

1 Mobbing behaviour varies according to predator
2 dangerousness and occurrence

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4 Mylène Dutour*, Jean-Paul Lena, Thierry Lengagne

5 Université de Lyon ; UMR5023 Ecologie des Hydrosystèmes Naturels et Anthropisés ;
6 Université Lyon 1 ; ENTPE ; CNRS ; F- 69622 Villeurbanne, France.

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8

9 *Corresponding author:* M. Dutour, email: mylene.dutour@univ-lyon1.fr

10 telephone number: +336.72.18.27.27 fax number: +334.72.43.11.41

11

12 *Correspondence:* Université de Lyon ; UMR5023 Ecologie des Hydrosystèmes Naturels et
13 Anthropisés ; Université Lyon 1 ; ENTPE ; CNRS ; 6 rue Raphaël Dubois, 69622
14 Villeurbanne, France ; jean-paul.lena@univ-lyon1.fr; thierry.lengagne@univ-lyon1.fr

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

36 Even though mobbing is not uncommon among vertebrates, how predation risk drives
37 the expression of this behaviour is still poorly understood. Most studies have suggested that
38 animals adjust the strength of their mobbing behaviour according to the perceived risk
39 associated either to predator dangerousness or to local predation pressure (Kobayashi, 1987;
40 Koboroff, 2004; Graw & Manser, 2007; Kaplan et al., 2009; Koboroff et al., 2013). Predator
41 dangerousness, i.e. the rate at which predators kill prey, can greatly vary between predator
42 species, while predatory pressure mostly depends on the abundance of a local predator
43 species. Although mobbing is thought to positively correlate to predator dangerousness,
44 studies on mobbing have only compared prey responses to predators and non-predatory
45 species (Kobayashi, 1987; Koboroff, 2004; Lind et al., 2005). For example, Lind et al. (2005)
46 has experimentally shown that great tits (*Parus major*) do not exhibit mobbing against the
47 European robin (*Erithacus rubecula*), i.e. a non-predatory species, but approach and mob
48 Eurasian pygmy owls (*Glaucidium passerinum*), a predator which is particularly dangerous
49 for great tits. However, inoffensive species such as the European robin can be easily
50 discriminated acoustically from predatory species. Hence, it is still unclear whether mobbing

51 is specific to dangerous predators or more broadly intended to predatory species whatever
52 their dangerousness. It is thus important to investigate the accuracy of prey discrimination
53 facing predatory species of different dangerousness levels (see for instance Griesser 2009
54 working at an intraspecific level on the Siberian jay *Perisoreus infaustus*). Many studies have
55 emphasized that local predation pressure is an excellent predictor of the strength of mobbing
56 responses, with birds exhibiting stronger mobbing responses in locations where predators are
57 common and weaker responses where predators are rare (Sandoval & Wilson, 2012; Tilgar &
58 Moks, 2015). This is in agreement with the study of Reudink et al. (2007) suggesting that
59 birds mob only predatory species they have previously experienced (Reudink et al., 2007).
60 Interestingly, studies also indicate that prey respond to mobbing calls even in areas where
61 their natural predator is absent (Johnson et al., 2004; Randler, 2012) suggesting that the
62 convergent features themselves would facilitate interspecific communication (Marler, 1955,
63 1957). Nevertheless, it is worth noticing that comparing behavioural responses between
64 different localities should be interpreted with caution. For instance, prey communities may
65 greatly vary between localities which can make comparisons irrelevant. This can be
66 particularly problematic if the prey species richness or the relative abundance of most
67 commonly depredated species vary according to the predator occurrence. Unfortunately, to
68 our knowledge, previous studies did not control for such variations in prey communities
69 between the compared sites.

