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Mylène Dutour, Jean-Paul Léna, Thierry Lengagne

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# 1 Mobbing calls: a signal transcending species boundaries

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3 Mylène Dutour, Jean-Paul Léna, Thierry Lengagne

4 Université de Lyon, UMR5023 Ecologie des Hydrosystèmes Naturels et Anthropisés,

5 Université Lyon 1, ENTPE, CNRS, Villeurbanne, France

6

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

8 telephone number: +336.72.18.27.27 fax number: +334.72.43.11.41

9

10 *Correspondence:* Université de Lyon ; UMR5023 Ecologie des Hydrosystèmes Naturels et

11 Anthropisés ; Université Lyon 1 ; ENTPE ; CNRS ; 6 rue Raphaël Dubois, 69622

12 Villeurbanne, France ; jean-paul.lena@univ-lyon1.fr; thierry.lengagne@univ-lyon1.fr

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14

## 15 **Mobbing calls: a signal transcending species boundaries**

16

17 When they perceive a potential predator, many species of birds and mammals emit specific

18 alarm calls (Seyfarth et al., 1980; Klump & Shalter, 1984; Rainey et al., 2004; Graw &

19 Manser, 2007; Magrath et al., 2007). These calls are often classified as flee alarm calls, which

20 are associated with an immediate escape of the emitter while spurring receivers to freeze or

21 flee, or mobbing calls, which are associated with the approach and harassment of the predator

22 by the emitter, while spurring receivers to join the caller (Hartley, 1950; Curio, 1978; Hurd,

23 1996; Kennedy et al., 2009; Magrath et al., 2015). Mobbing calls are usually intended toward

24 a potential non-hunting predator, and are expected to decrease its hunting efficiency, either

25 through distracting it or by chasing it away (Hoogland & Sherman, 1976; Curio, 1978;  
26 Pettifor, 1990; Flasskamp, 1994; Pavey & Smyth, 1998). Both the intensity of mobbing and  
27 its success in deterring the predator are positively related to the size of the crowd gathered by  
28 the caller (Becker, 1984; Robinson, 1985; Verbeek, 1985; Picman et al., 1988). Although  
29 mobs can be formed exclusively by conspecifics, they often involve heterospecifics prey  
30 (Hurd, 1996; Suzuki, 2016; Dutour, Lena, & Lengagne, 2017). Hence, this phenomenon  
31 makes them well-suited to investigate communication at the community level. Indeed, as it  
32 implies a cooperative act, i.e. joining the mob, this makes it easier to distinguish between  
33 “simple” eavesdropping on heterospecific signals and more elaborate interspecific  
34 communication. For instance, while some species will take part in the crowd, others will not,  
35 although they perceive the same threat (Davies & Welbergen, 2009; Ito & Mori, 2010). As for  
36 other alarm calls, mobbing calls require the ability to gather relevant information from  
37 heterospecific signals (i.e. interceptive eavesdropping, *sensus* Peake, 2005; see Magrath et al.,  
38 2015 for a review). In particular, individuals can recognize heterospecific mobbing calls.

39 Both learned and innate processes could be involved in the mechanisms enabling the  
40 recognition of heterospecific mobbing calls (Hurd, 1996; Ramakrishnan & Coss, 2000;  
41 Magrath et al., 2009; Fallow et al., 2011; Wheatcroft & Price, 2013). By nature, associative  
42 learning is more flexible than innate process but it requires a previous experience to take  
43 place. Such experience could occur when heterospecific preys encounter each other when  
44 detecting and mobbing the same predator. However, several innate processes could also play a  
45 central role in the recognition of heterospecific mobbing calls. In particular, as for other alarm  
46 calls, strong ecological constraints apply on the acoustic structure to enhance call efficiency.  
47 In the case of mobbing calls, loudness and repeated features can be expected to be selected in  
48 order to facilitate emitter location (Marler, 1955; Klump & Shalter, 1984; Ficken & Popp,  
49 1996; Bradbury & Vehrencamp, 1998; Jones & Hill, 2001). Hence, these calls can also be

50 used in other contexts for which an accurate localization of the emitter is necessary such as  
51 pair contact situation or food presence discovering (Marler, 1956; Mahurin & Freeberg, 2009;  
52 Suzuki, 2012). Moreover, calls inevitably incorporate some features such as harshness or  
53 broad-bandwidth pulses of sound related to the psychological state of the emitter, such as fright  
54 in the case of flee calls or arousal in the case of mobbing calls. All these characteristics can be  
55 expected to lead to acoustic similarity of mobbing calls across species, which could arise from  
56 phylogenetic conservation or evolutionary convergence of mobbing calls (Ficken & Popp,  
57 1996; Johnson et al., 2003; Randler, 2012). Finally, one may not exclude that both associative  
58 learning and innate process could enhance recognition of heterospecific mobbing calls. In  
59 particular, similitudes in acoustic features of mobbing calls among heterospecific species  
60 could greatly enhance heterospecific mobbing call recognition through the mechanism of  
61 generalization which is often involved in learning process (Weary, 1991; Sturdy, Bloomfield,  
62 Charrier, & Lee, 2007). Studies in some Paridae species suggest that they learn to recognize  
63 their own mobbing calls and that they generalize to other unfamiliar calls that are acoustically  
64 similar.

65         Mechanisms involved in the recognition of heterospecific alarm and mobbing calls are  
66 still poorly understood despite heterospecific responses becoming well documented (Magrath  
67 et al., 2015). One way to fill this gap is to investigate the variation in response to unfamiliar  
68 alarm calls. Unfortunately, such data remain scarce in the case of mobbing calls. While in one  
69 study, individuals did not respond to the allopatric mobbing calls (Nocera et al., 2008), in  
70 other cases individuals recognized the allopatric mobbing calls (Johnson et al., 2003;  
71 Langham et al., 2006; Randler, 2012; Wheatcroft & Price, 2013). Because almost all studies  
72 just focused on one pairwise comparison of emitter-receiver species, any comparison across  
73 species remains difficult, if not impossible. Moreover, while studies focused on more than one  
74 pair of emitter-receiver, heterospecific species responding to playbacks have not been

75 identified and prevent us from understanding responses in the light of the phylogeny. Hence,  
76 there is a need for a larger pairwise comparison of emitter-receiver species in order to unravel  
77 the importance of the relationship among species to explain their behavioural responses in an  
78 antipredator strategy.

