), at 105 sites in 35 localities within and outside the owl's breeding range. While the birds outside the owl's breeding range did not respond to the owl's call, they mobbed at about 60% of the sites within the owl's breeding range. At sites where the birds did not respond to the owl presentation, alarm calls of forest passerines were broadcasted to them. The birds always mobbed in response to the playback of these alarm calls. These results indicate that the birds' response to the owl call may be a plastic trait induced by learning, while the response to the alarm calls of birds may be innate, as predation pressure in general can be strong enough to cause directional selection on the prey's response to the alarm signalling of other birds.

Keywords Antipredator behaviour · Eurasian pygmy owl · Mobbing behaviour · Passerine birds · Playback

Introduction

Predation is one of the most important evolutionary forces, selecting for several morphological and behavioural adaptations in prey animals (Lima and Dill 1990), such as coloration (Murali 2018), building cryptic nests (Prokop and Trnka 2011), habitat selection (Stratmann and Taborsky 2014), death feigning (Li and Wen 2022) or mobbing a predator. In birds, mobbing is a behaviour in which a potential prey animal approaches a potential predator, usually an apparently non-hunting predator, by performing stereotyped movements—flicks with wings and tail and diving towards the predator—while emitting repeated and loud alarm calls, recruiting the majority of local conspecific and heterospecific prey around the predator, with the aim chasing the predator away (Hartley 1950; Altmann 1956; Curio 1978; Griffin 2004; Krams et al. 2007; Dutour et al. 2016; da Cunha et al. 2017).

Pattern of association between mobbing behaviour and predation risk is still not well understood, although mobbing is common in vertebrates (Kobayashi 1994; Dutour et al. 2016, 2017a; Pitman et al. 2017). Some bird studies suggest that predator recognition is innate (Veen et al. 2000; Göth 2001; Wiebe 2004; Sandoval and Wilson 2022), others have emphasised the importance of a non-genetic pre-hatching maternal background (Bize et al. 2012) and/or learning—through direct experience or social—behavioural copying (Lima 2009; Keen et al. 2020; Szymkowiak 2021). Similar patterns have been observed in other wild vertebrates or invertebrates (e.g. Åbjörnsson et al. 2004; Scheurer et al. 2007; Storm and Lima 2010; Coslovsky and Richner 2011; Stratmann and Taborsky 2014; Arnaud et al. 2017). Mobbing was found to be positively associated with predator dangerousness (proportion of prey in the predator's diet) or predation pressure (local abundance of a predator) (Sandoval and Wilson 2012; Tilgar and Moks 2015; Dutour et al. 2016, 2017b; Kalb and Randler 2019). However, Dutour et al. (2016) had noted that prey community composition can vary considerably spatially depending on the occurrence of prey predators; therefore, comparing behavioural responses between different localities can be irrelevant and should be interpreted with caution. Therefore, they compared identical

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bird communities in similar habitats and observed that mobbing varied depending on the local presence of the predator, the Eurasian pygmy owl (*Glaucidium passerinum*). They found that passerine birds mobbed where the predator was common, suggesting an innate or learned background to the behaviour; and that birds did not mob in response to the call of the pygmy owl in localities where this dangerous predator was not present, suggesting an experience-dependent origin of the mobbing behaviour and a high flexibility of the mobbing behaviour (Dutour et al. 2016). They conducted the study on a small spatial scale—within two study areas—in 20 sites with detected presence of the pygmy owl and in 15 sites without detected presence of pygmy owl, respectively (Dutour et al. 2016).

In the present study, I assessed a response of passerine birds to acoustic signal (territorial call) from their potential predator, Eurasian Pygmy owl, within and outside the predator's breeding range at a large spatial scale. Therefore, I conducted playback experiments at 105 sites in 35 localities in an area of 100 × 250 km (minimum convex polygon of 19,500 km^2) in the Western Carpathians, Slovakia, Central Europe. As the density of the Pygmy Owl is not homogeneous in its breeding range (Pačenovský and Šotnár 2010; Barbaro et al. 2016; Šotnár et al. 2020; Ševčík et al. 2021), I had expected that the relationship between the presence of predators (outside or within the predator's breeding range) and prey response should be weaker than in the small-scale study by Dutour et al. (2016), in which the pygmy owl had been present at all sites studied within the pygmy owl area. Studying the response of prey to predation pressure at a larger spatial scale may shed more light on the mechanisms underlying mobbing behaviour.

