

1 Acoustic cues and season affect mobbing responses in a bird

2 community

3 Short title: cues and context affect heterospecific communication

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27

28 **ABSTRACT**

29 Heterospecific communication is common for birds when mobbing a predator. However,  
30 joining the mob should depend on the number of callers already enrolled, as larger mobs  
31 imply lower individual risks for the newcomer. In addition, some ‘community informant’  
32 species seem more reliable regarding the information transferred in mobbing calls. Birds  
33 should therefore rely on both the number of callers and the species identity of the caller(s)  
34 when mobbing. In the present study, we tested the potential interaction between two acoustic  
35 cues (number of callers and the species identity of the caller). Overall, we found that  
36 soundtracks with three callers triggered more mobbing than soundtracks with one caller and  
37 that soundtracks with coal tits’ calls triggered more mobbing than soundtracks with crested  
38 tits’ calls. Our results therefore support the hypothesis that birds consider both the species and  
39 the number of callers when joining a mobbing chorus in winter. However, when the same  
40 experiments were replicated during spring, only soundtracks with three coal tits triggered a  
41 mobbing response, illustrating therefore how the seasonal context interacts can strongly affect  
42 the results of studies on heterospecific communication.

43 **Keywords: heterospecific communication, mobbing call, community response,**  
44 **cooperation, seasonal effect**

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46

## 47 INTRODUCTION

48 Clustering around a predator and actively harassing it instead of fleeing is a  
49 widespread phenomenon termed ‘mobbing’. Particularly common in birds (Carlson et al.  
50 2018), mobbing encourages the predator to give up hunting and move to another location in  
51 both the short and long term (the Move-On Hypothesis, Curio 1978, Flasskamp 1994). Other  
52 benefits, such as monitoring the predators and enhancing learning opportunities for offspring,  
53 have been proposed (Curio 1978). Costs associated with such behavior are however non-  
54 negligible: in addition to the loss of time and energy when responding to an individual calling,  
55 the direct confrontation with a predator could result in direct aggression from the predator  
56 (Curio and Regelmann 1986, Poian and Yorke 1989, Sordahl 1990). Mobbing efficiency (i.e.,  
57 the ratio of costs / benefits) can be improved by increasing the number of mobbing individuals  
58 (Krams et al. 2010, Wheatcroft and Price 2018). Indeed, larger groups decrease both the  
59 individual risk of being targeted by the predator (Hamilton selfish herd or dilution effect,  
60 Foster and Treherne 1981), and the overall success of the predator through confusion effect  
61 (Carlson et al. 2018). Larger groups also increase the chances of repelling the predator  
62 (Hendrichsen et al. 2006). Such an increase of participants can be achieved both with  
63 conspecific and heterospecific individuals, and heterospecific mobs are indeed well  
64 documented (e.g., Dutour et al. 2017a, Goodale and Kotagama 2005, Hua et al. 2016).  
65 Although heterospecific mobbing responses probably emerged as simple by-product  
66 mutualism (Kostan 2002), the relationships between species can be complex. Indeed,  
67 participation in such mobs is often unequal (Dutour et al. 2017b), with some species risking  
68 less by following the group at a distance (Magrath et al. 2015). In opposition, other species

69 seem particularly active and trustworthy regarding the information conveyed in the calls  
70 (Farine et al. 2015). For such species that are active, reliable, and highly responded to, the  
71 term ‘community informant’ has been proposed (Carlson et al. 2020).

72         The rationale to join mobbing birds should therefore depend on two main acoustic  
73 cues: (i) the number of birds already mobbing, as a greater number of birds indicates a lower  
74 risk for new participants, and (ii) the species identity of the caller(s), since some species  
75 convey more reliable and relevant information than others. To test these hypotheses, we built  
76 a set of playback experiments using a factorial design. We broadcast soundtracks of either one  
77 or three coal tits (*Parus ater*) and one or three crested tits (*Lophophanes cristatus*) to free-  
78 ranging birds of both species, and recorded their behavioral response (calling and  
79 approaching, the most conspicuous signs of mobbing in birds). Following a recent study  
80 (Carlson et al. 2020), coal tits and crested tits contrast in their call reliability (i.e., coal tits  
81 vary their calls when facing different threats) and heterospecific attraction when mobbing a  
82 predator.

83         Heterospecific communication related to mobbing is prevalent in winter in passerines  
84 communities (Dutour et al. 2019), notably because of an increased tendency to flock with  
85 heterospecifics to increase predator defense and foraging efficiency (Goodale et al. 2015). We  
86 therefore chose to test first and foremost birds during winter. Yet, we also replicated the same  
87 experiment in spring to test whether the same rules apply during the reproductive season for  
88 which interspecific communication is less prominent. Indeed, throughout the year, the  
89 physical and social environment of birds varies greatly, possibly impacting their  
90 communication. In spring, the increased aggressiveness due to territoriality and nest defense

91 could affect results on mobbing behavior (Betts et al. 2005, Jiang et al. 2020). By replicating  
92 this experiment in a different season, we test how environmental parameters such as season  
93 can affect our biological conclusions.

94 Our experiment therefore aims at determining the relative flexibility of heterospecific  
95 relationships and stability of acoustic cues throughout birds' seasonal activity. By looking at  
96 the mobbing response of both coal and crested tits to each other's calls, as much as the  
97 mobbing response of the overall community, we aim at determining how context affects the  
98 acoustic cues used by birds when investing in mobbing.

99

## 100 MATERIAL AND METHODS

### 101 General organization

102 We aimed at testing the mobbing response of free-ranging birds to different  
103 soundtracks. Playback tests were done in a 10 km<sup>2</sup> area of coniferous forest in the East of  
104 France (46°13'05.0"N 5°41'50.8"E). Densities of coal and crested tits are high in this area, as  
105 shown by the long-term ornithological census in the region: both species were detected in  
106 94% of points, spaced at 150 m from each other (participative database Faune-ain.org  
107 administered by the LPO AuRA DT Ain). To circumvent inherent spatial variability, we  
108 established 100 spots for the playback tests. Each spot was selected close to a tree allowing  
109 birds' approach and concealment of experimenters, following existing trails. All spots were  
110 separated by ~ 100 m (mean and standard deviation  $X = 110.9 \pm 27.2$  m) since this distance is  
111 sufficient to degrade bird sounds (Morton 1975). In addition, we performed a complementary

112 subset of experiments (n = 22 birds tested) to verify that birds do not follow the observer  
113 between successive spots. For this purpose, we followed the same methodology than the one  
114 used by Salis et al. on great tits (2022). More specifically, both observers were equipped with  
115 the acoustic material and binoculars, and after each test, while one observer was launching the  
116 playback experiments on a subsequent location, the other was following the birds from the  
117 previous location. We found that from one test to the next one, no bird followed us, and no  
118 bird moved farther than 50 meters from their original position (see details in Supplementary  
119 File 1). While birds can travel large distances in a short period, it is unlikely that we tested the  
120 same birds in consecutive tests in the present experiment given the absence of human  
121 following and the absence of attraction from the subsequent playbacks.

