



26

27 **ABSTRACT**

28 Heterospecific communication is common for birds when mobbing a predator. However,  
29 joining the mob should depend on the number of callers already enrolled, as larger mobs  
30 imply lower individual risks for the newcomer. In addition, some ‘community informant’  
31 species seem more reliable regarding the information transferred in mobbing calls. Birds  
32 should therefore rely on both the number of callers and the species identity of the caller(s)  
33 when mobbing. In the present study, we tested the potential interaction between two acoustic  
34 cues. In a playback experiment, we modified the number of callers (through an increased  
35 number of calling individuals correlated to an increased duty cycle) and the emitter species  
36 (crested tits versus coal tits). Overall, we found that soundtracks with three callers triggered  
37 more mobbing than soundtracks with one caller and that soundtracks with coal tits’ calls  
38 triggered more mobbing than soundtracks with crested tits’ calls. Our results therefore support  
39 the hypothesis that birds consider both the species and the number of callers when joining a  
40 mobbing chorus in winter. Finally, we replicated the experiment in spring and did not record  
41 the same responses from the bird community. Indeed, only soundtracks with three coal tits  
42 triggered a mobbing response, suggesting therefore that the seasonal context can affect the  
43 results of studies on heterospecific communication. The potential mechanisms implicated in  
44 the varying responses to different acoustic cues and different seasons are discussed and should  
45 deserve further investigations.

46 **Keywords: heterospecific communication, mobbing call, community response,**  
47 **cooperation, seasonal effect**

## 48 INTRODUCTION

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

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

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

84         Heterospecific communication related to mobbing is prevalent in winter in passerines  
85 communities (Dutour et al. 2019), notably because of an increased tendency to flock with  
86 heterospecifics to increase predator defense and foraging efficiency (Goodale et al. 2015). We  
87 therefore chose to test first and foremost birds during winter. Yet, we also replicated the same  
88 experiment in spring to test whether seasonal context could influence experiments about  
89 heterospecific communication. Indeed, throughout the year, the physical and social  
90 environment of birds varies greatly, possibly impacting their communication (e.g., Clucas et  
91 al. 2004, Jiang et al. 2020). In spring, the increased aggressiveness due to territoriality and

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

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

100

## 101 **MATERIAL AND METHODS**

### 102 **Study site & Species**

103 The **playback** experiments described below were all done **in** the Haut-Bugey region,  
104 France. This region is a small mountain environment (altitude: ~800m), with mixed  
105 deciduous-coniferous forests. Densities of coal and crested tits are high in this area, as shown  
106 by the long-term ornithological census in the region: both species were detected in 94% of  
107 points, spaced at 150 m from each other (participative database Faune-ain.org administered by  
108 the LPO AuRA DT Ain). In this region, small birds are often predated by several predator  
109 including the Eurasian pygmy owl *Glaucidium passerinum*. Previous experiments in the  
110 region have shown a mobbing response from a large number of species, including the coal  
111 and the crested tits (Dutour et al. 2016; Dutour et al. 2017b). When mobbing occurs, birds

112 approach the predator cue and produce calls often with specific aggressive postures (e.g.,  
113 wing flicks and frequent hops), but direct attack is rare (Carlson & Griesser, 2022).

114

## 115 **General organization**

116 We aimed at testing the mobbing response of free-ranging birds to different  
117 soundtracks. To this aim, we established 100 spots for the playback tests in a 10 km<sup>2</sup> area of  
118 coniferous forest in the East of France (46°13'05.0"N 5°41'50.8"E). Each spot was selected  
119 along an existing trail but close to a tree allowing birds' approach and concealment of  
120 experimenters. All spots were separated by ~ 100 m (mean and standard deviation: 110.9 ±  
121 27.2 m) since this distance is sufficient to degrade bird sounds (Morton 1975). In addition, we  
122 performed a complementary subset of experiments (n = 22 birds tested, 9 crested tits and 13  
123 coal tits) to verify that birds do not follow the observer between successive spots. For this  
124 purpose, we followed the same methodology than the one used by Salis et al. on great tits  
125 (2022). More specifically, both observers were equipped with the acoustic material and  
126 binoculars, and after each test, while one observer was launching the playback experiments on  
127 a subsequent location, the other was following the birds from the previous location. We found  
128 that from one test to the next one, no bird followed us, and no bird moved farther than 50  
129 meters from their original position (see details in Supplementary File 1). While birds can  
130 travel large distances in a short period, it is unlikely that we tested the same birds in  
131 consecutive tests in the present experiment given the absence of human following and the  
132 absence of attraction from the subsequent playbacks.