79 In this study, we conducted playback experiments to investigate the variation in the  
80 response of four passerine birds exposed to three allopatric species mobbing calls.  
81 Additionally, we measured similarity among mobbing call of the studied species to determine  
82 if acoustic similarity could be viewed as a general mechanisms involved in heterospecific  
83 communication. To this aim, we selected the four receiver species among European passerine  
84 birds and the three emitter ones among North American birds, since mobbing is well  
85 documented in both communities and found to be based on a similar alarm-calling system  
86 (Langham et al., 2006; Templeton & Greene, 2007; Sieving et al., 2010; Dutour et al., 2016).  
87 Then, according to a first study suggesting a possible phylogenetically conserved response  
88 among Paridae family (Randler 2012), we used sound track of three American Paridae  
89 species: two of them corresponding to mobbing call while the third one was a control one (i.e.  
90 territorial call). Additionally we choose to use a non Paridae call to compare mobbing  
91 responses obtained from two different families.

92

## 93 **METHODS**

### 94 *Study Species*

95 To test whether a response to mobbing calls can occur without a learning process  
96 linked to these calls, we tested four European species with playbacks of three North American  
97 passerine species. The following European species were selected because they are known to  
98 exhibit mobbing behaviour when confronted with a predator and give specific mobbing calls:  
99 great tit (*Parus major*), blue tit (*Cyanistes caeruleus*), coal tit (*Periparus ater*) and common

100 chaffinch (*Fringilla coelebs*) (hereafter chaffinch) (Thompson, 1969; Curio, 1971;  
101 Zimmermann & Curio, 1988 ; Krams & Krama, 2002; Lind et al., 2005; Berzins et al., 2010;  
102 Randler, 2011; Randler & Vollmer, 2013; Dutour et al., 2016; Carlson et al., 2017). These  
103 European species were exposed to mobbing calls of three North American passerine species,  
104 black-capped chickadee (*Poecile atricapillus*), tufted titmouse (*Baeolophus bicolor*) and  
105 Carolina wren (*Thryothorus ludovicianus*). All of them are known to mob predators (Morton  
106 & Shalter, 1977; Hurd, 1996; Sieving et al., 2004; Betts et al., 2005; Templeton et al., 2005;  
107 Templeton & Greene, 2007; Bartmess-LeVasseur et al., 2010; Hetrick & Sieving, 2011).  
108 Tests involved 132 different European individuals (for the detailed number of tests conducted  
109 for each combination, see Table 1). Additionally, to ensure that the response was not due to  
110 call novelty (i.e. that the individuals did not simply respond to any novel sound) we used  
111 territorial call of the boreal chickadee (*Poecile hudsonicus*), an American songbird found  
112 throughout Canada and northern United States (Ficken et al., 1996), as a control (50 tests, see  
113 Table 1). Finally, to compare the relative intensity of mobbing response obtained to American  
114 species, we also broadcast conspecific mobbing calls to each of the four European species  
115 studied (44 tests, see Table 1).

116

### 117 *Acoustic Analysis*

118 Recordings were in 16-bit WAV format and analyzed with Avisoft SASLab© software. We  
119 used spectrograms with a FFT length of 512 points for the measurements. We selected 5  
120 recordings per species and analyzed up to 10 songs per recording (on average  $5.97 \pm 2.43$   
121 SD). To properly characterize the mobbing production of each studied species and to measure  
122 the variation across species, seven shared acoustic properties were measured on each call  
123 sound track: (1) duration (s); (2) peak frequency (the frequency for which amplitude is  
124 maximum in Hz); (3) maximum frequency (highest frequency of the call in Hz); (4) minimum

125 frequency (lowest frequency of the call in Hz); (5) frequency bandwidth (differences in Hz  
126 between maximum frequency and minimum frequency measure on a linear amplitude  
127 spectrum (threshold -20dB)); (6) number of elements; (7) number of different elements per  
128 song, an indicator of call complexity (frequency modulated element or dee element or both,  
129 see Fig 1).

130

### 131 *Study Sites and Playback Experiments*

132 All experiments were conducted on wild passerines inhabiting a large mixed  
133 deciduous-coniferous forest (c.a. 570 km<sup>2</sup>) located in South-East France (45°80'N, 4°52').  
134 We never went back twice on the same forest path and two successive playbacks were always  
135 separated by more than 100 m (200 m for two tests performed on the same species). Hence  
136 although birds were not individually ringed the probability to test a second time a given  
137 individual remain very low. Moreover, all tests were conducted over a relatively short period  
138 during the breeding season (end of April to mid-July) in order to avoid a seasonal effect. In  
139 addition, we avoided any temporal effect during our experiments by evenly distributing the  
140 playbacks of the different species across the study period.

141 Once a focal bird was identified, we placed the loudspeaker used to broadcast the  
142 acoustic signal 30 m away from the bird at the bottom of a tree. The focal subject was always  
143 the one that was nearest to the playback source. We performed our playback experiments only  
144 at times when there were no other passerines observed near the focal individual, to avoid any  
145 interference with the behaviour of other passerines. All tests for which another bird mobbed  
146 before the focal one were discarded because we could not determine whether the focal  
147 individual responded to our playback test or to the mobbing call emitted by the other bird.  
148 Two observers with binoculars were positioned opposite each other at vantage points at least  
149 15 m from the loudspeaker and observed bird response during the test. In order to limit the