70 In this study, we conducted a series of playback experiments to determine whether
71 passerine mobbing behaviour depends on local predation risk. First, we studied birds'
72 response to two morphologically similar owl species to evaluate whether mobbing is specific
73 to predator dangerousness. We used passerine responses to Eurasian pygmy owl (hereafter
74 pygmy owl), a predator specialized in passerine birds which constitutes an ideal model
75 species for studying mobbing behaviour (Likhachev, 1971; Kellomäki, 1977; Solheim, 1984;

76 Kullberg, 1995; Muller & Riols, 2013; Stonar et al., 2015). We also used the boreal owl
77 (*Aegolius funereus*), a less dangerous species as indicated by the low prevalence of birds in its
78 diet (Korpimäki, 1986). We predicted that passerines should respond more strongly to the
79 pygmy owl than to the boreal owl. Second, we tested mobbing in two forest patches – one
80 with and one without pygmy owls – of the same mountain range and identical bird
81 communities, to compare mobbing behaviour with different predation pressures. We predicted
82 that birds would not mob in response to predator vocalizations where the predator is absent,
83 because owls calls are not associated with predation. Yet, it was important to control that the
84 absence of response would not be due to a loss of mobbing ability; hence, we tested in both
85 forest patches (with or without pygmy owls) that birds responded to the playback of a
86 mobbing chorus.

87

88 **MATERIALS AND METHODS**

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90 *Site and species studied*

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92 The study was conducted in mixed deciduous-coniferous forests in the Jura mountains
93 (Ain, France) in two study areas. The first is located near Oyonnax (46°15' N, 5° 39' E, mean
94 altitude 850m) where the Eurasian pygmy owl (*Glaucidium passerinum*), a dangerous
95 predator of passerine birds and the boreal owl (*Aegolius funereus*), a less dangerous predator
96 of passerine birds, are both common. The second study area, in which owls are absent, is
97 located 40 km away from the first (45° 57' N, 5° 20' E, mean altitude 260 m). Four listening
98 sessions were performed at each site to control owl occurrence using site occupancy models
99 (Supplementary Materials 1). While owls were detected in each site of the first area ($N = 20$),
100 none was detected in the second area ($N = 15$), confirming previous information (Lengagne &

101 Bulliffon, 2014) and making the two sampled areas (hereafter referred as area with owls
102 *versus* area without owls) highly relevant to investigate the influence of owl predation
103 exposure on mobbing. The distance between the different sites was at least 500 m to avoid
104 that a responding individual would contribute more than once to the analyses. At each of the
105 35 sites, bird species diversity was surveyed through a 20 minutes acoustic census of a ~ 100
106 m radius around the observer. A census was performed before any experiment (Blondel et al.,
107 1970). In total, 32 passerine species were identified in the area where pygmy owls were
108 present and 22 passerine species in the area where pygmy owls were absent. In all cases, we
109 focused on the eight bird species that were most commonly depredated by pygmy owls
110 (Muller & Riols, 2013): common chaffinch (*Fringilla coelebs*), coal tit (*Periparus ater*),
111 European crested tit (*Lophophanes cristatus*), great tit (*Parus major*), blue tit (*Cyanistes*
112 *caeruleus*), goldcrest (*Regulus regulus*), common firecrest (*Regulus ignicapilla*) and European
113 robin (*Erithacus rubecula*). This passerine community most commonly depredated did not
114 significantly vary among the two study areas (see Supplementary Fig. S1).

115

116 *Experimental Design*

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118 Data were collected during playback experiments conducted between May-July
119 2014 (experiment 1) and September-November 2014 (experiment 2).

120 Response specificity (experiment 1) was tested in different sites of the area with
121 owls ($N = 20$). For this purpose, we applied a crossover design: at each site, the bird
122 community was offered a broadcast sequence of the following three experimental stimuli,
123 pygmy owl calls, mobbing chorus and boreal owl calls. Such a study design is particularly
124 convenient to minimize the error variance resulting from the subject effect (i.e. the bird
125 community present at the site), since the relative effect of stimuli can be assessed within each

126 bird community (Jones & Kenward, 2003). A latency period of five minutes was
127 systematically observed between each experimental test (see test procedure for the complete
128 description) in order to avoid carry-over effects (i.e. a residual effects of the experimental
129 stimuli tested during the previous period on the next one). The sequence order of the three
130 playback stimuli was also alternated between sites to avoid any bias that could result from the
131 sequence order.