122 We created a factorial design in which our four different treatments (different emitter  
123 species and number of callers, see paragraph Playbacks for details) were broadcast on each  
124 spot. These experiments were first carried out in winter, and then replicated in spring. Each  
125 spot consequently received eight playback tests. We avoided spatial and temporal  
126 autocorrelation by (i) alternating the four treatments at consecutive spots, and (ii) doing the  
127 same number of tests of each treatment, each day. The 400 tests in each season were done in a  
128 short period (two weeks) to avoid a potential intra-seasonal effect, and each consecutive test  
129 spaced by at least five minutes. We changed the order in which the spots were tested each day  
130 (different beginning point each day and different directions in the trails). Post hoc analyses  
131 (Sup. File 2) show no effect of order of playback treatment nor of the repeated presentation of  
132 playbacks on our results.

133

## 134 **Playbacks**

135 We created four treatments: soundtrack with only one calling coal tit (1CO), three coal  
136 tits calling simultaneously (3CO), only one calling crested tit (1CR), and lastly, three crested  
137 tits (3CR). We did not use a negative control (e.g., heterospecific song or background noise)  
138 since we were interested in the difference between our treatments. Moreover, background  
139 noise has been used in several studies (Dutour et al. 2019, Salis et al. 2022, Suzuki et al.  
140 2016) and never triggered a response from Parids. To prepare our soundtracks, we elicited  
141 mobbing calls from wild crested tit and coal tit by broadcasting a mobbing chorus of various  
142 birds (including coal and crested tits, Dutour et al. 2016). Once birds arrived to mob they were  
143 recorded with a ME-67 Sennheiser microphone connected to a K6 basis and a Fostex FR2LE  
144 recorder. At last, the recordings were then cleared of any other bird call, their amplitude  
145 homogenized at 50% on the entire file with AvisoftSasLab (Avisoft Bioacoustics, Glienicke,  
146 Germany), and saved as WAV files. We selected recordings with a number of calls around the  
147 mean ( $\pm 1$  SD) of previous recordings obtained by our team (coal tit:  $82 \pm 26$  notes per min,  $N$   
148 = 30, crested tit:  $134 \pm 44$  notes per min,  $N = 10$ ). For the treatments with three birds (trio  
149 treatments), we superimposed recordings of three different birds calling to simulate a chorus.  
150 As a result, the final duty cycle (i.e., the amount of signal present in the playbacks) was higher  
151 for the three-birds treatment ( $\sim 9$  seconds) than for the one-bird treatments ( $\sim 6.5$  seconds,  
152 details in Sup. File. 3). Nevertheless, the calls substantially overlapped, reducing the risk for  
153 the focal birds to consider the three-birds treatments as only one bird calling intensely. For  
154 each treatment, we built five different soundtracks to circumvent the idiosyncrasy of recorded  
155 subjects (Kroodsma 1989).

156

157 **Test procedure**

158 One test consisted in playing 30 sec of a mobbing call sequence at each spot with a  
159 Bose Soundlink Revolve loudspeaker perched on a tripod (H: 1m), put near a tree and at an  
160 amplitude of  $84.01 \pm 2.70$  dB (calculated at 1 m with Lutron SL-4001, C weighting, slow  
161 settings, re. 20  $\mu$ Pa, Templeton et al., 2016). 30 sec is enough to trigger a mobbing response  
162 from nearby birds (previous recordings were obtained with such a stimulation), who can  
163 approach and call as a response, sometimes with additional aggressive behavior (e.g., wing  
164 flicking, Salis et al. 2021). A stimulation of only 30 seconds also limited the influence of the  
165 first birds to call on the following birds recruited. The two observers positioned themselves at  
166 10 m from the tripod at vantage points before launching the soundtrack with an NW-A45  
167 Sony. Before launching any test, we made sure that no bird was already in the vicinity nor  
168 uttering mobbing calls in a distance. **If a bird was detected, we waited only it left the area**  
169 **(~10m around the loudspeaker).** We observed the area with binoculars and all birds either  
170 calling and/or approaching from the beginning of the test to 15 sec after the end of the  
171 soundtrack. One bird was considered as approaching if it came in the 10 m radius around the  
172 tripod (Dutour et al. 2017b). Only birds uttering specific and known mobbing calls (see Sup.  
173 File 4 for spectrograms) were noted as calling. If a bird displayed the complete sequence of  
174 mobbing behavior (i.e., simultaneously calling and approaching the loudspeaker), it was then  
175 considered as giving a mobbing response. **The two observers agreed on the lowest number of**  
176 **birds seen simultaneously by both experimenters.**

177



178 **Statistical analyses**

179 All statistical analyses were done with R studio (R v.3.6.1, R core team 2022).

180 Since the number of responding birds during the winter cannot be strictly compared to  
181 the one observed during the spring, analyses were done separately for each season. We used  
182 three response variables: the number of responding birds at the community level, the number  
183 of responding coal tits, and the number of responding crested tit. All these three response  
184 variables were thus analyzed separately for each season and following the same model  
185 framework. More specifically, for each response variable, we constructed an initial Hurdle  
186 mixed model. Hurdle models are two stage mixture models enabling to take into account  
187 excess of zero for count data (Zuur et al. 2009). This model framework is particularly suitable  
188 in our case since it involves a first process that determine the occurrence of an event (here the  
189 presence of at least one responding bird, i.e., mobbing occurrence) using a Binomial  
190 distribution, and a second one that determine the number of events (here when the number of  
191 responding birds is  $> 0$ , i.e. mobbing intensity) using a truncated count distribution. Such  
192 models are notably used in parasitology to segregate the effects on the host susceptibility and  
193 those affecting the infection intensity (e.g., Planade et al. 2009). We used a truncated  
194 Negative Binomial distribution to model the second stage (i.e. Hurdle Negative Binomial  
195 model, hereafter referred as HNB model) since preliminary analyses revealed that a truncated  
196 Poisson distribution performed less well than the HNB models, and the residuals of the latter  
197 did not indicate a lack of fit (function *testResiduals* of the package *DHARMA*, v. 0.4.5, Hartig  
198 and Hartig 2017). Both the effect of the emitter species, the one of the number of callers and  
199 their interactive effect were introduced in both fixed parts of the initial model. Moreover, both

200 the spot location and the soundtracks' ID were introduced as random effects in the model. The  
201 random effects were not added in the models analyzing the response of crested tits because of  
202 a general lower response precluding the correct estimation of the random effects. All initial  
203 full models were implemented using the package *glmmTMB* (v.1.1.2.3, Brooks et al. 2017),  
204 and were further reduced to construct all nested models (i.e., a set of 25 models including the  
205 full one for each response variable). Multimodel inference (Anderson and Burnham 2002)  
206 was used to select the best supported models for each response variable. For this task, we used  
207 the Bayesian Information Criterion (BIC) instead of the AIC since the former is more  
208 sensitive to the sample size than the latter (although both criteria gave a similar model  
209 selection, results not shown). We calculated the weighted BIC (wBIC) to calculate the  
210 evidence ratio between two models (i.e., calculate how much better is the best model  
211 compared to the other ones). The delta BIC (difference between two consecutive models) are  
212 given (a delta >2 is commonly considered to represent a significant difference between  
213 models). Effects sizes of the differences between treatments were calculated with odds ratios  
214 (OR).