150 risk of interference with non focal birds, the experimental duration was voluntary shortened  
151 compared to what it is usually done (including our own previous studies, Dutour et al. 2016,  
152 see also Randler & Vollmer, 2013). More precisely, each experimental test was divided into a  
153 1 min baseline of silence followed by playback of signal containing a series of individual calls  
154 following a natural rhythm (1 min). We found no evidence that our arrival disturbed the  
155 behaviour of the focal individual before the playback. During the playback, focal birds either  
156 did not approach the loudspeaker (i.e. staying around 30 m apart from it) and continued  
157 their usual activity (i.e. singing, foraging or resting) or approached it within a 15 m radius.  
158 We therefore used this distance of approach to assess the mobbing propensity of focal birds as  
159 Hua et al. (2016). A preliminary analysis confirmed that animals approaching the soundtrack  
160 within a 15 m radius were 20 times more likely to emit mobbing calls than animals that did  
161 not approach it (CI 95%: 21.75 – 59.15). Furthermore, approaching birds also exhibited other  
162 mobbing behaviours (circling the loudspeaker, restless movements), although these  
163 behaviours were not quantified. Neither the latency to approach (i.e. time of arrival), nor the  
164 closest approach (i.e. the minimal distance from the loudspeaker) were found related to the  
165 emission of mobbing call among approaching birds (see supplementary material 1, Table A1).  
166 Data on species identity and mobbing response of the focal birds were collected mainly by  
167 one observer (MD), and were supplemented by a second observer who recorded behavioral  
168 observations on bird individuals.

169

#### 170 *Choice of Experimental Stimuli and Playback Materials*

171 In the field, the amplitude level of mobbing call emitted by these species has never  
172 been measured accurately (precise distance between the bird and the sound level meter taking  
173 into account the exact position of the head of the bird). Hence, we decided to match by ear  
174 signal amplitude of the signals used during our test to a natural calls emitted by passerine



175 birds while mobbing. Then, the average amplitude used for the playback experiment was  
176 obtained by way of a sound level meter placed at one meter from the loudspeaker ( $86.2 \pm 3.07$   
177 dB, mean  $\pm$  SD, Lutron SL-4001, C weighting, slow settings, re:  $20 \mu$  Pa). The same volume  
178 was used for all species. We broadcast sound tracks using a Shopinnov 20 W loudspeaker  
179 (frequency response 100 Hz -15 kHz) that include a memory to store sound file.

180         Concerning the signal used during playback, we used mobbing calls produced by  
181 passerines in response to an Eurasian pygmy owl (*Glaucidium passerinum*) and to conspecific  
182 mobbing calls. Calls were recorded with a Fostex FR2LE digital recorder connected to a  
183 Sennheiser ME67-K6P microphone. We also used mobbing calls obtained from the Macaulay  
184 Library (Cornell Lab of Ornithology, <http://macaulaylibrary.org>) or from the Xeno Canto  
185 online database ([www.xeno-canto.org](http://www.xeno-canto.org)). In order to avoid pseudoreplication (Hurlbert, 1984;  
186 Kroodsma, 1989, 1990), calls from 40 individuals were used (five from each species). Each  
187 stimulus was played back at the same volume to copy natural calling amplitudes.

188

### 189 *Statistical Analyses*

190         To compare the acoustic similarity of European calls to those of the North American  
191 species, we carried out four Principal Components Analysis (PCA) using acoustic  
192 measurements taken from mobbing calls of the 7 species (Fig. 1). These four PCA analyses  
193 including peak frequency, minimum frequency, frequency bandwidth, number of different  
194 elements and number of elements. Furthermore, the PCA of great tit and blue tit including  
195 duration. For chaffinch and coal tit this acoustic measurement was excluded because it was  
196 strongly correlated with number of elements (chaffinch:  $r^2 = 0.89$ , coal tit:  $r^2 = 0.86$ ,  $P <$   
197  $0.001$ ). Maximum frequency was excluded for each of the four European species because it  
198 was strongly correlated with frequency bandwidth ( $0.84 < r^2 < 0.99$ ,  $P < 0.001$ ). Analyses

199 were done in R v.2.15.1 (R Development Core Team 2012) using the ade4 package (Dray &  
200 Dufour, 2007).

201         Because none of the focal bird (whatever the receiver species) mobbed when exposed  
202 to the novelty signal (i.e. the territorial call of the boreal chickadee;  $N = 50$ ), it was not  
203 possible to include this experimental treatment in a parametric analysis. For each receiver  
204 species, we therefore used a Fisher exact or Chi-square homogeneity tests to compare the  
205 mobbing propensity, as revealed by the relative frequency of mobbing birds, between the  
206 novelty signal and the other three heterospecific mobbing stimuli (black-capped chickadee,  
207 tufted titmouse and Carolina wren mobbing calls). For each receiver species, a similar test  
208 was also performed to compare the mobbing propensity between the novelty signal and the  
209 conspecific mobbing stimulus. We then used a generalized mixed models (GLMM) to  
210 investigate the variation in mobbing propensity among the receiver species and according to  
211 the mobbing stimuli broadcast, thus discarding the novelty signal treatment from the analysis.  
212 More specifically, the individual binary response (mobbing response = 1; no mobbing  
213 response = 0) was introduced as the dependent variable using a logit link and a binomial  
214 distribution for the error term, and the receiver species, the mobbing stimuli and their  
215 interactive effect were introduced as explanatory terms in the fixed part of the model. Because  
216 five different playback soundtracks of each mobbing stimulus were used twice for each  
217 receiver species, soundtracks were introduced in the model as random effects. All coal tits  
218 mobbed when a conspecific mobbing call was offered that resulted in aliasing between this  
219 explanatory term combination and a complete set of soundtrack random effects (i.e. the coal  
220 tits mobbing calls). We therefore used the Laplace optimization method to circumvent the  
221 optimization problem and to allow a log-likelihood estimation of the model required to  
222 perform likelihood ratio tests (LRT). The significance of the random effect was tested using a  
223 likelihood ratio test (LRT) on the full model. LRT were also used to test the significance of