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

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139 *Test procedure*

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

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150 *Experimental Stimuli*

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We broadcast playbacks via an amplified loudspeaker (SMC8060, Beyma) connected to a digital playback device (WAV player). Playbacks were restricted to 06:00-12:00, which corresponds to a period of high activity in birds. In order to avoid pseudoreplication, we previously tested if prey response was specific to a specific 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 sound tracks recorded in two populations located on both side of the specie range in order to encompass the call variation range that could experience a local prey community. Both the call variability within each soundtrack and the call variations among pairs of soundtracks were *a posteriori* controlled (results not shown). Results showed that passerine responses (i.e. number of species observed) to pygmy owl calls recorded in Swiss or Sweden were the same whatever the sound track used (permutation test: $t = -1.48$, $N = 12$, $P = 0.20$). In addition, the proportion of species which 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 peculiar soundtrack (no pseudoreplication). Although it was easy to ensure that pygmy owl or boreal owl soundtracks had the same « predator value » for passerines, mobbing chorus recorded in the field may have presented differences (intensity, species composition) difficult to measure for a human observer. 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.

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178 All analyses were done using the SAS 9.3 software. In order to investigate the relative
179 effect of predator dangerousness and mobbing chorus (experiment 1), we tested whether the
180 proportion of mobbing species varied within each site according to the experimental stimuli
181 sequentially presented (i.e. pygmy owl call, boreal owl call and mobbing chorus). These
182 analyses were performed using a log linear mixed model (LLMM, Procedure GLIMMIX,
183 SAS Institute Inc. 2012). More specifically, we modelled the proportion of mobbing species
184 using the number of responding species as the dependent variable with a Poisson distribution
185 for the error term specification and the number of bird species inventoried at the experimental
186 location (i.e. site) as the offset covariate. The experimental stimulus was introduced as an
187 explanatory factor in the fixed part of the model. Since our experimental design was done to
188 assess the relative effect of the three stimuli within the bird community located at each site,
189 we treated the site as a random effect. To check for a possible carry-over effect, the
190 presentation order of the experimental stimuli (i.e. three modalities: first, second or third) and
191 the sequence order of the three stimuli (i.e. 6 combination orders) were also included as
192 factors in the fixed part of the model. The significance of each explanatory term was tested
193 using a non-sequential F test and the Kenward-Roger method was used to estimate the degree
194 of freedom. Non-significant terms were then removed to obtain the final model. Proportions
195 of mobbing species were then compared between the experimental stimuli using the contrast
196 method. We used a similar approach to investigate whether the local occurrence of the
197 predator had any effect on the proportion of species responding either to the predator stimuli
198 or to a mobbing chorus. As above, sites were introduced in the model as a random effect. The
199 experimental stimulus (i.e. pygmy owl call *versus* mobbing chorus), the study area (with

200 *versus* without predator) and their interactive effect were introduced as explanatory terms in
201 the fixed part of the model.

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203 *Ethical Note*

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205 Although our playbacks experiments changed the behaviour of the targeted birds, we
206 do not feel that these experiments were stressful. Indeed, birds recovered a normal activity
207 and were not present near the loudspeaker 5 minutes after our experiments. All behavioural
208 observations performed during this study complied with the legal requirements in France and
209 followed the ASAB/ABS Guidelines for the Use of Animals in Research. The study was
210 approved by DREAL supervisor and permit n°69266347 of the Direction des Services
211 Vétérinaires.

212

213 **RESULTS**

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215 *Mobbing response and predator dangerousness (experiment 1)*

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217 There was no significant carry-over effect in bird responses (LLMM: treatment
218 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
219 variation in mobbing according to the presentation order between pygmy owl and mobbing
220 chorus playbacks ($t = 1.94$, $P = 0.12$). The playback type (call of pygmy owl, call of mobbing
221 chorus and call of boreal owl) had a significant effect on bird responses (LLMM: $F_{2,39.83} =$
222 10.51 , $P = 0.0002$; Fig. 1). Indeed, bird species mobbed more intensely the pygmy owl than
223 the boreal owl ($F_{1,45.6} = 20.92$, $P < 0.0001$). Bird species also responded more to mobbing
224 chorus playback than to boreal owl playback ($F_{1,45.29} = 19.61$, $P < 0.0001$), the latter response

225 being close to zero (0.01278). In addition, mobbing did not differ between pygmy owl and
226 mobbing chorus playbacks (proportion of species 22.85% for pygmy owl, 24.85% for
227 mobbing chorus; $F_{1,34.54} = 0.15$, $P = 0.70$). The average number of bird species detected in the
228 test was 2.30 ± 1.30 (corresponding to 5.1 ± 3.67 individuals) during pygmy owl playback
229 and 2.25 ± 0.97 (corresponding to 4.8 ± 2.88 individuals) during mobbing chorus playback.