Material and methods

Study area, localities and sites

I conducted the study in deciduous, mixed deciduous-coniferous and coniferous forests in the Western Carpathians and the Pannonian Basin in Slovakia in 35 localities, 3 sites per locality (Fig. 1, Table S1). I tested the mobbing behaviour of passerine birds at three sites in each locality. The minimum distance between localities was at least 5 km and between sites at one locality was at least 0.5 km, so I consider my observations to be independent of each other (see Dutour et al. 2016, 2017a; Kalb and Randler 2019). At the studied sites, the elevation ranged from 100 to 1440 m a.s.l, the age of forests stands ranged from 15 to 230 years and proportion of coniferous trees ranged from 0 to 100% (Table S1).

Experimental design

I conducted the behavioural experiment during the non-breeding season between September 2021 and February 2022, with most of tests were conducted in December 2021 and January 2022.

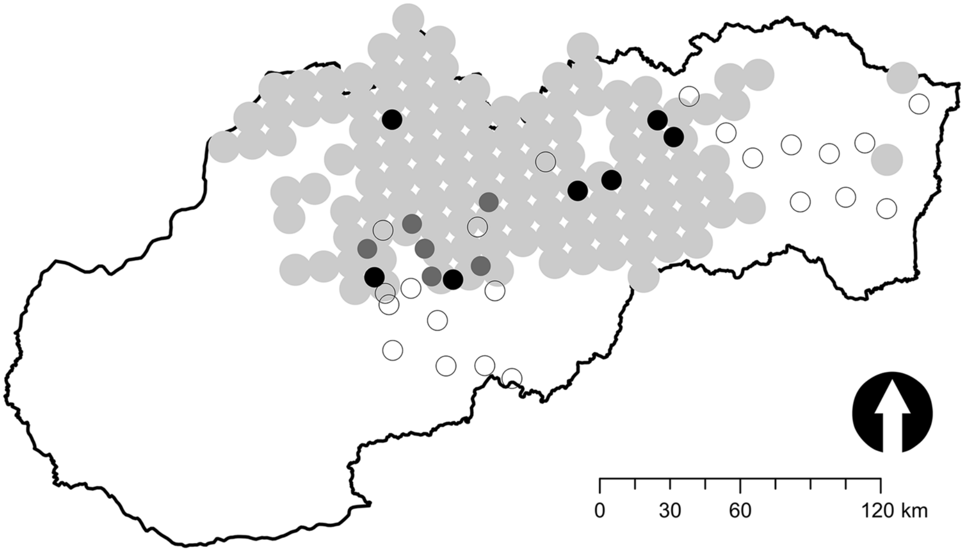

Fig. 1 Map of the breeding range of the Eurasian pygmy owl and surveyed localities in Slovakia, Central Europe. Mapping squares with confirmed breeding from Pačenovský (2002) are shown as light grey circles. In each locality, the call of the pygmy owl was broadcast at three sites to investigate the response of small forest passerine birds, which are potential prey of this predator. The localities studied where the birds did not respond to the pygmy owl's call are shown as smaller empty circles, the localities where the birds responded by mobbing are shown as black circles and the localities with mixed response (i.e. localities with sites where both mobbing and no bird response was detected) are marked as dark grey circles

As the aim of the present study was to assess the response of passerine birds to acoustic signal from their potential predator within and outside the predator breeding range, I randomly selected 17 localities within the pygmy owl breeding range in Slovakia and 18 localities outside the breeding range of this species. To define the breeding range of the pygmy owl in Slovakia (Fig. 1), I used confirmed breeding in mapping squares (each square has a size of 12.0 × 11.1 km) published in the last atlas of birds' distribution in Slovakia (Pačenovský 2002), as recommended by Moudrý et al. (2017). I consider these data to be reliable, as the population trend of the pygmy owl in Slovakia is considered stable both in the short term (2007–2018) and in the long term (1980–2018); the range of the species is estimated to be about 17,500 km^2 with 1300–2000 breeding pairs in the country (Černecký et al. 2020).