224 explanatory terms, and non-significant explanatory terms were removed to obtain the final  
225 model. We then performed an analysis of deviance to examine the relative importance of the  
226 variation explained by the heterospecific status of the stimuli. For this purpose, we  
227 constructed a concurrent but reduced model for which all heterospecific stimuli were  
228 regrouped within a unique category and compared to the conspecific one. An F statistic was  
229 then calculated in order to test the significance of the variation caught by this group. We used  
230 a similar approach to investigate whether the difference of response between the conspecific  
231 and the heterospecific mobbing calls observed among receiver species could be explained by  
232 their phylogenetic relationship at the family level (hereafter family origin). For this purpose,  
233 the mobbing stimuli were regrouped into two classes (heterospecific versus conspecific calls)  
234 and the receiver species were regrouped according to their family origin. Finally, we  
235 performed a separate analysis on the conspecific mobbing call treatment to control for  
236 variation of mobbing propensity according to the receiver species. We also performed a  
237 partial analysis for each receiver species in order to investigate the variation of mobbing  
238 propensity according to the mobbing stimuli using LRT based contrasts. For both these two  
239 analyses, the soundtrack random effect could not be estimated reducing the models to  
240 generalized linear models (GLM). Analyses were done using SAS 9.3 (SAS Institute Inc.,  
241 Cary, NC, U.S.A.) software.

242

### 243 *Ethical Note*

244 All tested birds returned to normal activity relatively quickly after our experiments  
245 (usually within one minute), so we were confident that our experiments were not unduly  
246 stressful. All behavioural observations performed during this study complied with the legal  
247 requirements in France and followed the ASAB/ABS Guidelines for the Use of Animals in  
248 Research. The study complied with the ethical rules set by University Lyon 1 concerning the

249 use of wildlife species in research programs. The study was conducted with the approval of  
250 the Prefecture du Rhône (Ref 2015-13).

251

## 252 **RESULTS**

### 253 *Acoustic similarity of mobbing calls*

254 A PCA was performed on acoustic characteristics for each of the four European  
255 species in order to determine the similarity of their mobbing calls with those emitted by  
256 allopatric species (Fig. 2). In two cases, chaffinch and coal tit, we observed a strong  
257 dissimilarity between the focus species and allopatric ones (Fig. 2a and 2b). Concerning great  
258 tit, PCA revealed an important overlapping with allopatric mobbing calls of the three  
259 allopatric species (Fig. 2c). At last, blue tit mobbing calls showed a strong similarity with  
260 black-capped chickadee but no overlapping with mobbing calls emitted by Carolina wren and  
261 tufted titmouse (Fig. 2d).

262

### 263 *Response to Mobbing Calls*

264 As highlighted in the methods section, none of the European species responded to the  
265 novelty signal (i.e. the territorial call of the boreal chickadee). Nonparametric tests showed  
266 that all European species responded significantly less to the novelty signal than to conspecific  
267 mobbing calls (Nonparametric tests: territorial call versus. conspecific mobbing calls; great  
268 tit:  $N = 25$ ,  $P < 0.001$ ; blue tit:  $N = 21$ ,  $P = 0.001$ ; coal tit:  $N = 24$ ,  $P < 0.001$ ; chaffinch:  $N =$   
269  $24$ ,  $P < 0.001$ ). Furthermore, our results showed that all three tit species responded  
270 significantly less to the novelty signal than to the three mobbing calls of American species  
271 (black-capped chickadee, tufted titmouse and Carolina wren grouped) (Nonparametric tests:  
272 territorial call versus. mobbing calls; great tit:  $N = 48$ ,  $P < 0.001$ ; blue tit:  $N = 41$ ,  $P = 0.002$ ;  
273 coal tit:  $N = 44$ ,  $P = 0.009$ ). Concerning chaffinch, the response did not differ significantly

274 between the novelty signal and mobbing calls ( $N = 49$ ,  $P = 0.167$ ). Responses to the novelty  
275 signal were thus discarded for the rest of the analyses.

276 According to the generalized linear mixed model (GLMM) used to analyze the  
277 response variation among the receiver species and across the different mobbing signals, we  
278 detected a significant soundtrack random effect ( $\chi^2 = 3.60$ ,  $P = 0.03$ ; see Table 2). The  
279 pattern of responses to the different mobbing signals also varied significantly among the  
280 receiver species, as indicated by a significant interactive effect between the receiver species  
281 and the mobbing signals ( $\chi^2 = 18.92$ ,  $P = 0.03$ ; see Table 2). As revealed by a deviance  
282 analysis, a significant part of this interactive effect could be explained by the variation among  
283 the receiver species of the relative response difference between heterospecific and conspecific  
284 mobbing calls ( $F_{7,8} = 4.04$ ,  $P = 0.03$ ; see Table 2 for details). Although all species responded  
285 to conspecific mobbing calls (see partial analysis below), the relative strength of this response  
286 when compared to all grouped heterospecific calls varied significantly across receiver species  
287 (Fig. 3). Furthermore, this variation of response between the conspecific and the  
288 heterospecific calls observed among receiver species was at least partly explained by their  
289 family origin ( $F_{3,12} = 5.42$ ,  $P = 0.01$ ; see Table 2 for details). The chaffinch showed a higher  
290 response to conspecific rather than heterospecific mobbing calls, whatever the emitter species,  
291 while this difference was relatively less and more heterogeneous within the tit species (Fig. 3;  
292 Table 3). Partial analysis of the response towards conspecific mobbing calls did not indicate a  
293 significant variation in mobbing propensity among species ( $\chi^2 = 6.93$ ,  $P = 0.074$ ), although  
294 the response exhibited by the coal tit was stronger than that of the other three species.

295 Separate analyses performed for each receiver species indicate that both coal tit and chaffinch  
296 were significantly more prone to respond to conspecific calls than to heterospecific ones while  
297 this was not the case of both the great tit and the blue tit (see Table 3 and Fig. 3). Contrarily to  
298 the great tits and the chaffinches, both the blue tit and the coal tit exhibited some variations in

299 their response towards the three different heterospecific calls despite these variations were not  
300 statistically significant (see Table 3 and Fig. 3).