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231 *Mobbing response and predation pressure (experiment 2)*

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233 Bird species response was significantly affected by the interaction between the type of
234 stimulus that was broadcast and the presence of the pygmy owl (LLMM: $F_{1,45.88} = 32.48$, $P <$
235 0.0001 ; Fig. 2). Species observed in the area where the pygmy owl was present were 12.8
236 times more likely to respond to a pygmy owl call than species observed in the area where the
237 pygmy owl was absent (contrast test: $F_{1,55.79} = 32.54$, $P < 0.0001$). However, we found that the
238 proportion of species responding to a mobbing chorus did not differ significantly between the
239 two study areas (contrast test: $F_{1,55.79} = 0.37$, $P = 0.21$).

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241 **DISCUSSION**

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

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248 Several studies have shown that prey respond to predators by adopting behaviours
249 specific to the perceived risk (Kobayashi, 1987; Koberoff, 2004; Lind et al., 2005; Graw &

250 Manser, 2007; Kaplan et al., 2009; Koboroff et al., 2013). However, most of these studies
251 have opposed predator species and inoffensive species like quails (*Coturnix sp.*), tortoises
252 (*Pseudemys scripta*) or parrots (*Platycercus eximius*). In the present study, we have shown
253 that birds responded selectively to the presentation of predator calls according to predator
254 dangerousness: passerine birds mob the pygmy owl (i.e. a dangerous predator) but not the
255 boreal owl (i.e. a far less dangerous species). Although we used only two distinct soundtracks
256 per species, it is unlikely that our results are confounded by pseudoreplication because the
257 bird response did not differ between soundtracks despite the substantial difference between
258 soundtracks. Our results therefore indicate that prey adjusted the strength of their mobbing
259 behaviour according to the perceived risk. The low predatory risk associated to the boreal owl
260 is likely related to its hunting strategy. Indeed, while pygmy owls are diurnal (Mikkola, 1983;
261 Cramp, 1985) and have flexible hunting strategies, boreal owls are nocturnal and display a
262 single hunting strategy. Hence, it is not surprising that passerine birds display a differential
263 mobbing response according to owl species. Our results are also congruent with the field
264 study of Morosinotto et al. (2010) showing that pied flycatchers (*Ficedula hypoleuca*)
265 strongly avoid the territories of pygmy owls but not of boreal owls for settling. If it is now
266 clear that bird mobbing varies with predator dangerousness, which level of dangerousness is
267 required to elicit mobbing in the prey community remains unclear. In our study, birds do not
268 respond to the boreal owl while the proportion of passerines in the diet of this predator
269 estimated near our study area is about 3% (Henrioux, 2014a) (*versus* 58% in pygmy owl diet;
270 Henrioux, 2014b). Although comparisons between studied models should be interpreted with
271 caution, Kaplan et al. (2009) have found that birds mob the monitor lizard (*Varanus varius*)
272 while these birds constitute only 14-16% of the predator diet. It seems therefore likely that the
273 threshold value of “dangerousness” above which mobbing is elicited is relatively low.
274 Similarly, one should also expect some variations of mobbing across the prey community,

275 since the relative risk of predation may vary between prey species. For instance, field studies
276 conducted on commonly preyed bird species have found a relationship between how often a
277 species mob predators and how often predators prey upon this species (Gehlbach, 1994;
278 Courter & Ritchison, 2012). Investigating more precisely the correlation between the relative
279 prevalence of a species in a predator's diet and its relative involvement in mobbing could thus
280 be particularly insightful.