215

## 216 **RESULTS**

### 217 **Mobbing responses in winter**

218 Eleven different species were attracted to our soundtracks (Figure 1A), with a  
219 maximum diversity of six species at one test. The two main species, apart from coal and  
220 crested tits, were the Goldcrest (*Regulus regulus*, present in 39% of our tests) and the Marsh

221 tit (*Poecile palustris*, 23%). As indicated by the best supported model (lowest BIC and an  
222 evidence ratio of 10, Table 1A), mobbing occurrence (the probability that at least one bird  
223 responded to the playback), irrespective of the species (i.e., at the community level, Figure 2A)  
224 was affected by an additive effect of both the number of callers in the playback and the caller  
225 species (Table 1A). Indeed, birds mobbed more often the coal tit soundtracks compared to the  
226 crested tit soundtracks, and more to soundtracks with three birds rather than only one bird  
227 calling (1CO: 64%, 3CO: 77%, 1CR: 33%, 3CR: 59%). This additive effect was also detected  
228 when looking at the mobbing intensity (i.e., the number of mobbing birds when mobbing  
229 occurs, Figure 2B). Indeed, the largest mobs were initiated by playbacks with three coal tits  
230 ( $4.22 \pm 3.65$  birds, mean  $\pm$  standard deviation) while the smaller mobs were initiated by  
231 playbacks with one crested tit ( $1.88 \pm 1.24$  birds).

232 When focusing on the response of coal tits or the one of the crested tits, the best  
233 supported model comprised an additive effect of the number of callers and the emitter species  
234 (Table 1B and 1C), resulting in a lower response toward singletons of crested tits (8% of  
235 points attracted coal tits or crested tits), intermediate scores toward trios of crested tits and  
236 singletons of coal tits, and the highest occurrence of response toward soundtracks with three  
237 coal tits (46% triggered a response from coal tits and 41% triggered a response from crested  
238 tits, Figure 2C and 2E). However, for the crested tit, the model with an interaction between  
239 number of callers and emitter species was also well supported (Delta < 2 and evidence ratio of  
240  $0.35/0.29 = 1.21$ , Table 1C). Indeed, the difference between 1CR and 3CR was higher (OR:  
241 4.74, 95%CI: [1.92; 10.40]) than the difference between 1CO and 3CO (OR: 1.35, 95%CI:  
242 [0.76; 2.40]). Regarding mobbing intensity, no difference was detected between any of the

243 four playback treatments for the coal tit's response nor for the crested tit's response (Figure  
244 2D and 2F).

245

## 246 **Mobbing responses in spring**

247 In spring, we detected a lower mobbing propensity: the occurrence of response to any  
248 treatment did not reach 25%, compared to almost 50% in winter. 15 different species were  
249 attracted to our soundtracks (Figure 1B), with a maximum diversity of five species at one test.  
250 The two most common species that responded were the Goldcrest (present in 24% of our  
251 tests) and the Common Chaffinch (*Fringilla coelebs*, 18%). The mobbing occurrence at the  
252 community level was not impacted by any of the four playback treatments (Table 1D, Figure  
253 3A). However, both the model with an interaction between number of callers and emitter  
254 species and the model with the number of callers alone were also well supported (similar BIC  
255 and wBIC, Table 1D). As a consequence, there is not strong evidence for any impact of either  
256 number of callers nor emitter species in our playbacks on the community response. The effect  
257 sizes depict a higher response towards the 3CO treatment than towards any of the three other  
258 playbacks (e.g., 3CO vs 3CR: 3.03, 95%CI: [1.70; 5.38]), while the three other playbacks  
259 triggered a similar response (e.g., 3CR vs 1CO: 1.14, 95%CI: [0.64; 2.05]). When focusing on  
260 the intensity of response (Figure 3B), only the emitter species impacted the size of the mobs,  
261 with coal tits' playbacks attracting more birds (respectively  $1.69 \pm 0.98$  birds and  $2.23 \pm 1.51$   
262 for 1CO and 3CO, and  $1.27 \pm 0.63$  birds and  $1.44 \pm 0.96$  birds for 1CR and 3CR).

263 The best supported model regarding the presence of at least one coal tit included the  
264 emitter species of the playback (Figure 3C, Table 1E), while the presence of at least one  
265 crested tit was more impacted by the number of callers in the playback (Figure 3E, Table 1F).  
266 We did not detect a difference in mobbing intensity between the four playbacks (Figure 3D  
267 and 3F).