301

## 302 **DISCUSSION**

303 We found that European birds responded selectively to the broadcast of mobbing calls  
304 of North American passerines but not to the boreal chickadee territorial call, which is usually  
305 directed at conspecifics, whereas the mobbing calls are addressed to both conspecifics and  
306 heterospecifics. These results corroborate the study of Randler (2012) showing that great tits  
307 responded more strongly towards allopatric chick-a-dee mobbing calls than towards the  
308 allopatric territorial call. In that study, 31.3% of individuals (5 out of 16) approached the  
309 loudspeaker during the black-capped chickadee territorial call playback, while during our  
310 boreal chickadee territorial call playback, no individual (0 out of 50) mobbed the  
311 loudspeaker. Unlike us, the author started their trials at the beginning of the territorial phase  
312 of great tits (Hölzinger, 1997). The stronger response to an allopatric territorial call at the  
313 beginning of the territorial phase could be explained by a modification of mobbing response  
314 according to the stage in reproduction behaviour.

315 Our results clearly show that among three out of four receiver species studied, i.e. the  
316 three species of tit, prior experience of the heterospecific mobbing call is not required to elicit  
317 a response. Moreover, during our experimental tests, American mobbing call playbacks  
318 elicited mobbing responses from 9 other bird species, including different genera, such as  
319 *Troglodytes*, *Regulus*, *Sitta*, *Lophophanes*, *Poecile*, *Turdus* and *Garrulus*. As expected, as  
320 natural selection might favour the strongest response to their own mobbing calls. Indeed,  
321 European passerines reacted most strongly towards European conspecific mobbing calls than  
322 those of North American species. Nevertheless, focusing on differences among species, we  
323 found great variations in their behavioural response. In particular, the propensity of the

324 chaffinch to respond to heterospecific mobbing calls is clearly lower than that found for the  
325 three tit species. Furthermore, although tits responded well to heterospecific mobbing calls, to  
326 some extent their responses remained heterogeneous. Like the chaffinch, the coal tit  
327 responded less to the allopatric calls than the conspecific calls. Therefore, these results  
328 strongly suggest variability among species, which could well explain the incongruence among  
329 previous studies (Johnson et al., 2003; Nocera et al., 2008; Randler, 2012).

330 Three hypotheses, not mutually exclusive, could be suggested to explain the responses  
331 observed to unfamiliar mobbing calls: (i) phylogenetic conservatism of the signal structure, (ii)  
332 evolutionary convergence due to similar constraints exerted on the signal structure, and (iii)  
333 acoustic communication system complexity.

334 (i) Several studies suggest a phylogenetic relatedness on existing sensory bias in the  
335 receiver and in the call structure used by the emitter (Ryan & Rand, 1993; Ryan, 1998; de  
336 Kort & ten Cate, 2001). Calls of different species can be acoustically similar as a result of  
337 calls retaining features of their acoustic structure from a common ancestor (de Kort & ten  
338 Cate, 2001), thus enabling interspecific responses among related species. Such a hypothesis  
339 could well explain the response of the chaffinch to allopatric mobbing calls we observed in  
340 our study, since none of the three emitter species we used came from its own family. The  
341 response of the European tit species to the American tit species could also be due to the highly  
342 conserved call structure of the Paridae throughout the Holarctic (Langman, 2006; Randler,  
343 2012). According to the study conducted by Randler (2012) suggesting that response of great  
344 tit to allopatric mobbing calls could be phylogenetically conserved, we observed in the  
345 present study a strong overlapping between characteristics of mobbing call emitted by this  
346 species and three other allopatric species. Surprisingly, all three tit species responded as  
347 strongly to the Carolina wren mobbing call as to the mobbing calls of the two tit species.

348 Hence, the difference in response across the heterospecific mobbing calls may not be  
349 explained by the family concordance between the receiver and emitter species.

350 (ii) The second mechanism to explain the responses observed to allopatric mobbing  
351 calls could be due to a similarity of the acoustic features resulting from an evolutionary  
352 convergence (Johnson et al., 2003). In order to facilitate emitter localization and recruitment  
353 for mobbing, acoustics signals frequently involved repeated calls, strongly modulated in  
354 amplitude, with a large frequency band and emitted with high amplitude (Brown, 1982;  
355 Marler, 1955; Bradbury & Vehrencamp, 1998; Aubin & Jouventin, 2002). In the same way,  
356 many studies suggest that flee alarm calls emitted by several species share the same acoustic  
357 structures due to the fact that the emitter should not be localized by the predator while calling  
358 (Shalter, 1978; Brown, 1982; Jones & Hill, 2001). The strong selective pressure imposed by  
359 predators on the communication process (being localized in the case of mobbing calls or  
360 being not localized in the case of flee alarm calls) may lead many species to share the same  
361 acoustic structures and could at least partially explain heterospecific communication (Marler,  
362 1955; Bradbury & Vehrencamp, 1998; Johnson et al., 2003; Fallow et al., 2011). Previous  
363 studies suggest that both acoustic similarity and learning are important for interspecific  
364 responses to alarm calls (Fallow et al., 2011; Haff & Magrath, 2012). In the present study the  
365 fact that three out of four European species responded to mobbing emitted by allopatric  
366 American species suggests that acoustic structure similarities could explain our results  
367 (Fallow et al., 2011). Nevertheless, our acoustic analysis revealed a contrasted situation (Fig.  
368 2). Acoustic similarity could explain behavioural response to allopatric species both in  
369 chaffinch (strong acoustic differences with allopatric call and low behavioural responses) and  
370 in great tit (strong acoustic similarities and strong behavioural responses to allopatric species).  
371 Great tits responded to calls that were acoustically similar to their own. This suggests that  
372 they generalize responses from conspecific calls to unfamiliar calls that are acoustically



373 similar (Ghirlanda & Enquist, 2003). Indeed, if a great tit learns to recognize its own mobbing  
374 calls, then with generalized responding, any calls that it hears that are acoustically similar  
375 enough to those mobbing calls would be treated as "mobbing calls" (Weary, 1991; Sturdy,  
376 Bloomfield, Charrier, & Lee; 2007). On the other hand, acoustic similarity did not explain  
377 behavioural response to allopatric species in coal tit (strong behavioural responses to  
378 allopatric call in spite of strong acoustic differences with them) and blue tit although for this  
379 species results are more complex (Fig. 2d and Fig. 3). To sum up, similarity of the acoustic  
380 features seems not to be a universal hypothesis to explain our results as suggested by  
381 Wheatcroft and Price (2013).