133           We created a factorial design in which our four different treatments (different emitter  
134 species and number of callers, see paragraph Playbacks for details) were broadcast on each  
135 spot. These experiments were first carried out in winter, and then replicated in spring. Each  
136 spot consequently received eight playback tests. We avoided spatial and temporal  
137 autocorrelation by (i) alternating the four treatments at consecutive spots, and (ii) doing the  
138 same number of tests of each treatment, each day. The 400 tests in each season were done in a  
139 short period (two weeks) to avoid a potential intra-seasonal effect, and each consecutive test  
140 spaced by at least five minutes (each consecutive test was at a different spot, so that each spot  
141 was tested only once per day). We changed the order in which the spots were tested each day  
142 (different beginning point each day and different directions in the trails). Post hoc analyses  
143 (Sup. File 2) show no effect of order of playback treatment nor of the repeated presentation of  
144 playbacks on our results.

145

## 146 **Playbacks**

147           We created four treatments: soundtrack with only one calling coal tit (1CO), three coal  
148 tits calling simultaneously (3CO), only one calling crested tit (1CR), and lastly, three crested  
149 tits (3CR). We did not use a negative control (e.g., heterospecific song or background noise)  
150 since we were interested in the difference between our treatments. Moreover, background  
151 noise has been used in several studies (Dutour et al. 2019, Salis et al. 2022, Suzuki et al.  
152 2016) and never triggered a response from Parids. To prepare our soundtracks, we elicited  
153 mobbing calls from wild crested tit and coal tit by broadcasting a mobbing chorus of various  
154 birds (including coal and crested tits, Dutour et al. 2016). Once birds arrived to mob they were

155 recorded with a ME-67 Sennheiser microphone connected to a K6 basis and a Fostex FR2LE  
156 recorder (recording distance of 5 m to 15 m). At last, the recordings were then cleared of any  
157 other bird call, their amplitude homogenized at 50% on the entire file with AvisoftSasLab  
158 (Avisoft Bioacoustics, Glienicke, Germany), and saved as WAV files. We selected recordings  
159 with a number of calls around the mean ( $\pm 1$  SD) of previous recordings obtained by our team  
160 (coal tit:  $82 \pm 26$  notes per min,  $N = 30$ , crested tit:  $134 \pm 44$  notes per min,  $N = 10$ ). For the  
161 treatments with three birds (trio treatments), we superimposed recordings of three different  
162 birds calling to simulate a chorus. As a result, the final duty cycle (i.e., the amount of signal  
163 present in the playbacks) was higher for the three-birds treatment ( $\sim 9$  seconds) than for the  
164 one-bird treatments ( $\sim 6.5$  seconds, details in Sup. File. 3). Nevertheless, the calls  
165 substantially overlapped, reducing the risk for the focal birds to consider the three-birds  
166 treatments as only one bird calling intensely. For each treatment, we built five different  
167 soundtracks to circumvent the idiosyncrasy of recorded subjects (Kroodsma 1989).

168

## 169 **Test procedure**

170 One test consisted in playing 30 sec of a mobbing call sequence at each spot with a  
171 Bose Soundlink Revolve loudspeaker perched on a tripod (H: 1m), put near a tree and at an  
172 amplitude of  $84.01 \pm 2.70$  dB (calculated at 1 m with Lutron SL-4001, C weighting, slow  
173 settings, re.  $20 \mu\text{Pa}$ , Templeton et al., 2016). 30 sec is enough to trigger a mobbing response  
174 from nearby birds (previous recordings were obtained with such a stimulation), who can  
175 approach and call as a response, sometimes with additional aggressive behavior (e.g., wing  
176 flicking, Salis et al. 2021). A stimulation of only 30 seconds also limited the influence of the