281 Our results also reveal that mobbing varies in relation to the local presence of the
282 predator. In the locations where the pygmy owl is absent, calls of this dangerous predator fail
283 to elicit mobbing among passerine birds. This result is in agreement with Reudink et al.
284 (2007). In their study, tropical birds living in environments devoid of predators often express
285 inappropriate antipredator behaviours. Moreover, recent studies have experimentally shown
286 that local predation pressure can predict the strength of mobbing responses in birds,
287 individuals exhibit a stronger mobbing response when local predation pressure is high (Krams
288 et al., 2010; Sandoval & Wilson, 2012; Tilgar & Moks, 2015). However, these authors have
289 not taken into consideration the number of species which was present before tests began. In
290 our study, considering the number of species present, we have been able to control available
291 prey and predators. Predatory response where pygmy owl is a common predator is linked
292 either to selection process (local adaptation) or to learning process. In the first case, only one
293 recent study has shown that the antipredator behaviour of Alpine swifts (*Apus melba*) is
294 heritable (Bize et al., 2012). In many situations, the most probable is that offspring may learn
295 to adjust their behaviour and to express a mobbing response by observing their conspecifics'
296 mobbing behaviour (Curio et al., 1978; Francis et al., 1989; Graw & Manser, 2007). For
297 example, in an experimental study, Campbell and Snowdon (2009) has shown that captive-
298 reared cotton-top tamarins (*Saguinus oedipus*) do not innately recognize predators and a
299 demonstrator seems to be necessary to acquire predator recognition. Hence, the fine-tuning of

300 this behaviour is probably experience-dependent. In our case, we cannot determine if bird
301 mobbing behaviour observed in areas with pygmy owls result from an innate or a learned
302 process. Experiments involving passerines eggs transferred from areas where pygmy owls are
303 present to areas without owls would answer this question.

304 As predicted, prey respond to a mobbing chorus whatever the occurrence of pygmy
305 owls in the area, a result which is in agreement with previous studies on other predators
306 known to elicit mobbing (Johnson et al., 2004; Randler, 2012). The most likely explanation
307 for the conservation of the response to mobbing chorus whatever the local occurrence of the
308 studied predator species is that numerous predator species are known to elicit a mobbing
309 behaviour (Curio et al., 1983; Bartmess-LeVasseur et al., 2010). Thus, in a multi-predator
310 environment, mobbing behaviours could be maintained even in the absence of a specific
311 predator species. This is probably particularly true for avian prey given the ubiquity of
312 opportunist nest predators. These predators can be expected to favour mobbing since they do
313 not usually represent an immediate danger for the adults but are particularly dangerous for
314 offspring. More surprisingly, our results have also shown that the strength of passerine
315 response to a mobbing chorus is not significantly higher than the response to the pygmy owl
316 calls in the area where this predator is present. Indeed, a previous study has reported the
317 mobbing calls to elicit a stronger response than the one elicited by a specific dangerous
318 predator, suggesting that mobbing calls give information not only on the presence of the
319 predator, but also on the response of other prey species perceiving the situation as threatening
320 (Sandoval & Wilson, 2012). Previous studies have also suggested that mobbing calls contain
321 information about the degree of threat that a predator represents (Naguib et al., 1999;
322 Templeton et al., 2005; Graw & Manser, 2007; Griesser, 2009; Koboroff et al., 2013, Suzuki,
323 2014; Billings et al., 2015). The difference in the method used to infer the strength of the
324 response may well explain why our results differ from those reported in previous studies

325 (Sandoval and Wilson 2012). In particular, our measure of mobbing response is probably
326 more conservative than the one used by Sandoval and Wilson (2012) since we did not use the
327 number of individuals attracted by the mobbing call but the proportion of responding species
328 among species present at the experimental location.

329 Mixed-species avian mobbing is a widely recognized phenomenon. Mobbing calls can
330 communicate the presence of a predator to heterospecifics as well as conspecifics (Marler,
331 1957; Zimmermann & Curio, 1988; Hurd, 1996; Forsman & Mönkkönen, 2001; Templeton &
332 Greene, 2007; Randler and Förschler, 2011; Hetrick & Sieving 2012; Sandoval & Wilson,
333 2012; Randler & Vollmer, 2013). Indeed, our soundtrack of mobbing chorus with four species
334 has elicited a response not only from these four species but also from all the other species
335 strongly predated by the pygmy owl. In our study, the proportion of conspecific species (i.e.
336 four species of the mobbing chorus playback) which respond to mobbing choruses was
337 69.66% whereas the proportion of heterospecific species (i.e. four species not included in the
338 mobbing chorus playback) was 37.50%. However, responses to mobbing choruses greatly
339 vary among heterospecific passerines species. For example, in our experiments, the goldcrest
340 (*Regulus regulus*) has responded in 20/24 tests where it was present whereas European robin
341 has responded in only 2/32 tests where it was present. Hence, we emphasize heterospecific
342 communication and our results suggest that responses are asymmetrical across species. Future
343 experiments will investigate the underlying processes of response to mobbing calls.