As an acoustic signal, I broadcasted a soundtrack merged from calls of three different individuals of the pygmy owl downloaded from the online database of bird sounds Xeno Canto (www.xeno-canto.org; XC124610, XC399248 and XC505342). The length of the soundtrack was 3:19 min; calling rate = 0.50 calls/s. It has been shown that passerine response to the pygmy owl soundtracks was the same regardless of the soundtrack used (see Dutour et al. 2016). To control for the possibility that the absence of response was due to a loss of mobbing ability, I tested whether birds responded to the playback of alarm calls. As the control, I used a soundtrack (length 2:48 min) built as a mixture of (partially) overlapping alarm calls from five bird species (*Parus major*, XC409935, calling rate = 0.54 calls/sec.; *Periparus ater*, XC297792, 2.50 elements/s; *Poecille palustris*, XC624079, 0.37 calls/s; *Lophophanes cristatus*, XC245848, 1.73 calls/s; and *Cyanistes caeruleus*, XC448480, 0.50 calls/s). I used these species because at least two to three of them can be found at each site in the studied area. The alarm calls used can be classified as mobbing alarm calls or alert alarm calls (according to Magrath et al. 2015a), alarm calls hereafter. The soundtracks were merged or mixed using the freeware Audacity 2.4.2 (Audacity Team 2018).

Playback experiment was performed during calm weather without rain or snow from sunrise to sunset. I used a Lamax Sounder2 portable Bluetooth loudspeaker (Lamax, Czech Republic). The sound tracks were broadcast at a volume of about 80 dB (measured at 1 m from the speaker using the smartphone app Sound Meter before fieldwork), which corresponds to the natural calls of the pygmy owl (Dutour et al. 2017b) and the natural volume of alarm calls of the great tit (Templeton et al. 2016). During the quiet walk in the field, I visually and acoustically checked for the presence of small passerine birds—Paridae, *Regulus regulus*, *Certhia familiaris*, *Sitta europaea*, *Aegithalos caudatus*, the most common potential prey species of the pygmy owl in the study area (Šotnár et al. 2015)—within a radius of about 30–40 m. When at least one individual of the focal species was detected, I stopped walking and started broadcasting experimental stimulus—the pygmy owl calls' soundtrack—while observing the response of the individual(s) of the detected bird species to this stimulus. I considered a response to be positive (i.e. mobbing) if the individual(s) approached towards me within a 10 m radius while the pygmy owl soundtrack was playing, performing typical stereotypic movements (flapping wings and tails) or making alarm/mobbing calls. If no such response was detected during broadcasting the pygmy owl soundtrack, I started broadcasting of the control soundtrack of the passerines alarm call mixture after a short (one-minute) pause. I counted all the birds that approached me during broadcasting the pygmy owl or alarm calls. Still and quit I keep the loudspeaker during the broadcast of the soundtracks. I observed no obvious signs that my presence disturbed the birds' behaviour before the playback emission.

At two localities (one within the predator breeding range, another outside the breeding range), the experiment was repeated several times during the non-breeding season (locality in the predator breeding range = three visits, locality outside the breeding range = five visits).

Explanatory variables

Besides (i) location of the site in relation to the breeding range of the pygmy owl (categorical—binary variable: within or outside; "location within/outside the breeding range" hereafter) and (ii) occurrence of the pygmy owl in the site's mapping square surroundings ("pygmy owl in the surrounding landscape" hereafter), expressed as the number of neighbouring mapping squares with confirmed breeding of the pygmy owl (continuous variable, range 0–8, where "0" means, that the square is outside the pygmy owl breeding range, "8" means that the square is within the breeding range), I assessed other environmental variables that could influence the presence of the predator and thus the response of passerines to the predator vocalisation: (iii) site elevation (m a.s.l.) was determined from a topographic map. (iv) Stand age (years) and (v) proportion of coniferous trees (%) of sites in managed forests were determined for the respective forest management units and taken from forest management plans (https://gis.nlcsk.org/islhp/mapa); these variables were estimated for woody vegetation on non-forest sites (e.g. successional forest on former pastures, riparian woody vegetation). I used these variables as explanatory factors, as it is known that pygmy owl occupies higher elevations and prefers forests with a higher proportion of conifers (Barbaro et al. 2016; Šotnár et al. 2020; Ševčík et al. 2021). Stand age may be positively correlated with the proportion of tree cavities and habitat quality (Barbaro et al. 2016; Baroni et al. 2020).