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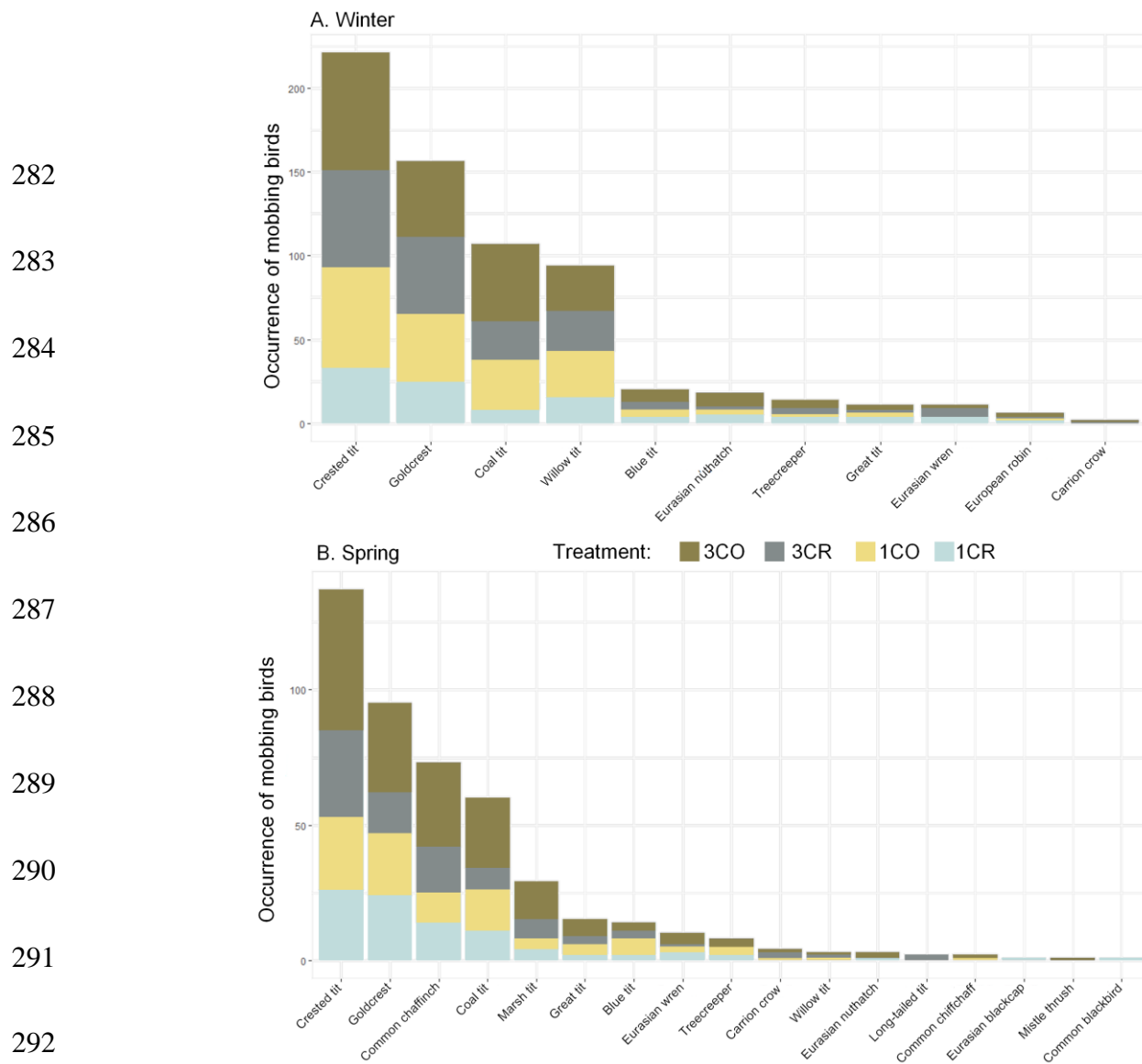
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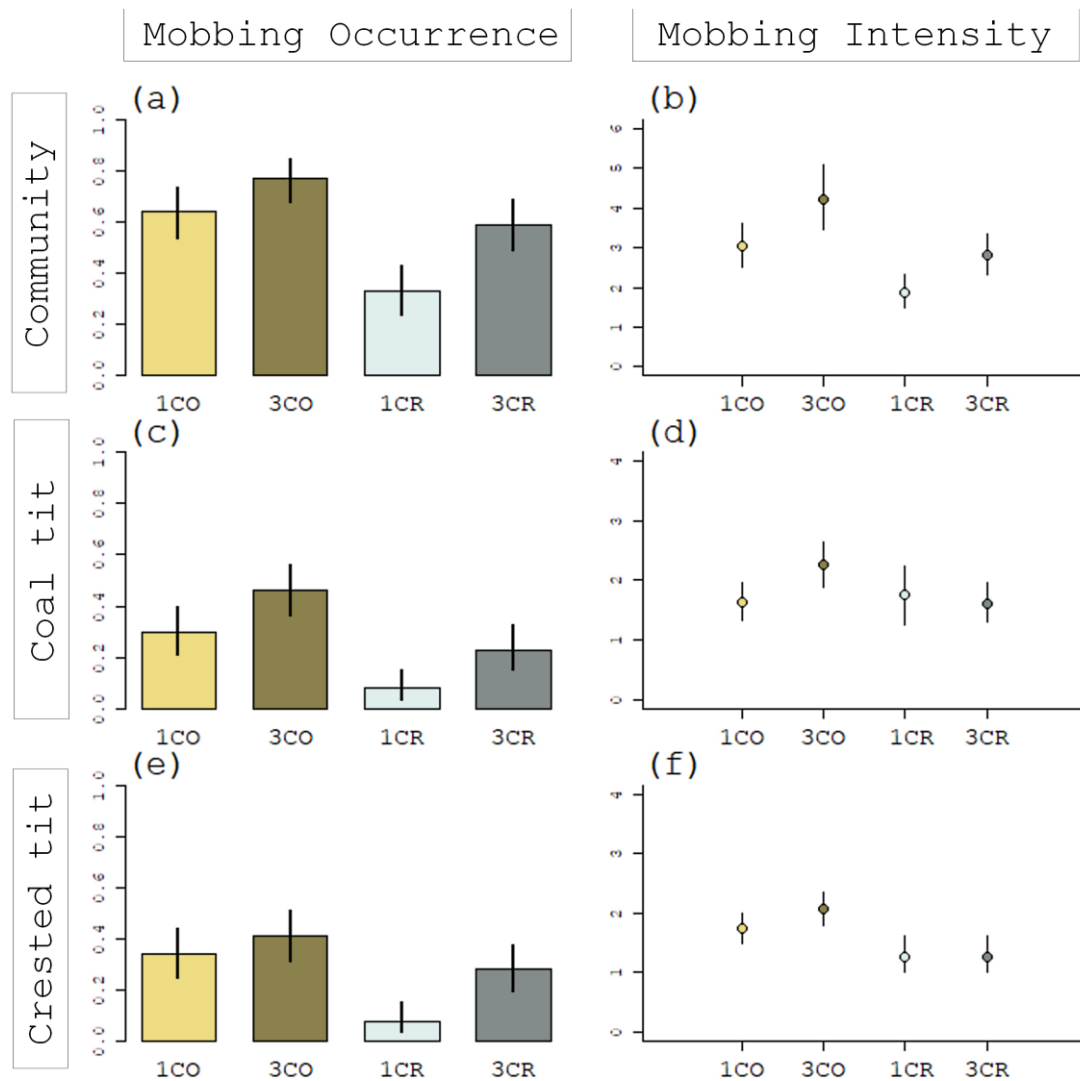
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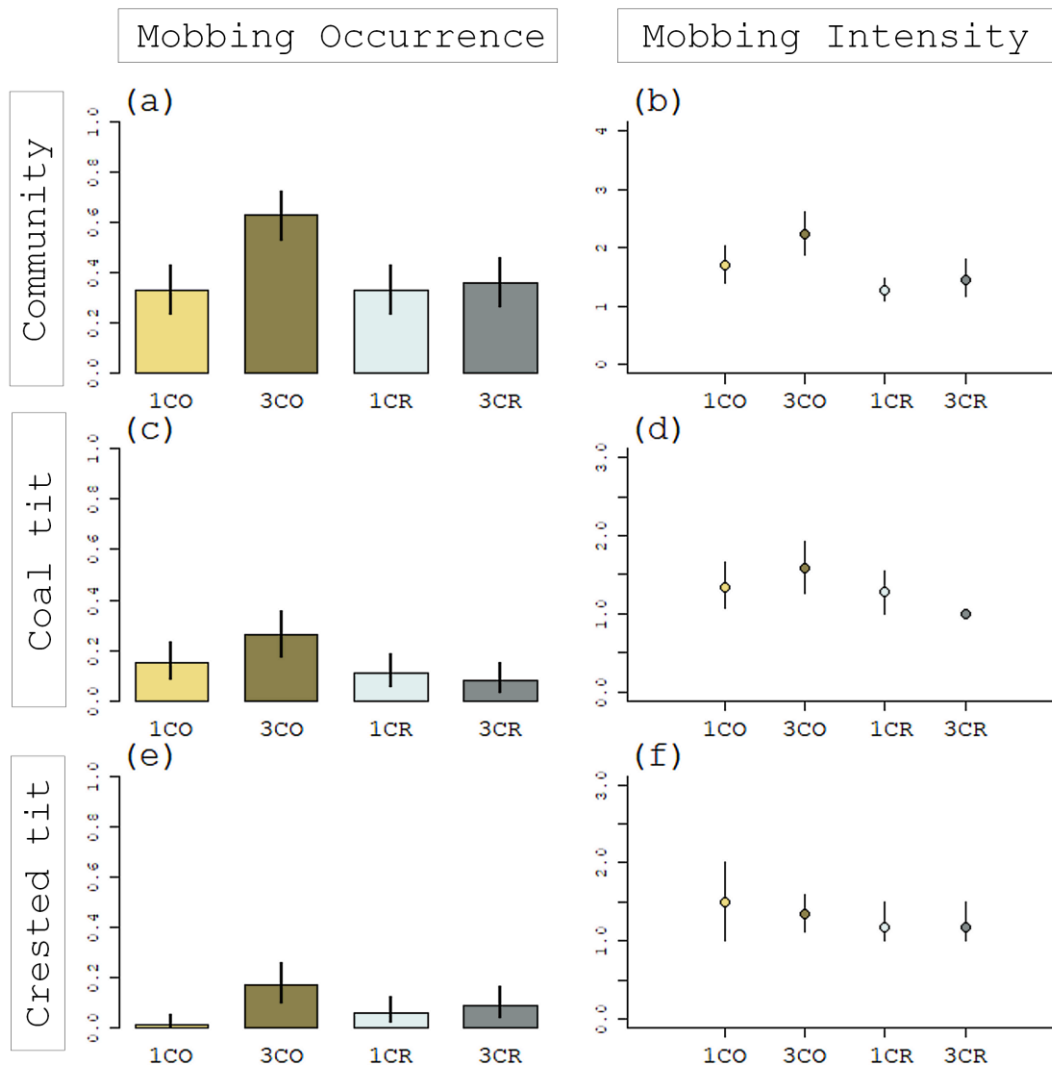
293 **Figure 1.** Number of spots (100 per acoustic treatment) in which at least one bird of each species  
 294 mobbed (i.e., approached and called), when facing each of our four acoustic treatments (3CO: three  
 295 coal tits, 1CO: one coal tit, 3CR: three crested tits, 1CR: one crested tit). Species taxonomy : Blue tit =  
 296 *Cyanistes caeruleus*, Carrion crow = *Corvus corone*, Crested tit = *Lophophanes cristatus*, Coal tit =  
 297 *Periparus ater*, Common blackbird = *Turdus merula*, Common chaffinch = *Fringilla coelebs*,  
 298 Common chiffchaff = *Phylloscopus collybita*, Eurasian nuthatch = *Sitta europaea*, Eurasian wren =  
 299 *Troglodytes troglodytes*, European blackcap = *Sylvia atricapilla*, European Robin = *Erithacus*  
 300 *rubecula*, Goldcrest = *Regulus regulus*, Great tit = *Parus major*, Long-tailed tit = *Aegithalos caudatus*,  
 301 Marsh tit = *Poecile palustris*, Mistle thrush = *Turdus viscivorus*, Treecreeper = *Certhia familiaris*,  
 302 Willow tit = *Poecile montanus*.