177 first birds to call on the following birds recruited. The two observers positioned themselves at  
178 10 m from the tripod at vantage points before launching the soundtrack with an MP4 player  
179 (NW-A45 Sony). Before launching any test, we made sure that no bird was already in the  
180 vicinity nor uttering mobbing calls in a distance. If a bird was detected, we waited only it left  
181 the area (~10m around the loudspeaker). We observed the area with binoculars and all birds  
182 either calling and/or approaching from the beginning of the test to 15 sec after the end of the  
183 soundtrack. One bird was considered as approaching if it came in the 10 m radius around the  
184 tripod (Dutour et al. 2017b). Only birds uttering specific and known mobbing calls (see Sup.  
185 File 4 for spectrograms) were noted as calling. If a bird displayed the complete sequence of  
186 mobbing behavior (i.e., simultaneously calling and approaching the loudspeaker), it was then  
187 considered as giving a mobbing response. The two observers agreed on the highest number of  
188 birds seen simultaneously by both experimenters.

189

## 190 **Statistical analyses**

191 All statistical analyses were done with R studio (R v.4.1.1, R core team 2022).

192 Since social conditions for our study species differ between winter and spring and  
193 factors influencing rates of response presumably therefor differ, the analysis was done  
194 separately for each season. We used three count response variables: the number of responding  
195 birds of any species (“community level”), the number of responding coal tits, and the number  
196 of responding crested tits. Given the high densities of both species in the study area, we  
197 considered that the absence of responding birds is due to the absence of response (i.e.

198 structural zero) rather than the absence of bird (i.e. sampling zero). We therefore used Hurdle  
199 mixed models which are more convenient than zero inflation models to handle an excess of  
200 zeros of count data in such a situation (Zuur et al. 2009, Feng 2021). More specifically,  
201 Hurdle models are two stage models using a Bernoulli probability mass function to treat the  
202 zero outcomes as the result of a first process driving the occurrence of response (in our case,  
203 the mobbing occurrence), and a left truncated probability mass function to treat the positive  
204 outcomes as the result of a second process driving the response intensity (in our case the  
205 intensity of mobbing). For each count variable, we first constructed an initial full hurdle  
206 model implemented in the package *glmmTMB* (v.1.1.2.3, Brooks et al. 2017), with the effect  
207 of the emitter species, the effect of the number of callers, and their interactive effect in both  
208 parts of the model (occurrence and intensity). Moreover, both the spot location and the  
209 soundtracks' ID were introduced as random effects as an intercept in the model. All models  
210 were constructed with a quasi-Newton optimization method ('BFGS') to circumvent  
211 convergence failure. Nevertheless, the random effects were discarded from the model when  
212 analyzing the response of crested tits because of a general lower response precluding the  
213 correct estimation of the random effects. In order to control for potential overdispersion in our  
214 positive count data, we first selected between two alternative left truncated probability mass  
215 functions to handle positive counts, a truncated Poisson distribution and a truncated negative  
216 binomial one allowing the variance to increase more rapidly than the Esperance (note that we  
217 tested both *nbinom1* and *nbinom2*, the former having a linear parameterization and the second  
218 having a quadratic parameterization, Hardin & Hilbe 2007). For this purpose, both models  
219 were constructed and compared using Bayesian Information Criterion (BIC) and AIC. Since  
220 BIC is more sensitive to the sample size but less sensitive to the unobserved heterogeneity

221 than AIC (Brewer et al 2016), we only reported BIC. For the community response, a truncated  
222 negative binomial distribution led to the lowest BIC and was therefore chosen. Indeed, the  
223 dispersion parameter  $\Theta$  (i.e., the inflation factor associated to the truncated negative binomial  
224 distribution: when  $\Theta \rightarrow 0$ , the distribution is closer to a Gamma distribution, while when  $\Theta \rightarrow$   
225  $\infty$ , the distribution is closer to a Poisson distribution) was 1.16 for the community model in  
226 winter and 0.79 for the community model in spring. For the isolated response of coal tits and  
227 crested tits, the truncated Poisson distribution led to the lowest BIC and was therefore chosen  
228 to analyze these responses. The fit of the structure selected for the initial model was then  
229 checked by the inspection of its residuals using the package DHARMA (v 0.4.5, Hartig and  
230 Hartig 2017).