Data analysis

All statistical analyses were performed using the statistical software R 3.6.3 (R Development Core Team 2020), implemented in the RStudio 1.2.1335 (RStudio Team 2019) environment. Statistical significance was set at $p = 0.05$ for all tests.

First, I examined the differences between the continuous variables at each level of the categorical explanatory variable, i.e. breeding range, using the Kruskal–Wallis rank sum test. I then calculated the Spearman rank correlation (r_s) between pairs of continuous variables to assess the collinearity between these variables.

Preliminary analyses indicated the presence of quasi-complete separation in my data (i.e. no mobbing response outside the pygmy owl breeding range), so I used a Bayesian form of logistic regression (Gelman et al. 2008; Mansournia et al. 2018) (i.e. Bayesian generalised linear model with the binomial family and logit link function) to assess the response of passerine species to acoustic signal from their potential predator. This model does not allow random effect terms to be included in the model, so locality was not used as a random effect in the analyses. The binary input variables were converted to 0/1 format to have a mean of 0 and differ by 1 in their lower and upper conditions. The non-binary input variables were standardised to have a mean of 0 and a standard deviation of 0.5 to ensure a commonly-interpretable scale (Gelman et al. 2008). In addition, Student-t-family prior distributions—the Cauchy prior distribution with centre 0 and scale 2.5—were placed on the coefficients (Gelman et al. 2008). To determine which variable(s) were stronger predictors of birds mobbing behaviour, I created several a priori models from the variables assessed—null model, main effect models with single and two explanatory variables. Continuous variables with $|r_s| \geq 0.60$ were not used together in a model to minimise collinearity (Dormann et al. 2013). Furthermore, as a statistically significant difference was found in all continuous variables for the two levels of breeding range, the site location in relation to pygmy owl breeding range was only used in the simple regression. A total of nine models were analysed and ranked using the calculated values of the Akaike information criterion corrected for small sample size (AICc), Akaike weights and Bayesian information criterion (BIC). For these analyses, I used the function "bayesglm" from the package arm 1.13.1 (Gelman and Su 2022), the functions "AICC" and "Weights" from the package MuMIn 1.43.6 (Bartoń 2019) and the function "BIC" from the package flexmix 2.3–18 (Gruen and Leisch 2008). The association between breeding range and bird response was also tested by the χ^2-independence test—a maximum statistic of Pearson residuals (function "mosaic", implemented in package vcd 1.4–10 (Meyer et al. 2022)).

To link the assemblage composition of mobbing birds to explanatory variables, I additionally performed Distance-based redundancy analysis (dbRDA) and a partial dbRDA performed in the R package vegan 2.5–5 (Oksanen et al. 2019) using the functions "capscale", "anova.cca" and "RsquareAdj". The Bray–Curtis dissimilarity index was used as a response variable representing bird species composition. Species were not scaled (standardised) as this could give too much weight on rare species in the analysis. As independent variables, I used all the explanatory variables mentioned above together with the mobbing response to the pygmy owl. First, I ran several dbRDAs to model association of (i) birds' mobbing response to the pygmy owl call, (ii) site location within or outside the pygmy owl breeding range + number of neighbouring mapping squares, (iii) elevation + stand age + proportion of conifers, and (iv) all these explanatory variables on mobbing bird species abundance. I then ran multiple partial dbRDAs to model the pure effect of variable groups (i–iii) while controlling for other/remaining explanatory variables. The permutation test with 999 unrestricted permutations was used to test the significance of the explanatory variables.

The R packages GGally 2.0.0 (Schloerke et al. 2020), ggpubr 0.2.1 (Kassambara 2019), vcd, tidyverse 1.2.1 (Wickham 2017), ggrepel 0.8.1 (Slowikowski 2019), dplyr 0.8.1 (Wickham et al. 2019) and ggplot2 3.3.2 (Wickham 2016) were used to plot the results of the analyses, and ArcGis 10.4 software (Esri, USA) was used to produce a map of the study area.