303

304 **Figure 2.** Mobbing response of the bird community tested in winter to our four different  
 305 mobbing soundtracks (1CO: one coal tit, 3CO: three coal tits, 1CR: one crested tit, 3CR: three  
 306 crested tits). Error bars are 95% confidence intervals. Graphs on the left represent mobbing  
 307 occurrence: the proportion of spots in which at least one bird mobbed (i.e., approach and  
 308 called,  $N = 100$  per treatment). Graphs on the right represent mobbing intensity: the number  
 309 of birds that responded when there was a mobbing response (sample sizes are the proportion  
 310 of the graphs on the left). The upper graphs are the response of the general bird community,  
 311 middle graphs responses from coal tits, and lower graphs are response from crested tits.

312



313 **Figure 3.** Mobbing response of the bird community tested in a replication of the first  
314 experiment, during the reproductive season (spring). Birds' responses are recorded when  
315 facing four different mobbing soundtracks (1CO: one coal tit, 3CO: three coal tits, 1CR: one  
316 crested tit, 3CR: three crested tits). Error bars are 95% confidence intervals. Graphs on the left  
317 represent mobbing occurrence: the proportion of spots in which at least one bird mobbed (i.e.,  
318 approach and called,  $N = 100$  per treatment). Graphs on the right represent mobbing intensity:  
319 the number of birds that responded when there was a mobbing response (sample sizes are the  
320 proportion of the graphs on the left). The upper graphs are the response of the general bird  
321 community, middle graphs responses from coal tits, and lower graphs are response from  
322 crested tits.



323

324 **Table 1.** Hurdle models selection tables. A full mixed Hurdle model was constructed for each  
 325 response variable (number of responding birds at the community level, number of responding  
 326 coal tits, number of responding crested tits), and further reduced to construct the whole set of  
 327 reduced models. The full model included both the effect of the emitter species, the one of the  
 328 number of callers as well as their interactive effect in both fixed parts of the model (i.e.  
 329 mobbing occurrence modeled using a Binomial distribution, and mobbing intensity using a  
 330 truncated Negative Binomial distribution). We provide the three best supported models  
 331 according to the Bayesian Information Criterion (BIC), and the ones with the lowest BIC are  
 332 in bold. The weighted BIC (wBIC) represent the relative likelihood of our models. With  
 333 wBIC we can calculate evidence ratio between two models (e.g., the first model is 0.76 /  
 334 0.076 = 10 times more supported than the second model). The delta BIC (difference between  
 335 two consecutive models) are given (a delta >2 is commonly considered to represent a  
 336 significant difference between models).

337

	Occurrence (Presence of mobbers)	Intensity (Number of mobbers)	BIC	wBIC	Delta
<b>Winter</b>					
<b>A. Community</b>	<b>Emitter Species + Number of callers</b>	<b>Emitter Species + Number of callers</b>	1471.13	0.76	0
	Emitter Species + Number of callers	Emitter Species	1475.73	0.076	4.6
	Emitter Species * Number of callers	Emitter Species + Number of callers	1476.03	0.065	4.9
<b>B. Coal tit</b>	<b>Emitter Species + Number of callers</b>	<b>∅</b>	758.13	0.61	0
	Emitter Species + Number of callers	Number of callers	761.04	0.14	2.91
	Emitter Species + Number of callers	Emitter Species	761.56	0.11	3.43
<b>C. Crested tit</b>	<b>Emitter Species + Number of callers</b>	<b>∅</b>	732.47	0.35	0
	Emitter Species * Number of callers	∅	732.83	0.29	0.35
	Emitter Species + Number of callers	Emitter Species	735.36	0.08	2.89

Spring					
D. Community	∅	Emitter Species	962.94	0.18	0
	Number of callers	Emitter Species	963.17	0.17	0.21
	Emitter Species * Number of callers	Emitter Species	963.47	0.14	0.53
E. Coal tit	Emitter Species	∅	473.21	0.54	0
	∅	∅	475.71	0.16	2.5
	Emitter Species	Emitter Species	475.83	0.15	2.63
F. Crested tit	Number of callers	∅	281.35	0.75	0
	Number of callers	Emitter Species	285.37	0.10	4.03
	Emitter Species * Number of callers	∅	286.37	0.06	5.02

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341

## 342 **DISCUSSION**

343           In winter, coal tits' soundtracks triggered more mobbing response from conspecifics  
344 and heterospecifics than crested tits' soundtracks; and soundtracks with three callers triggered  
345 more mobbing response from the bird community than soundtracks with only one caller.  
346 However, when replicating the experiment in spring, we found a lower general response but  
347 also difference between playbacks, with increased responses only toward the 3 coal tits'  
348 playbacks. This interaction between context and acoustic cues demonstrates the flexible  
349 nature of heterospecific communication.