231 For each of the three response variables (at the level of community, crested tits and  
232 coal tits) and for each season, we then created four candidate models, each of them with all  
233 the explanatory terms of interest (number of callers and emitter species), but for which the  
234 interaction term was kept or not, in the occurrence part and the intensity part of the model.  
235 Weighted BIC (wBIC) was then computed for the four candidate models and used to assess  
236 and compare their relative support using evidence ratios (i.e., ratio of wBIC between two  
237 models, Anderson and Burnham 2002). Effects sizes of the differences between treatments  
238 were calculated with odds ratios (OR).

### 239 **Ethical note**

240 We used a sample size that is higher than in other recent studies (commonly around  
241 20-30 tests per treatment) to circumvent common problems of lack of power in animal  
242 behavior studies, and because presence/absence data usually require larger sample sizes

243 (Jennions, 2003). To limit the impact on birds' welfare, we ran short playback tests (1 min-  
244 long). All birds returned to a foraging behavior in less than 5 minutes after our tests. No direct  
245 contact between birds and humans nor any concealment of the birds were needed in this  
246 experiment.

## 247 **RESULTS**

### 248 **Mobbing responses in winter**

249 Eleven different species were attracted to our soundtracks (Figure 1A), with a  
250 maximum diversity of six species at one test. The four main species were the goldcrest  
251 (*Regulus regulus*, present in 29.5% of our tests), the crested tit (present in 27.8% of our tests),  
252 the coal tit (26.7%) and the marsh tit (*Poecile palustris*, 16.3%). As indicated by the best  
253 supported model (lowest BIC and an evidence ratio of 8.3, Table 1A), mobbing occurrence  
254 (the probability that at least one bird responded the playback), irrespective of the species (i.e.,  
255 at the community level, Figure 2A) was affected by an additive effect of both the number of  
256 callers in the playback and the caller species (Table 2A). Indeed, birds mobbed more often the  
257 coal tit soundtracks compared to the crested tit soundtracks, and more to soundtracks with  
258 three birds rather than only one bird calling (1CO: 64%, 3CO: 77%, 1CR: 30%, 3CR: 59%).  
259 This additive effect was also detected when looking at the mobbing intensity (i.e., the number  
260 of mobbing birds when mobbing occurs, Figure 2B, Table 2A). Indeed, the largest mobs were  
261 initiated by playbacks with three coal tits ( $4.01 \pm 3.17$  birds, mean  $\pm$  standard deviation, with  
262 a maximum of 15 birds) while the smaller mobs were initiated by playbacks with one crested  
263 tit ( $1.90 \pm 1.21$  birds).

264           When focusing on the occurrence of response of coal tits or the one of the crested tits,  
265 the best supported model comprised an additive effect of the number of callers and the emitter  
266 species (Table 1B and 1C, Table 2B and 2C), resulting in a lower response toward singletons  
267 of crested tits (8% of points attracted coal tits or crested tits), intermediate scores toward trios  
268 of crested tits and singletons of coal tits, and the highest occurrence of response toward  
269 soundtracks with three coal tits (46% triggered a response from coal tits and 41% triggered a  
270 response from crested tits, Figure 2C and 2E). However, for the crested tit, the model with an  
271 interaction between number of callers and emitter species was also well supported (evidence  
272 ratio of  $0.51/0.43 = 1.19$ , Table 1C). Indeed, the difference between 1CR and 3CR was higher  
273 (OR: 4.74, 95%CI: [1.92; 10.40]) than the difference between 1CO and 3CO (OR: 1.35,  
274 95%CI: [0.76; 2.40]). Regarding mobbing intensity (Figure 2D and 2F), for both the coal tits'  
275 and crested tits' response, the additive effect of number of callers and emitter species was less  
276 stringent than for the occurrence of mobbing (the effect of emitter species for the coal tit, and  
277 the effect of number of callers for the crested tits did not reach statistical significance when  
278 reporting the estimates, Table 2B and 2C).