Results

Characteristics of the study sites

The studied sites within and outside the pygmy owl breeding range differed significantly in all explanatory variables assessed: presence of the breeding pygmy owl in the surrounding landscape, expressed by the number of mapping squares with confirmed breeding, was higher in the breeding area ($\chi^2 = 70.476$, $p < 0.001$), the same pattern held for elevation ($\chi^2 = 57.725$, $p < 0.001$), proportion of conifers ($\chi^2 = 55.998$, $p < 0.001$) and forest age ($\chi^2 = 5.970$, $p < 0.001$), although the age difference was small (Fig. S1). Consequently, the correlation between elevation, the proportion of conifers and presence of the pygmy owl in the surrounding landscape ranged from 0.68 to 0.71; the strength of the correlation between forest age and these variables ranged from 0.13 to 0.33 (Fig. S2).

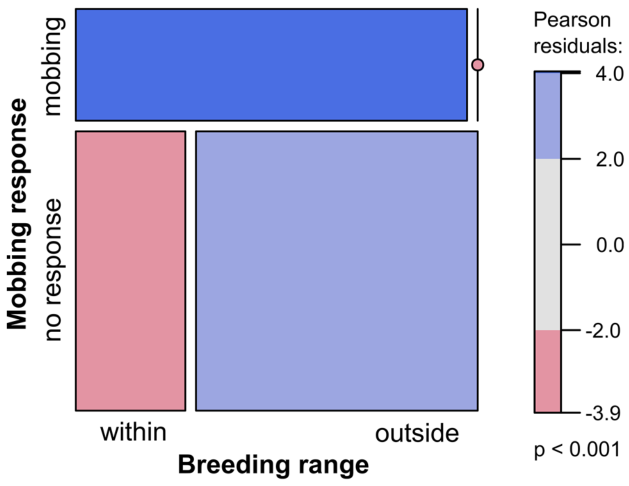

Fig. 2 Mosaic plot of the association between the mobbing behaviour of small passerine birds in response to the call of their potential predator, Eurasian pygmy owl, at sites within or outside the breeding range of the predator in Slovakia. Pearson χ^2 independence test: $\chi^2 = 41.635$, $p < 0.001$. (Coloured figure online.)

Response of the birds

I observed no response of birds to the pygmy owl call outside the pygmy owl breeding range. Within its breeding range, birds mobbed in response to the pygmy owl call at 30 of 51 sites (Fig. 2). At the locality level, in the breeding range, birds mobbed at all sites per locality in 7 localities, did not mob at all sites in each of 4 localities and their response was mixed in 6 localities. At all sites where birds did not respond to the pygmy owl call, they mobbed in response to the broadcasting of other birds alarm calls.

The importance of site location within/outside pygmy owl breeding range on bird response to the pygmy owl call was also confirmed by logistic regression. The best-fitting model (AICc = 73.8) included site location only. Other models had a ΔAICc ≥ 12.64 indicating relatively weak support (Table 1).

At the two localities—one within the predator breeding range, another outside the breeding range—where the experiment was repeated several times, bird responses were the same at both localities for all visits: at the locality within the pygmy owl's breeding range, birds mobbed in response to the pygmy owl, whereas at locality outside the pygmy owl's

Table 1 Results of a priori models analysed with logistic regression analysis with the Akaike's information criterion model ranking corrected for small sample size (AICc) and Bayesian inference (BIC) to assess mobbing behaviour small passerine birds in response to vocal cue of their potential predator, the Eurasian pygmy owl, in Slovakia