350

351 **In winter, both the number of caller and emitter species influence mobbing responses**

352 The mobbing response towards soundtracks with three individuals calling triggered  
353 higher responses than soundtracks with only one individual calling. These results corroborate  
354 the hypothesis that a greater number of birds mobbing a predator represents a lower risk for a  
355 potential mobber, as it probably represents a lower risk of attack from the predator (confusion  
356 and dilution effect, Sridhar et al. 2009). One previous study found similar results with the  
357 Australian magpie (*Gymnorhina tibicen*, Igc et al. 2019), but with flee calls. Magpies flew  
358 and scanned more in response to soundtracks with more individuals. Birds can consider  
359 several acoustic criteria to assess the number of birds calling. First, birds can consider the  
360 number of spatially different acoustic sources (Bradbury and Vehrencamp 2011). In our  
361 study, we launched the soundtracks with only one loudspeaker whatever the treatment to  
362 suppress this effect. Therefore, in our tests, the acoustic criteria that remain available are the  
363 duty cycle (i.e., the proportion of the calling sequence when the signal is present), and the  
364 count of calling individual through individual signatures. Our experiment does not add any  
365 insights on which criteria was used by birds. Based on the current literature, the duty cycle is  
366 probably one major coding strategy for increased risk in Parids (Landsborough et al. 2020,  
367 Salis et al. 2022), and Parids modify their response to unknown non-Parids calls with different  
368 duty cycles (Dutour et al. 2022). Regarding caller identity, great tits (*Parus major*) increased  
369 their mobbing response toward soundtracks made with calls of several individuals compared  
370 to soundtracks with only one individual calling (Dutour et al. 2021). In this latter experiment,  
371 the duty cycles of the different treatments were strictly equal. This result was however not  
372 replicated when testing the response to different number of heterospecifics (chaffinches  
373 *Fringilla coelebs*, Dutour and Randler 2021). In our experiments, we believe that the  
374 overlapping of the calls in the three birds treatments avoid the risk of interpreting these

375 treatments as only one bird calling intensely. However, experiments with non-overlapping  
376 calls and similar duty cycles could provide insight on this issue.

377 A mobbing response occurred more often when broadcasting coal tits' mobbing calls  
378 compared to crested tits' calls, but also more birds responded to it. Unexpectedly, even  
379 crested tits responded more to coal tits' mobbing calls than to calls from their own species.  
380 Coal tits therefore appear to be listened to and heavily responded to, leading to larger (and  
381 possibly more efficient) mobs. This is in line with the hypothesis that species from the same  
382 community show different levels of reliability (Magrath et al. 2015). The notion of  
383 "community informant" was developed for Parids in Carlson et al. (2020). They investigated  
384 whether the birds possessed a reliable way of encoding predator information, and if several  
385 heterospecifics relied on these calls. They showed that the great tit (*Parus major*) best fitted  
386 the definition of community informant. The coal tit approached the definition, with only one  
387 caveat: the dunnock (*Prunella modularis*) did not respond to it. As the authors suggested, the  
388 lack of response from one species does not mean that other species from the community do  
389 not respond to it (Carlson et al. 2020). Indeed, in our study, 14 species responded to coal tits'  
390 soundtracks. In opposition, the crested tit did not meet any of the criteria set by Carlson and  
391 colleagues. Coal tits appear therefore to be one important species regarding predator  
392 information in the community, and this is congruent with their increased sensibility to  
393 predation by pygmy owls (*Glaucidium passerinum*) in winter (Suhonen et al. 1993).

394

395 **Replicating the experiment in spring: A lower general response**

396 In winter, Parids living in temperate regions often flock with heterospecifics,  
397 sometimes leading to impressive mobs (up to 20 birds in the present experiment). In  
398 opposition, during the reproductive period (May-July), Parids nest and defend their territory  
399 with intensity (Hinde 1952). Spring territoriality may explain one of our results: we detected a  
400 lower number of birds mobbing to the different soundtracks in spring. We here propose that in  
401 spring, when all birds defend their territory, the number of birds that can respond is restricted  
402 to the neighbors. Moreover, in spring, aggressivity toward conspecifics is high and may  
403 therefore reduce the number of potential birds responding to mobbing calls. This aggressivity  
404 may also explain why not so many birds responded to conspecific mobbing calls in spring  
405 (coal tits to coal tits and crested tits to crested tits). Secondly, our results depict an apparent  
406 decrease in mobbing occurrence in spring compared to winter. This difference must be taken  
407 with cautiousness, as the community and the density of the population may vary with the  
408 seasons: a decrease in mobbing response may simply be related to fewer individuals in the  
409 territory. An order effect due to tests in winter being done before the tests in spring is unlikely  
410 given the absence of order effect in our experiment at a short time scale (see Sup. Mat. For  
411 details). In addition, in spring, we were able to hear coal tits singing at the 100 spots studied.  
412 We are therefore confident that, in spring, each spot could have recorded one coal tit's  
413 mobbing response. This suggests that at least for the coal tit, the response to conspecific and  
414 heterospecific mobbing calls decreases in spring. This result is consistent with Dutour et al.  
415 (2019) who detected in Parids a higher mobbing response toward heterospecific calls in  
416 winter compared to summer. The proximal reasons for such a decrease can be various.  
417 Increased territoriality and aggression in spring may very well limit cooperative  
418 communication, since the mobbing calls may resemble intra-specific aggression/territoriality

419 calls, leading to a lower relevance for heterospecifics. Other factors such as decreased  
420 predator pressure in spring (Dutour et al. 2017b) could also result in a lower investment in  
421 mobbing in spring. The ratio cost/benefits in responding to distanced mobbing calls is  
422 therefore probably flexible through different times of the year. Given that most of these  
423 factors are intercorrelated, determining which one is responsible for the difference in mobbing  
424 is unfeasible in natural conditions.

425

426 **Replicating the experiment in spring: Almost no response to crested mobbing**  
427 **calls**

428 In addition to a general lower mobbing response in spring, the differences between  
429 treatments were also impacted by the season. Indeed, while we selected similar models for the  
430 community, coal tits', and crested tits' response in winter (additive effect of number of caller  
431 and emitter species), we found different models in spring. A general tendency was detected,  
432 with only the playbacks with three coal tits triggering more response than the three other  
433 playbacks. This suggests that the crested tit is not considered as informative in spring, even  
434 when mobbing in groups, and unexpectedly, even to conspecifics. Three explanations can be  
435 proposed. Firstly, a group of three crested tits in spring may be too rare to bear meaning, as  
436 they are in pairs and defending their nest. However, this hypothesis does not stand as this is  
437 also the case for the coal tit, but that the difference between one and three callers still stands  
438 in spring for this species. **Alternatively, the contact with crested tits may be reduced in spring**  
439 **if crested tits densities are lower during this season, hence decreasing learning opportunities**  
440 **for heterospecifics. However, crested tits stay on the same territory throughout the year**

441 (Ekman 1979) making this hypothesis unlikely despite our experiments do not allow us to  
442 formally rule out it. We rather suggest that this lack of mobbing response may emerge from  
443 reduced reliability of the calls. To be efficient, an acoustic signal needs to be easily  
444 distinguishable from other signals (Bradbury and Vehrencamp 2011). The song and mobbing  
445 calls of the crested tits are extremely similar (Cramp and Perrins 1993, Hailman 1989). As  
446 crested tits produce both songs and mobbing calls in spring, we can hypothesize that the  
447 global vocal production of crested tits therefore becomes less reliable from an external  
448 individual, hence leading to a decreased response to such calls. In contrast, the coal tit appears  
449 to be reliable and responded to in both seasons. This result is in adequacy with Jiang et al.  
450 (2020) who also found that between seasons differences in playback responses did not affect  
451 the nuclear status of some particular species (in their case, David's Fulvetta *Alcippe davidi*).  
452 The difference between the response of the bird community to coal tits' playbacks compared  
453 to crested tits' playbacks may also be due to a higher aggressiveness from crested tits. Crested  
454 tits are known to be more aggressive during spring (Campbell 1958), and crested tits, larger  
455 than coal tits, have higher rank dominance status (Suhonen et al. 1993). We have however  
456 little data on whether the heterospecific aggressivity is higher than coal tits' aggressivity since  
457 dominance status are not necessarily linked to increased aggressiveness (Wilson 1992).  
458 Finally, difference in nest predation may impact the reliability of the information produced,  
459 but to our knowledge, nest predators are very similar between Parid species (Cramp and  
460 Perrins 1993).