279

## 280 **Mobbing responses in spring**

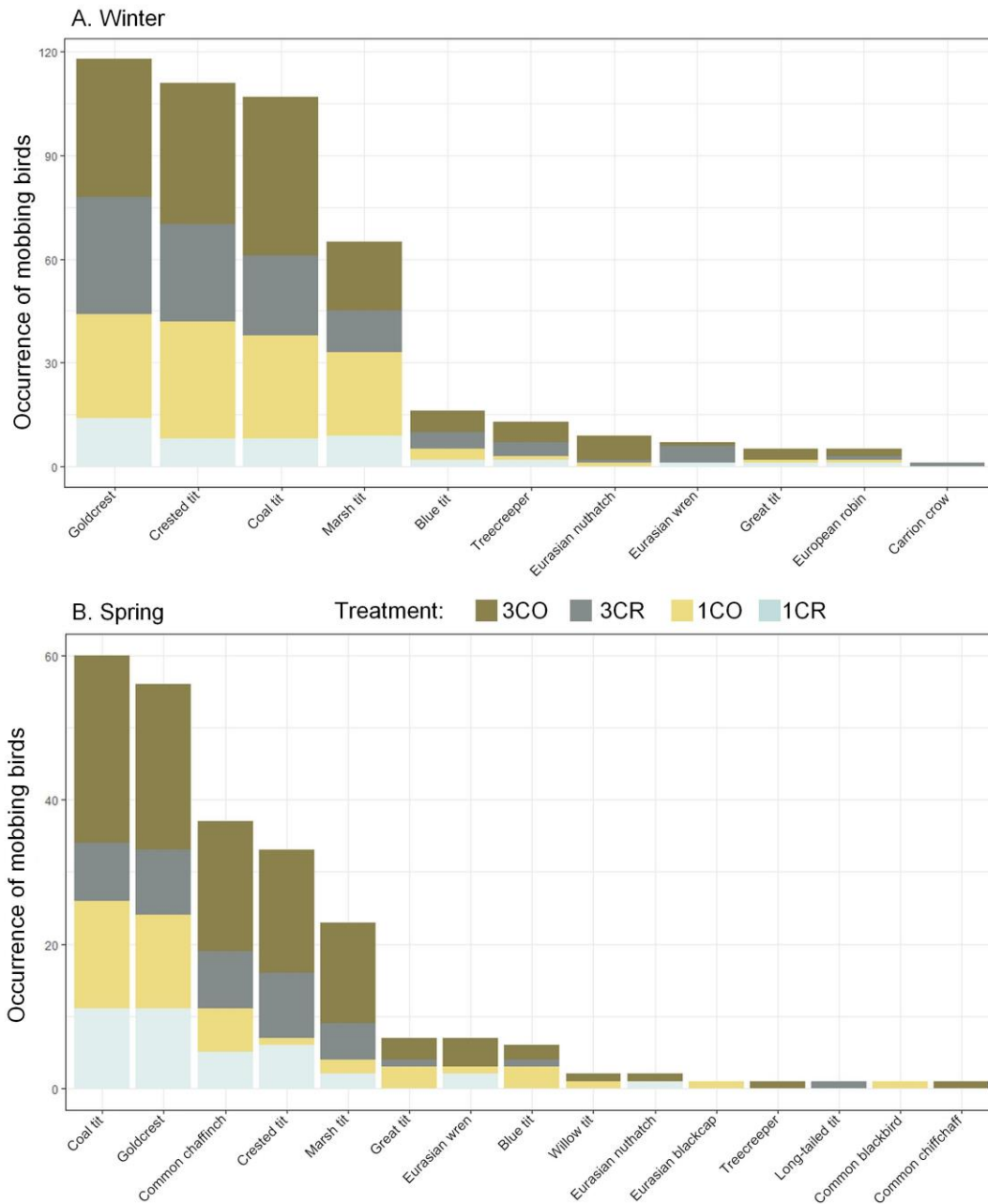
281           In spring, we detected a lower mobbing propensity: 58% of our tests did not trigger  
282 any mobbing behavior, while this proportion was of 42.5% in winter. 15 different species  
283 were attracted to our soundtracks (Figure 1B), with a maximum diversity of four species at  
284 one test. The four most common species that responded were the coal tit (present in 15% of

285 our tests), the goldcrest (present in 14% of our tests), the common chaffinch (*Fringilla*  
286 *coelebs*, 9.25%), and the crested tit (8%).