Model	AICc	ΔAICc	BIC	ΔBIC	w_i	Variables	β	SE	z	Pr(>|z|)	Odds ratio
Breeding range	73.8	0.00	79.0	0.00	0.08	Intercept	−0.3361	0.2835	−1.186	0.236	0.715
						Breeding range (outside)	5.5067	1.6865	3.265	0.001	246.347
Elevation	86.5	12.64	91.7	12.64	0.00	Intercept	4.3601	0.7765	5.615	< 0.001	78.267
						Elevation	−0.0051	0.0010	−5.137	< 0.001	0.995
Forest age and elevation	88.3	14.50	96.1	17.03	0.00	Intercept	4.1096	0.9449	4.349	< 0.001	60.925
						Forest stand age	0.0031	0.0070	0.449	0.654	1.003
						Elevation	−0.0052	0.0010	−5.139	< 0.001	0.995
# squares	95.7	21.89	100.9	21.89	0.00	Intercept	2.9514	0.5502	5.364	< 0.001	19.133
						Occupied squares	−0.4720	0.0965	−4.891	< 0.001	0.624
Forest age and # squares	97.8	23.99	105.6	26.53	0.00	Intercept	2.8867	0.8130	3.551	< 0.001	17.935
						Forest stand age	0.0007	0.0069	0.108	0.914	1.001
						Occupied squares	−0.4742	0.0984	−4.819	< 0.001	0.622
Conifers	105.3	31.49	110.5	31.49	0.00	Intercept	2.2602	0.4276	5.286	< 0.001	9.585
						Conifers	−0.0284	0.0064	−4.443	< 0.001	0.972
Age and conifers	106.6	32.76	114.3	35.30	0.00	Intercept	2.7793	0.7394	3.759	< 0.001	16.109
						Forest stand age	−0.0055	0.0061	−0.903	0.367	0.995
						Conifers	−0.0282	0.0064	−4.407	< 0.001	0.972
Null	127.7	53.84	130.3	51.26	0.00	Intercept	0.9154	0.2159	4.240	< 0.001	2.498
Forest age	128.4	54.57	133.6	54.57	0.00	Intercept	1.4821	0.5561	2.665	0.008	4.402
						Forest stand age	−0.0058	0.0052	−1.128	0.259	0.994

w_i, model weight, β, standardised coefficient estimate, SE, standard error. Variables: Breeding range = Site location in relation to the pygmy owl breeding range (within/outside the breeding range). Occupied squares = presence of the pygmy owl breeding in surrounding landscape around the site's square (number of mapping squares with confirmed breeding of the owl). Elevation = site elevation (m a.s.l.). Forest age = age of forest stand (years). Coniferous = proportion of coniferous trees (%)

breeding range, the opposite was true: here, birds mobbed in response to the birds' alarm calls.

Mobbing bird assemblages

A total of 12 species and 602 individuals were quantified as mobbed in the surveyed sites in response to either the pygmy owl call or bird alarm calls. The most common species (> 80 individuals) were *Parus major*, *Regulus regulus* and *Periparus ater* (Table S1). All independent variables together explained 19% of the composition of the mobbing bird assemblages (Table S2, Fig. 3). Partial distance-based redundancy analyses showed that most of this explained variation was shared between all independent variables. While mobbing response to pygmy owl call was the only independent variable in dbRDA explaining 10% of the assemblage composition, partial dbRDA showed no unique contribution of this variable to mobbing bird composition. On the other hand, site location within/outside the pygmy owl breeding range alone explained 3% of the mobbing species composition (Table S2).

Discussion

In this large spatial scale study, I investigated the behavioural response of passerine birds towards presence of their potential predator, the Eurasian pygmy owl. By broadcasting the pygmy owl call, I was able to show that the birds' responses depended on the expected presence of the predator: While the birds did not respond at all to the vocal signal outside the breeding range of the pygmy owl, they displayed mobbing behaviour at about 75% of localities/at about 60% of the sites within the breeding range. I also observed that if the birds did not respond to the pygmy owl call, they mobbed in response to broadcasted alarm calls of passerines.

The results of my study showed a similar pattern to the study that examined the strength of mobbing behaviour in small passerine birds as a function of perceived risk associated with local predation pressure of the pygmy owl, but at a smaller spatial scale (Dutour et al. 2016): the authors also observed the absence of mobbing in response to the pygmy owl in an area without the predator. In contrast, the proportion of bird species responding to the pygmy owl's call was higher in an area where the owl was locally present than in an area without the pygmy owl. The authors conclude that mobbing against the pygmy owl in the area with the owl present may be an innate or learned behaviour, and that the lack of a response by birds in the area with absent owl suggests that the response against the predator is experience-dependent and that mobbing is thus a flexible behavioural trait (Dutour et al. 2016). However, the behavioural pattern of birds in response to the pygmy owl presentation within and outside its breeding range can be explained by both genetic underpinning—which may reflect a degree of local adaptation—and phenotypic plasticity. Local adaptation is promoted by greater heterogeneity in selection (i.e. greater environmental heterogeneity), larger population sizes and lower migration rates (e.g. Blondel et al. 2006; Blanquart et al. 2012). For non-migratory small forest passerines, there are differences in dispersal between sexes, between adults and juveniles, and in intra-annual dispersal distance (i.e.