461 To conclude, individuals from different species rely on several acoustic cues when  
462 responding to conspecific or heterospecific mobbing calls. Both the number of callers and the

463 species calling are salient to the receivers, and those acoustic cues are not used in the same  
464 way throughout the year. These results emphasize the importance of seasons in studies  
465 investigating the complexity of heterospecific communication.

466

## 467 REFERENCES

468 Anderson DR, Burnham KP. 2002. Avoiding pitfalls when using information-theoretic  
469 methods. *J Wildl Manag.* 66:912–918.

470 Betts MG, Hadley AS, Doran PJ. 2005. Avian Mobbing Response is Restricted by Territory  
471 Boundaries : Experimental Evidence from Two Species of Forest Warblers. *Ethology.*  
472 111:821–835. <https://doi.org/10.1111/j.1439-0310.2005.01109.x>

473 Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland, MA:  
474 Sinauer Associates.

475 Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ,  
476 Maechler M, Bolker BM (2017). glmmTMB Balances Speed and Flexibility Among Packages  
477 for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal.* 9:378–400.  
478 <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>

479 Broughton RK, Maziarz M, Hinsley SA. 2019. Social structure of Coal Tits *Parus ater* in  
480 temperate deciduous forest. *J Ornithol.* 160:117-126. [https://doi.org/10.1007/s10336-018-](https://doi.org/10.1007/s10336-018-1594-4)  
481 [1594-4](https://doi.org/10.1007/s10336-018-1594-4)

482 Campbell, B. 1958. The crested tit. Forestry commission leaflet, Her Majesty's stationery  
483 office.



484 Carlson NV, Healy SD, Templeton CN. 2018. Mobbing. *Cur Biol.* 28:R1081–R1082.  
485 doi:10.1016/j.cub.2018.06.025

486 Carlson NV, Healy SD, Templeton CN. 2020. What makes a ‘community informant’?  
487 Reliability and anti-predator signal eavesdropping across mixed-species flocks of tits. *Anim*  
488 *Behav Cogn.* 7:214–246. <https://doi.org/10.26451/abc.07.02.13.2020>

489 Cramp S, Perrins CM, Brooks DJ. 1993. Vol. VII: Flycatchers to shrikes. Oxford, UK:  
490 Oxford University Press.

491 Cully JF, Ligon JD. 1986. Seasonality of Mobbing Intensity in the Pinyon Jay. *Ethology*  
492 71:333–339. <https://doi.org/10.1111/j.1439-0310.1986.tb00597.x>

493 Curio E. 1978. The adaptive significance of avian mobbing: I Teleonomic hypotheses and  
494 predictions. *Z Tierpsychol.* 48:175–183. <https://doi.org/10.1111/j.1439-0310.1978.tb00254.x>

495 Curio E, Regelman K. 1986. Predator harassment implies a real deadly risk: A reply to  
496 Hennessy *Ethology.* 72:75–78. <https://doi.org/10.1111/j.1439-0310.1986.tb00607.x>

497 Dutour M, Lena JP, Lengagne T. 2016. Mobbing behaviour varies according to predator  
498 dangerousness and occurrence. *Anim Behav.* 119:119–124.  
499 <https://doi.org/10.1016/j.anbehav.2016.06.024>

500 Dutour M, Léna JP, Lengagne T. 2017a. Mobbing calls: a signal transcending species  
501 boundaries. *Anim Behav.* 131:3–11. <https://doi.org/10.1016/j.anbehav.2017.07.004>

502 Dutour M, Lena JP, Lengagne T. 2017b. Mobbing behaviour in a passerine community  
503 increases with prevalence in predator diet. *Ibis.* 159:324–330.  
504 <https://doi.org/10.1111/ibi.12461>

505 Dutour M, Cordonnier M, Léna JP, Lengagne T. 2019. Seasonal variation in mobbing  
506 behaviour of passerine birds. J Ornithol. 160:509–514. [https://doi.org/10.1007/s10336-019-](https://doi.org/10.1007/s10336-019-01630-5)  
507 [01630-5](https://doi.org/10.1007/s10336-019-01630-5)

508 Dutour M, Fernández GJ, Randler C. 2022. How great tits respond to urgency-based  
509 information in allopatric Southern house wren mobbing calls. Ethology. 128: 676-683.  
510 <https://doi.org/10.1111/eth.13329>

511 Dutour M, Kalb N, Salis A, Randler C. 2021. Number of callers may affect the response to  
512 conspecific mobbing calls in great tits (*Parus major*). Behav Ecol Sociobiol. 75:1–8.  
513 <https://doi.org/10.1007/s00265-021-02969-7>

514 Dutour M, Randler C. 2021. Mobbing responses of great tits (*Parus major*) do not depend on  
515 the number of heterospecific callers. Ethology. 127:379-384.  
516 <https://doi.org/10.1111/eth.13138>

517 Ekman J. 1979. Coherence, composition and territories of winter social groups of the willow  
518 tit *Parus montanus* and the crested tit *P cristatus*. Ornis Scand. 10:56–68.  
519 <https://doi.org/10.2307/3676345>

520 Farine DR, Aplin LM, Sheldon BC, Hoppitt W. 2015. Interspecific social networks promote  
521 information transmission in wild songbirds. Proc Royal Soc B. 282:20142804.  
522 <https://doi.org/10.1098/rspb.2014.2804>

523 Flasskamp A. 1994. The adaptive significance of avian mobbing V An experimental test of  
524 the ‘move on’hypothesis. Ethology. 96:322–333. [https://doi.org/10.1111/j.1439-](https://doi.org/10.1111/j.1439-0310.1994.tb01020.x)  
525 [0310.1994.tb01020.x](https://doi.org/10.1111/j.1439-0310.1994.tb01020.x)

526 Foster WA, Treherne JE. 1981. Evidence for the dilution effect in the selfish herd from fish  
527 predation on a marine insect. *Nature*. 293:466–467. <https://doi.org/10.1038/293466a0>

528 Goodale E, Kotagama SW. 2005. Testing the roles of species in mixed-species bird flocks of  
529 a Sri Lankan rain forest. *J Trop Ecol*. 21:669–676.  
530 <https://doi.org/10.1017/S0266467405002609>

531 Goodale E, Ratnayake CP, Kotagama SW. 2014. Vocal Mimicry of Alarm-Associated Sounds  
532 by a Drongo Elicits Flee and Mobbing Responses from Other Species that Participate in  
533 Mixed-Species Bird Flocks. *Ethology*. 120:266–274. <https://doi.org/10.1111/eth.12202>

534 Goodale E, Ding P, Liu X, Martínez A, Si X, Walters M, et al. 2015. The structure of mixed-  
535 species bird flocks, and their response to anthropogenic disturbance, with special reference to  
536 East Asia. *Avian Res*. 6:14. <https://doi.org/10.1186/s40657-015-0023-0>

537 Hailman JP. 1989. The organization of major vocalizations in the Paridae. *Wil Bull*. 101:305–  
538 343.

539 Hartig F, Hartig MF. 2017. Package ‘DHARMA’. Vienna, Austria: R Development Core  
540 Team.

541 Hendrichsen D, Christiansen PK, Nielsen E, Dabelsteen T, Sunde P. 2006. Exposure affects  
542 the risk of an owl being mobbed—experimental evidence. *J Avian Biol*. 37:13–18.  
543 <https://doi.org/10.1111/j.2005.0908-8857.03658.x>

544 Hinde, RA. 1952. The behaviour of the great tit (*Parus major*) and some other related species.  
545 *Behav Sup*. III:1–201.