382 (iii) A third hypothesis, dealing with acoustic communication system complexity, may  
383 explain the fact that the three European tit species responded strongly to American mobbing  
384 calls while the chaffinch did not. Indeed calling is structurally complex in tits and chickadees  
385 because of the presence of different elements (Suzuki et al., 2016), and the fact that the  
386 number of C or D notes elicited different responses (Freeberg & Lucas, 2002). Previous  
387 studies have suggested that mobbing calls contain information about the degree of threat that  
388 a predator represents (Baker & Becker, 2002; Templeton et al., 2005; Hetrick & Sieving,  
389 2011). Paridae exhibit two very different signals in response to flying or perched predators.  
390 Finally, most of these species exhibit rich territorial call repertoires. On the other hand, the  
391 chaffinch calling system seems to be less structurally complex than that of chickadees. For  
392 instance, the call rate was the most significant determinant on whether other birds interpreted  
393 the vocalization as a mobbing call (Randler & Förschler, 2011). Therefore, the complexity of  
394 call structures used by the emitter, which is probably associated with the cognitive capacity of  
395 the receiver to decode information, may explain the differences observed between the  
396 responses of European tits and chaffinches. Further studies focusing on species for which the

397 mobbing system is based on a simple variation in call rate would be interesting to assess how  
398 birds might respond differently to heterospecifics.

399         In conclusion, our study has emphasized that prior experience is not a prerequisite for  
400 heterospecific communication. The allopatric response to mobbing calls of three American  
401 species by four European ones shows that a mobbing response could be obtained without  
402 previous learning process of these calls. We found that among two out of four receiver species  
403 studied, acoustic similarity could explain behavioural response to allopatric species.  
404 Nevertheless, the complexity of the communication system in many passerine species  
405 probably prevents us to find a general phenomenon that can be applied to all species. For  
406 instance, in chickadee species, within a given mobbing call sequence, some elements involved  
407 early experience while other not (Hughes, Nowicki, & Lohr, 1998). Further studies, including  
408 the use of different passerine species with different complexity levels of their communication  
409 system are now necessary to assess differences in phylogenetic relationships, acoustic  
410 parameters and acoustic communication system complexity.

411

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413

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620

621 **Table 1**622 The number of tests conducted for each combination in this study.  $N = 226$ 

	Playbacks				Song
	Mobbing calls			Conspecific	
	Black-capped chickadee	Tufted titmouse	Carolina wren		
Coal tit	11	11	10	12	12
Blue tit	10	10	11	11	10
Great tit	13	10	10	10	15
Chaffinch	13	11	12	11	13

623

624

625

626 **Table 2**

627 Deviance and AIC according to the terms introduced in the fixed part of the generalized  
 628 mixed model

Explanatory terms in the fixed part of the models	Nb parm	Deviance	AIC
Receiver   E(conspecific versus heterospecific)	8	196.09	214.09
R(tits versus chaffinch)   E(conspecific versus	4	206.36	216.36
R(tits versus chaffinch) + E(conspecific versus	3	208.53	216.53
R(tits versus chaffinch)   Emitter	8	199.03	217.03
Receiver   Emitter	16	185.66	219.66
Receiver + E(conspecific versus heterospecific)	5	207.94	219.94
Receiver + Emitter	7	204.58	220.58
Receiver	4	218.41	228.41
Emitter	4	220.23	230.23
Intercept	1	235.32	239.32

629  
 630 The « | » character indicates the addition and interaction between the explanatory terms.  
 631 Receiver: 4 receiver species, Emitter: 4 mobbing call stimuli, R(tits versus chaffinch):  
 632 receivers species grouped into two class according to the family of origin, E(conspecific  
 633 versus heterospecific): mobbing call stimuli grouped into two classes, heterospecific versus  
 634 conspecific calls. Nb parm: Number of parameters in the fixed part of the model. The  
 635 significance of explanatory terms was tested using a likelihood ratio test or a F test in the case  
 636 of constrained structures for the receiver or the emitter effect (see main text). For all models,  
 637 the playback soundtrack of each mobbing stimulus as a random factor in the response.  $N =$   
 638 176

639 **Table 3**

640 Overall difference of responses between birds exposed to heterospecific calls and those  
 641 exposed to the conspecific one, and overall difference of responses among birds exposed to  
 642 different heterospecific calls.

comparison	receiver	df	$\chi^2$	<i>P</i>
Conspecific versus heterospecific calls	Blue tit	3	5.6	0.13
	Coal tit	3	21.86	< 0.0001
	Great tit	3	0.85	0.84
	Chaffinch	3	13.38	0.004
Difference between heterospecific calls	Blue tit	2	4.84	0.09
	Coal tit	2	4.92	0.09
	Great tit	2	0.85	0.65
	Chaffinch	2	1.46	0.48

643 All comparisons were based on a partial analysis for each receiver species using a LRT based  
 644 contrast. df: degrees of freedom. See supplementary material 3 Table A3 for detail pairwise  
 645 comparisons of responses between all mobbing call stimulus for each receiver species.

646 **APPENDIX**

647 **Table A1**

648 Influence of the latency and the closest approach on the mobbing call propensity. Df: degrees  
649 of freedom

Explanatory term	Numerator df	Residual df	F value	P value
Latency	1	60	0.04	0.8467
Closest approach	1	60	0.05	0.8235
Latency*Closest approach	1	60	0.33	0.566

650 A logistic model was used to examine whether the latency (i.e. time of arrival within the 15  
651 meter radius around the loudspeaker) and the closest approach (i.e. the minimal distance from  
652 the loudspeaker) were related to the emission of mobbing call among approaching birds.  
653 Neither the latency nor the closest approach was found related to the mobbing call propensity.