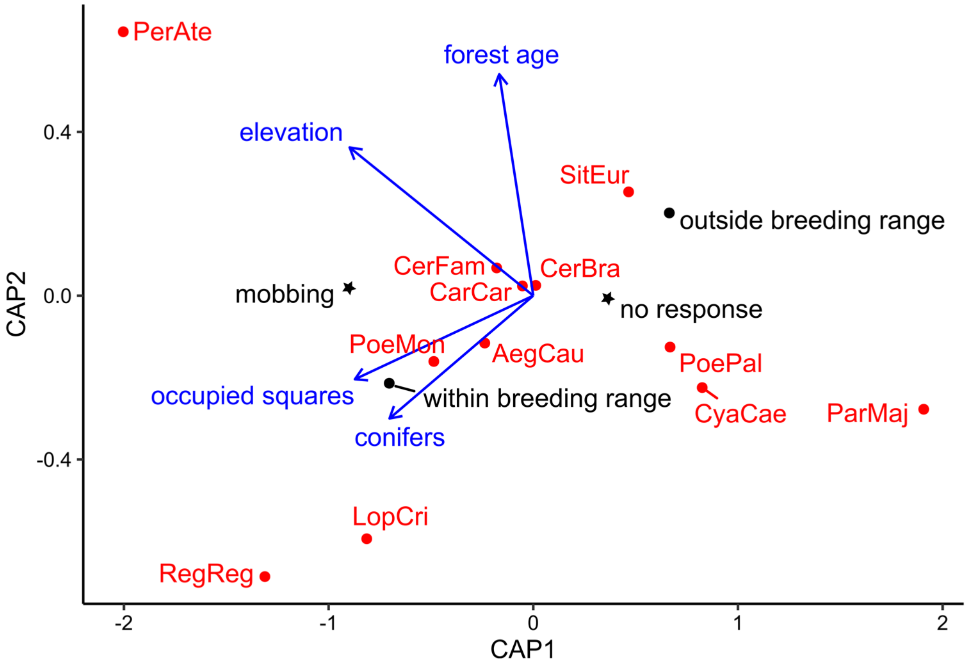

Fig. 3 Distance-based redundancy analysis (dbRDA) of the association between assemblages of small forest passerine birds mobbed in response to broadcasted call of the Eurasian pygmy owl ("mobbing") or in response to alarm calls of a small forest passerines ("no response"). For other variables, see Table 1. All independent variables explained 19% of the assemblages composition ($p = 0.001$; see Table S2). The scale represents the Bray–Curtis dissimilarities. Species abbreviations are composed of the first three letters of the scientific genus and species name (see header of Table S1 for species list). Note that the scale of the axes is different. (Coloured illustration online.)

territory fidelity) between species. Interspecifically, females can disperse greater distances than males (Verhulst et al. 1997; Andreu and Barba 2006; Wesołowski 2015), and natal dispersal distances are greater than breeding distances: in marsh tit, *Poecile palustris*), for example, natal dispersal distances were longer than breeding dispersal distances —hundreds of metres compared to a few tens of metres (Broughton et al. 2010; Wesołowski 2015); in great tit, *Parus major*, 95% nonphilopatric yearling individuals dispersed > 2 km (Verhulst et al. 1997), and in great tit, post-fledging movement accounted for much of the variation in natal dispersal distance (86% and 95% of average of natal dispersal distance for females and males, respectively) (Dingemanse et al. 2003). Great tits (Andreu and Barba 2006) and blue tits, *Cyanistes caeruleus* (Valcu and Kempenaers 2008), were also found to have a short dispersal distance during the breeding season. During the non-breeding season, great tits, blue tits and other non-migratory small passerine birds form mixed-species fission–fusion flocks (Ekman 1989; Silk et al. 2014). The patterns of these seasonal flocking movement resemble a partial migration between breeding and overwintering areas as these flocks can travel straight-line distances of more than 3 km (Matechou et al. 2015), although food supply or weather conditions may influence site fidelity during winter (Krištín and Kaňuch 2017; Pakanen et al. 2018). On the other hand, willow tit pairs stay in their territory all year round and remain mated across years (Hogstad 2015). In general, the mean dispersal range of small forest passerines such as tits is thought to be about 1 to 2 km from their natal site (Blondel et al. 2006); e.g. most tit species ringed in the Czech Republic and Slovakia were recovered within 10 km of the ringing site (within 1 km: 83–95%, within 1–10 km: 3–9%), with the longest distances recorded ranging from 8 km (willow tit) to 2295 km (great tit) (Cepák et al. 2008).