344 In conclusion, we have shown that passerines respond to mobbing chorus regardless of
345 the presence of dangerous predators in the area, suggesting that it is a conserved trait. In this
346 case, the removal of one predator should have limited effect on the persistence of the
347 antipredator strategy because predation pressure is usually not due to a single species. On the
348 other hand, the absence of passerine response to owls in the area where these predators are
349 absent suggest that mobbing behaviour against owls is an experience-dependent and highly

350 flexible trait. Future studies should explore the costs and benefits of mobbing at species level
351 to assess to which extent this trait is flexible.

352 **Acknowledgments**

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354 We warmly thank Francisque Bulliffon, Benoit Feuvrier and Florent Chaverot
355 for data collection. We are grateful to Bernard Kaufmann and Doris Gomez for English
356 corrections. We thank two anonymous referees whose comments helped us greatly improve
357 the quality of this article. This study was supported by a grant from the Conseil Général de
358 l'Ain.

359

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507

508 APPENDIX

509

510 **Supplementary Material 1: Site occupancy model (Eurasian pygmy owl)**

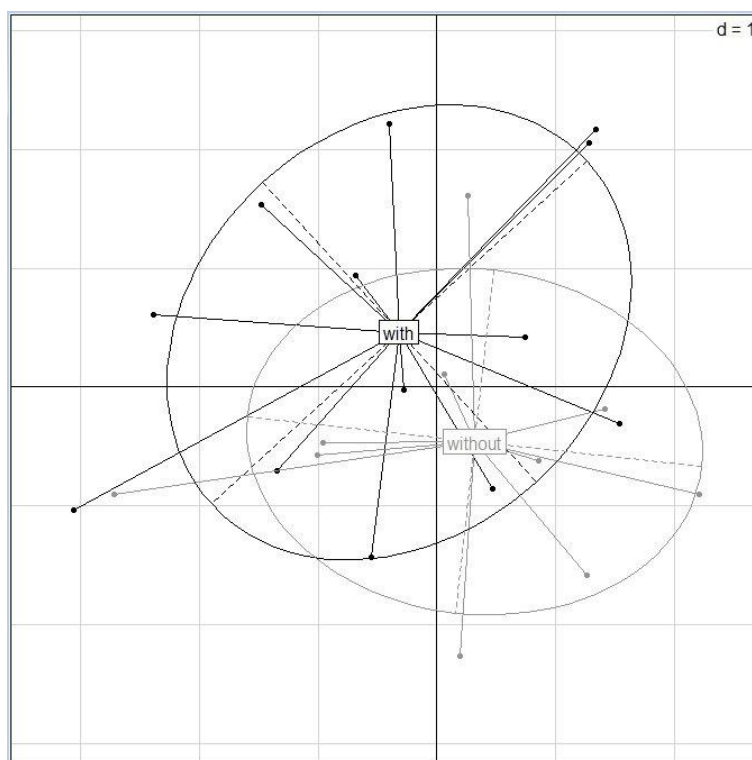
511

512 Model selection was based on Akaike's Information Criteria (AIC). Model including study
513 area covariable was considered best ($\Delta AIC = 29.26$) and showed that the occurrence of
514 pygmy owl was 1 in area where pygmy owl was present and 0 in area where pygmy owl was
515 absent.

516

517 **Supplementary Material 2: Species richness in areas with or without owl**

518



519

520 **Figure S1.** Schematic representation of factor correspondence analysis (FCA) of the most
521 frequently killed bird species by Eurasian pygmy owls (*Glaucidium passerinum*) in areas with
522 (black) and without (grey) owl (FCA1: 25.27%; FCA2: 21.45%).

523

524

FIGURE LEGENDS

525

526 **Figure 1.** Proportion of species in response to the presentations of a boreal owl (grey
527 diamond), a pygmy owl (black triangle) and mobbing chorus (white circle) calls at sites where
528 owls were present ($N = 20$ sites). Error bars represent standard errors.