546 Hua F, Yong DL, Janra MN, Fitri LM, Prawiradilaga D, Sieving KE. 2016. Functional traits  
547 determine heterospecific use of risk-related social information in forest birds of tropical  
548 South-East Asia. *Ecol Evol.* 6:8485–8494. <https://doi.org/10.1002/ece3.2545>

549 Igc B, Ratnayake CP, Radford AN, Magrath RD. 2019. Eavesdropping magpies respond to  
550 the number of heterospecifics giving alarm calls but not the number of species calling. *Anim*  
551 *Behav.* 148:133–143. <https://doi.org/10.1016/j.anbehav.2018.12.012>

552 Jiang D, Sieving KE, Meaux E, Goodale E. 2020. Seasonal changes in mixed-species bird  
553 flocks and antipredator information. *Ecol Evol.* 10:5368–5382.  
554 <https://doi.org/10.1002/ece3.6280>

555 Kostan KM. 2002. The evolution of mutualistic interspecific communication: Assessment and  
556 management across species. *J Comp Psychol.* 116:206–9. [https://doi.org/10.1037/0735-](https://doi.org/10.1037/0735-7036.116.2.206)  
557 [7036.116.2.206](https://doi.org/10.1037/0735-7036.116.2.206)

558 Krams I, Bērziņš A, Krama T, Wheatcroft D, Igaune K, Rantala MJ. 2010. The increased risk  
559 of predation enhances cooperation. *Proc Royal Soc B.* 277:513–518.  
560 <https://doi.org/10.1098/rspb.2009.1614>

561 Kroodsma DE. 1989. Suggested experimental designs for song playbacks. *Anim Behav.*  
562 37:600–609. [https://doi.org/10.1016/0003-3472\(89\)90039-0](https://doi.org/10.1016/0003-3472(89)90039-0)

563 Landsborough B, Wilson DR, Mennill DJ. 2020. Variation in chick-a-dee call sequences, not  
564 in the fine structure of chick-a-dee calls, influences mobbing behaviour in mixed-species  
565 flocks. *Behav Ecol.* 31:54–62. <https://doi.org/10.1093/beheco/arz155>

566 Magrath RD, Haff TM, Fallow PM, Radford AN. 2015. Eavesdropping on heterospecific  
567 alarm calls: from mechanisms to consequences. Biol Rev. 90:560–586.  
568 <https://doi.org/10.1111/brv.12122>

569 Morton ES. 1975. Ecological sources of selection on avian sounds. Am Nat. 109:17–34.

570 Planade B, Lena JP, Li H, Plénet S, Guegan JF, Thomas F, et al. 2009. Tracking a heterosis  
571 effect in the field: tadpole resistance to parasites in the water frog hybridogenetic complex.  
572 Parasitology. 136:1003–1013. <https://doi.org/10.1017/S0031182009006489>

573 Poian A, Yorke IM. 1989. Predator Harassment : More Evidence on the Deadly Risk.  
574 Ethology. 83:167–169. <https://doi.org/10.1111/j.1439-0310.1989.tb00526.x>

575 R Core Team, 2022. R: A language and environment for statistical computing. Vienna,  
576 Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.

577 Salis A, Léna JP, Lengagne T. 2022. Data & Supplemental information for manuscript  
578 "Acoustic cues and season affect mobbing responses in a bird community "\_ Review 1 PCI  
579 (Version 2). Zenodo. <https://doi.org/10.5281/zenodo.7271850>

580 Salis A, Léna JP, Lengagne T. 2021. Great tits (*Parus major*) adequately respond to both  
581 allopatric combinatorial mobbing calls and their isolated parts. Ethology. 127:213–222.  
582 <https://doi.org/10.1111/eth.13111>

583 Salis A, Léna JP, Lengagne T. 2022. Which acoustic parameters modify the great tit's  
584 response to conspecific combinatorial mobbing calls? Behav Ecol Sociobiol, 76:46.  
585 <https://doi.org/10.1007/s00265-022-03157-x>

586 Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and  
587 deception in signalling systems. Princeton, NJ: Princeton University Press.

588 Sordahl TA. 1990. The Risks of Avian Mobbing and Distraction Behavior: An Anecdotal  
589 Review. *Wilson Bull.* 102:349–352.

590 Sridhar H, Beauchamp G, Shanker K. 2009. Why do birds participate in mixed-species  
591 foraging flocks? A large-scale synthesis. *Anim Behav.* 78:337–347.  
592 <https://doi.org/10.1016/j.anbehav.2009.05.008>

593 Suhonen J, Halonen M, Mappes T. 1993. Predation Risk and the Organization of the Parus  
594 Guild. *Oikos.* 66: 94–100. <https://doi.org/10.2307/3545200>

595 Suzuki TN, Wheatcroft D, Griesser M. 2016. Experimental evidence for compositional syntax  
596 in bird calls. *Nat Com.* 7:10986. <https://doi.org/10.1038/ncomms10986>

597 Templeton CN, Zollinger SA, Brumm H. 2016. Traffic noise drowns out great tit alarm  
598 calls. *Cur Biol.* 26:R1173-R1174. <https://doi.org/10.1016/j.cub.2016.09.058>

599 Templeton CN, Greene E, Davis K. 2005. Allometry of alarm calls: black-capped chickadees  
600 encode information about predator size. *Science.* 308:1934–1937.  
601 <https://doi.org/10.1126/science.1108841>

602 Van Duyse E, Pinxten R, Eens M. 2002. Effects of Testosterone on Song, Aggression, and  
603 Nestling Feeding Behavior in Male Great Tits, *Parus major*. *Hormones and Behavior.*  
604 41:178–186. <https://doi.org/10.1006/hbeh.2001.1747>

605 Wheatcroft D, Price TD. 2018. Collective action promoted by key individuals. *Am Nat.*  
606 192:401–414. <http://dx.doi.org/10.1086/698874>

- 607 Wilson J. D. 1992. Correlates of agonistic display by great tits *Parus major*. Behaviour. 121:  
608 168–214.
- 609 Wingfield JC, Ramenofsky M. 1985. Testosterone and aggressive behaviour during the  
610 reproductive cycle of male birds. In: Gilles R, Balthazart J, editors. Neurobiology. Berlin,  
611 Germany: Springer. p. 92-104.
- 612 Woods RD, Kings M, McIvor GE, Thornton A. 2018. Caller characteristics influence  
613 recruitment to collective anti-predator events in jackdaws. Sci Rep. 8:1–8.  
614 <https://doi.org/10.1038/s41598-018-25793-y>
- 615 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and  
616 extensions in ecology with R. New York: Springer.