The pygmy owl prefers coniferous or mixed forests and avoids pure broadleaved stands at the landscape level; at smaller spatial scales, it is more likely to occur in older stands, with a positive correlation with the amount of dead or decaying standing trees (Strøm and Sonerud 2001; Shurulinkov et al. 2007; Barbaro et al. 2016; Šotnár et al. 2020; Ševčík et al. 2021). The distribution of habitats with features preferred by the pygmy owl is not uniform within the landscape, mainly due to forest management. Median home range size of adult pygmy owl covered 2.3 km^2 and ranged from 0.4 to 6.0 km^2 in Norway (Strøm and Sonerud 2001); the mean home range size of breeding adult male of the pygmy owl covered 0.67 km^2 and ranged from 0.46 to 0.98 km^2 in old-growth forests in the French Pre-Alps (Barbaro et al. 2016).

Thus, given the uneven distribution of the pygmy owl in its breeding range, the size of the owl's range, and small passerines' dispersal range which used to be larger than the owl range size, a uniform response to the pygmy owl at all sites within a locality should be expected if mobbing behaviour is the result of local adaptation to the owl in its breeding range. The results of my study may suggest that the pattern of birds' behaviour in response to presentation of passerines alarm calls may be genetic, while their response to the call of a potential predator may be a plastic trait induced by learning—through direct experience and/or social behavioural copying. Since predation is considered a major mortality risk for populations of prey species (Lima and Dill 1990), my results may indicate that the predation rate of the pygmy owl alone is not sufficient to impose directional selection and the evolution of local adaptation (i.e. the predator recognition followed by its mobbing) to that predator in its breeding range in the area studied. Migration—dispersal between populations may be positively associated with the evolution of phenotypic plasticity (Sultan and Spencer 2002). The opposite seems to be true for predation pressure in general, which was reflected in the mobbing of passerine birds in response to the presentation of passerines alarm calls, suggesting that this response may be innate—phylogenetically conserved or evolutionary converged (Randler 2012; Dutour et al. 2017a; Dutour 2022; Sandoval and Wilson 2022), but recognition of allopatric mobbing calls may also be partially explained by learning (Magrath et al. 2015b; Szymkowiak 2021). Blue tit juveniles did not exhibit adult-like mobbing behaviour in response to broadcasted conspecific or heterospecific alarm calls, which may suggest that adult-like mobbing develops over time in parts rather than as a whole (through associative learning, fine-tuning their responses, or observing conspecific behaviour and vocalisations) (Carlson et al. 2020). Moreover, opportunities for social learning to recognise previously unknown heterospecific sounds as alarm calls are higher than for recognising calls of the specific predator (Morand-Ferron and Quinn 2011). Several mechanisms could underlie the response to heterospecific mobbing calls (Dutour et al. 2017a). In addition to conspecifics, alarm calls are recognised and responded to by heterospecifics within and between animal classes (see Randler 2012 and references therein). Thus, the mobbing of birds in response to the pygmy call may not mean that all birds respond to the predator, but the response of some of them could be elicited by the mobbing of other conspecifics and/or heterospecific birds (i.e. epiphenomenon; Dutour et al. 2017a; Szymkowiak 2021). My study area, similar to that of Dutour et al. (2016), is located on the southwestern periphery of the pygmy owl distribution (BirdLife International 2022). It would be interesting to investigate whether the same pattern holds in the centre of the owl's range, where gene flow from pygmy owl-less populations of forest passerines should be lower and thus less constraining to local behavioural adaptation to predator signals.

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Availability of data and materials The raw data are available as an Online Supplementary Material (Table S1).

Declarations

Conflict of interest The author declares that he has no conflict of interest.

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