654  
655  
656

657 **Table A2**

658 Pairwise comparisons of the two principal components between each European birds mobbing  
 659 calls and the North American birds ones

	Tufted titmouse		Black-capped chickadee		Carolina wren	
	PC1	PC2	PC1	PC2	PC1	PC2
Chaffinch	<b>0.008</b>	<b>0.008</b>	<b>0.008</b>	0.151	<b>0.008</b>	0.151
Coal tit	<b>0.008</b>	0.548	<b>0.008</b>	0.309	<b>0.008</b>	0.548
Great tit	<b>0.032</b>	0.548	0.841	0.690	0.548	0.548
Blue tit	0.548	<b>0.008</b>	0.690	0.841	0.095	<b>0.008</b>

660 PC1 and PC2 respectively for the first and the second principal components. All comparisons

661 were done using a Wilcoxon exact test given the low sample size (i.e.  $N = 10$  for each test), p

662 values were not corrected for multiple comparisons. Significant  $P$  values are indicated in bold.

663

664



665 **Table A3**

666 Pairwise comparisons of responses between all mobbing call stimulus for each receiver  
 667 species

Receiver species	Pairwise comparison	$\chi^2$	<i>P</i>
Blue tit	conspecific vs BC	0.02	0.89
	conspecific vs CW	0	1
	conspecific vs TT	3.96	0.04
	BC vs CW	0.02	0.89
	BC vs TT	3.29	0.07
	CW vs TT	3.96	0.04
Coal tit	conspecific vs BC	6.83	0.009
	conspecific vs CW	12.32	0.0004
	conspecific vs TT	20.36	< 0.0001
	BC vs CW	1.18	0.28
	BC vs TT	4.92	0.03
	CW vs TT	1.24	0.27
Great tit	conspecific vs BC	0.01	0.94
	conspecific vs CW	0.22	0.64
	conspecific vs TT	0.2	0.65
	BC vs CW	0.18	0.67
	BC vs TT	0.31	0.58
	CW vs TT	0.84	0.36
Chaffinch	conspecific vs BC	11.81	0.0006
	conspecific vs CW	5.45	0.02
	conspecific vs TT	6.99	0.008
	BC vs CW	1.44	0.23
	BC vs TT	0.6	0.44
	CW vs TT	0.16	0.69

668 All comparisons were based on a partial analysis for each receiver species using a LRT based  
 669 contrast. BC for black-capped chickadee, TT for tufted titmouse and CW for Carolina wren.  
 670 df: degrees of freedom.

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## FIGURE LEGENDS

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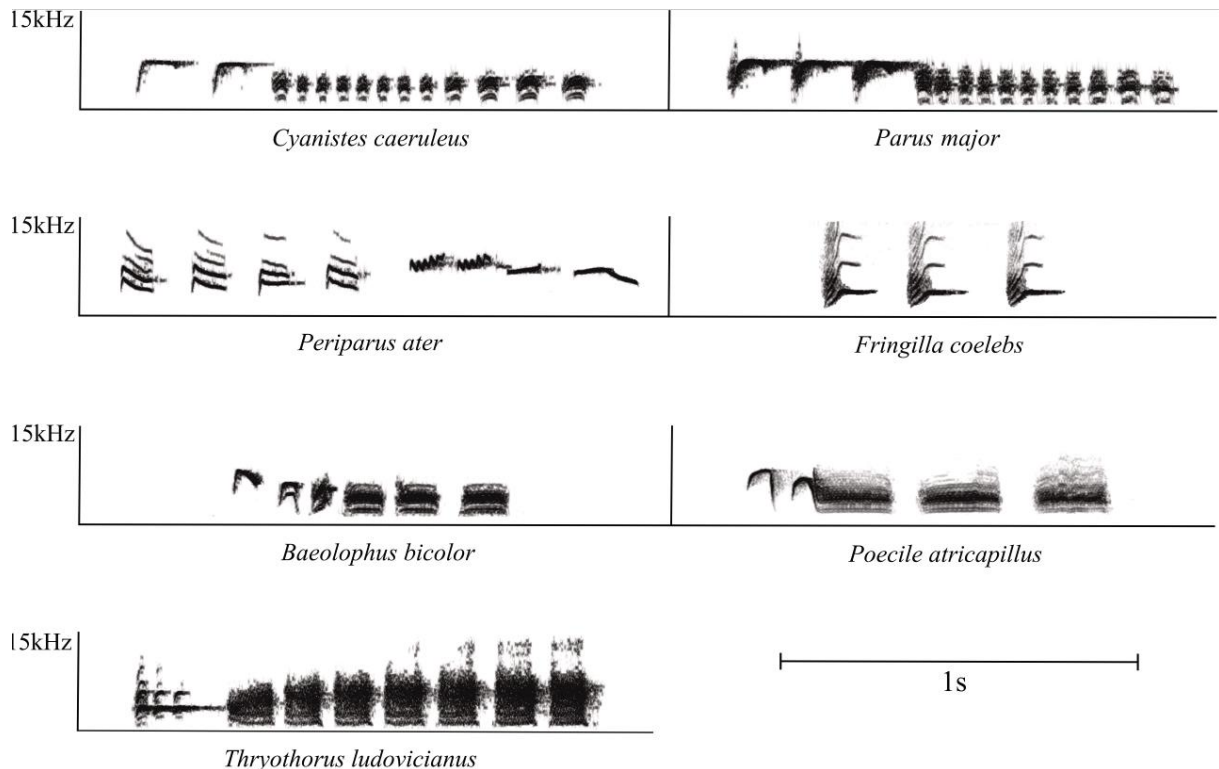
**Figure 1.** Spectrograms of the mobbing calls of studied species. Spectrograms were produced with Avisoft SASLab© (frequency sampling 44.1kHz, FFT length 512 points). See text for further details of measurements.