529

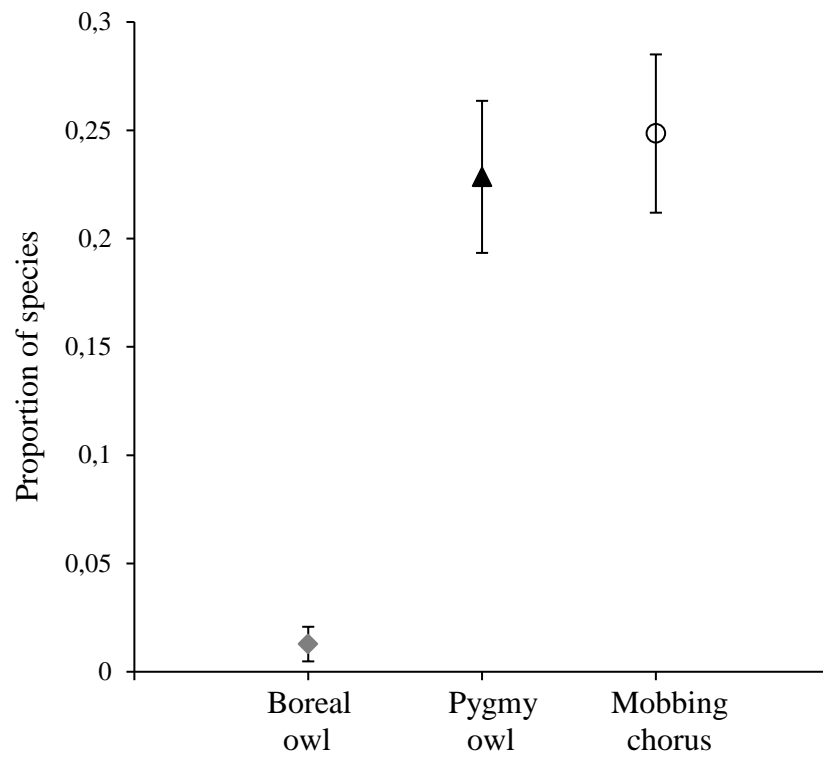
530 **Figure 2.** Proportion of species in response to the presentations of a pygmy owl (black
531 triangle) and a mobbing chorus (white circle) calls at sites where the pygmy owl was present
532 (on the left side, $N = 15$ sites) and sites where pygmy owl was absent (on the right side, $N =$
533 15 sites). Error bars represent standard errors.

534

535

FIGURES

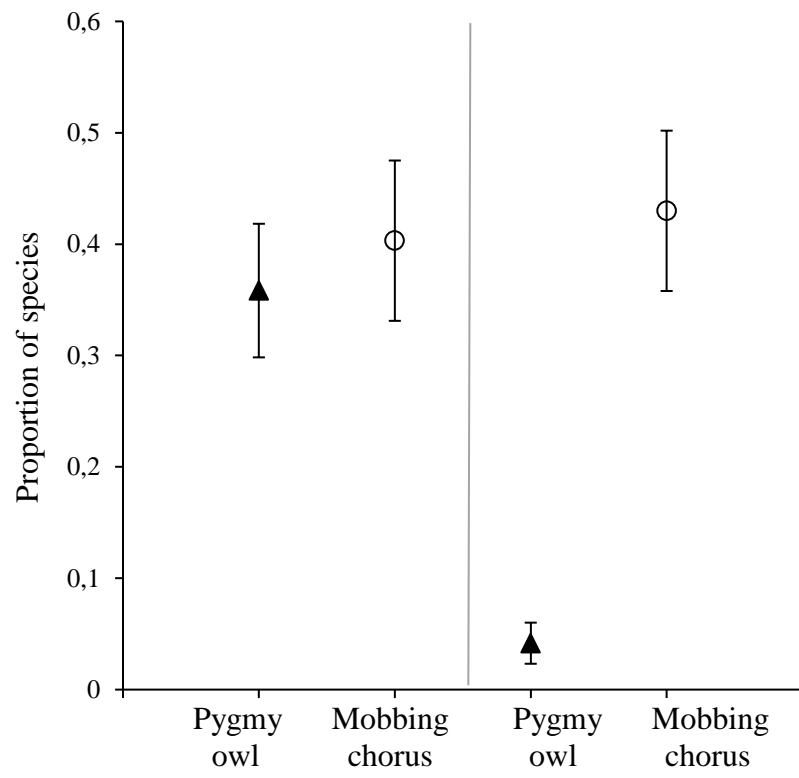
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