**Figure 2.** Principal Components plot of the acoustic characteristics of European birds mobbing calls (◆): (a) chaffinch (PC1: 40.9% and PC2: 23.2%), (b) coal tit (PC1: 50.3% and PC2: 22.3%), (c) great tit (PC1: 40.1% and PC2: 26.5%), (d) blue tit (PC1: 33.2% and PC2: 21.9%) with North American birds mobbing calls (tufted titmouse (■), a black-capped chickadee (▲), a Carolina wren (○)). The contour lines indicate the 68% probability of belonging to each putative cluster (i.e. species) which can be used to examine graphically the similitude between species. See supplementary material 2 Table A2 for pairwise comparisons performed separately on PC1 and PC2 between European and North American mobbing calls.

**Figure 3.** Proportion of European birds responding to the presentations of a tufted titmouse (light grey square), a black-capped chickadee (dark grey triangle), a Carolina wren (white circle) and a conspecific (black diamond) mobbing call. Error bars represent standard errors. See supplementary material 3 Table A3 for detail pairwise comparisons of responses between all mobbing call stimulus for each receiver species.

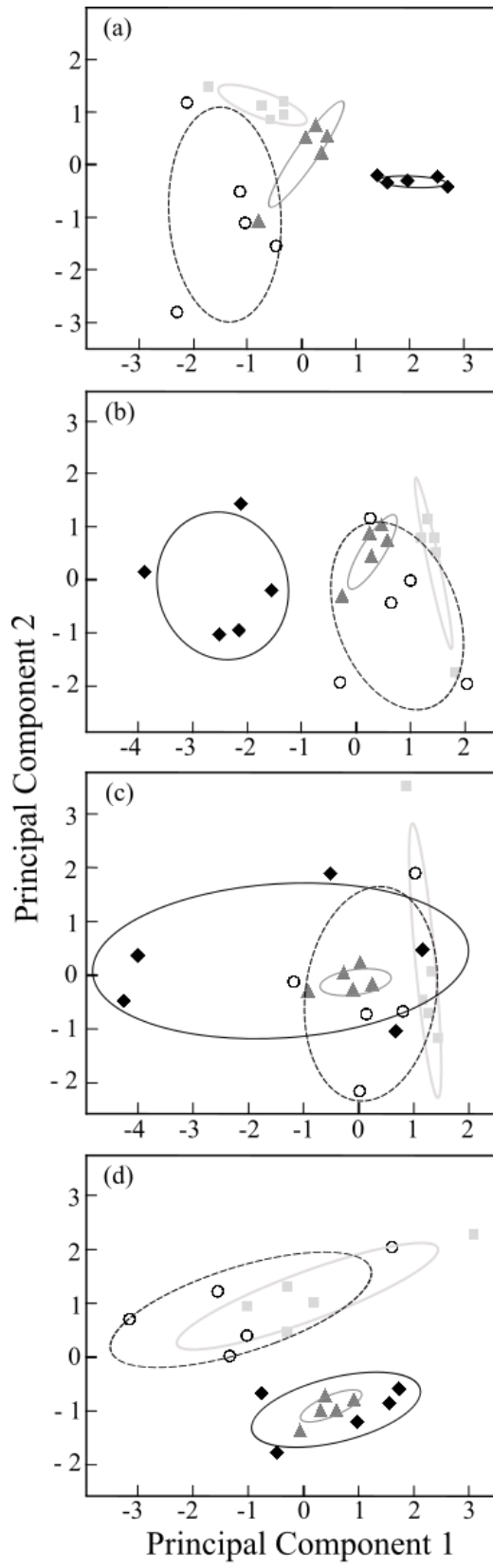
693 **Figure 1.**

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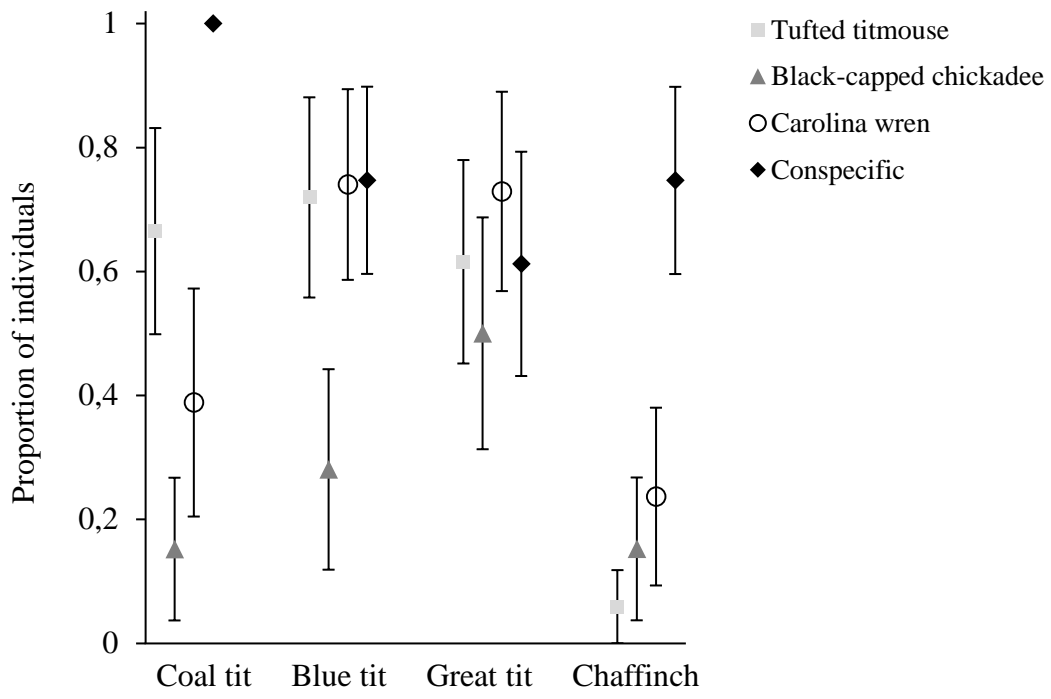


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699 **Figure 3.**



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