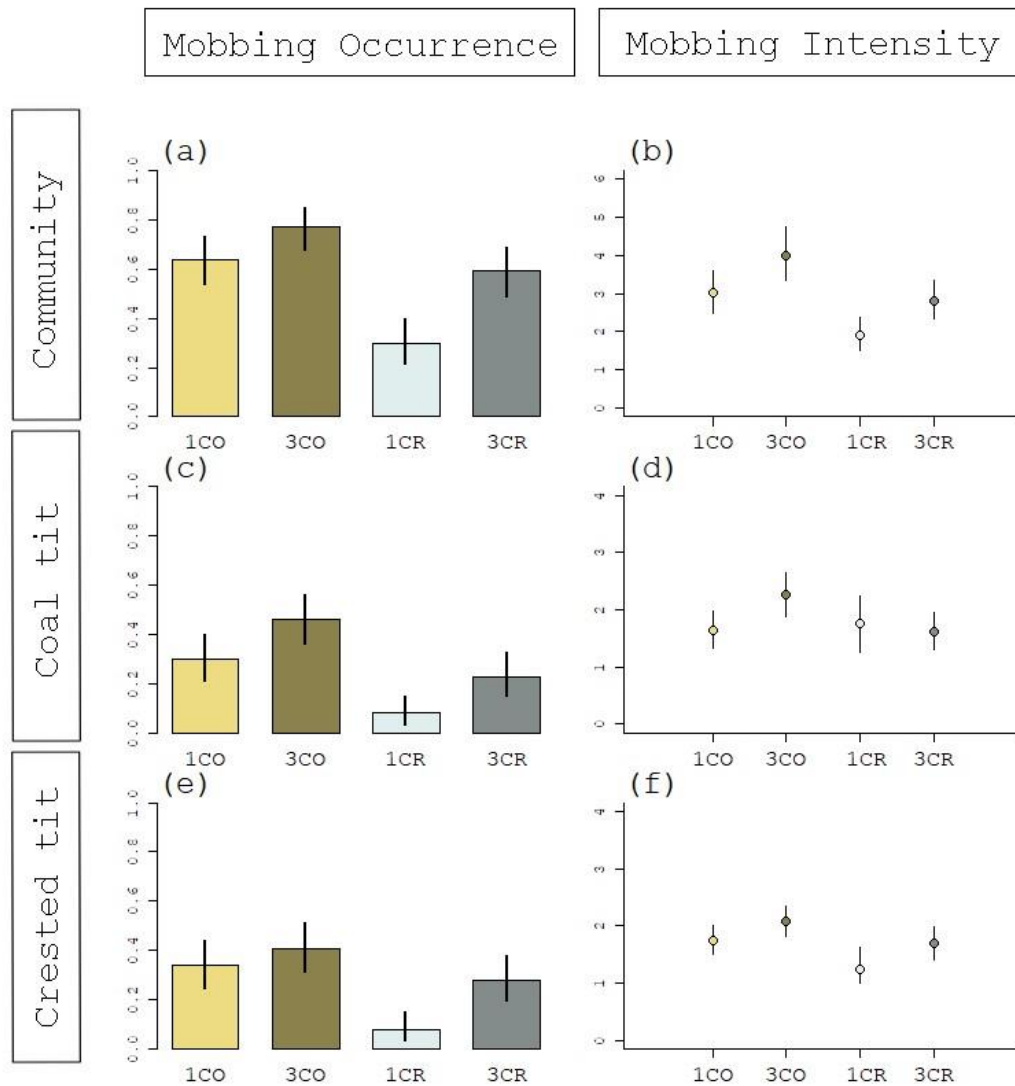
287         Regarding mobbing occurrence at the community level (Figure 3A), the model with  
288 the lowest BIC was the one including an interaction between emitter species and number of  
289 callers in the playbacks (Table 1D, Table 2D). Indeed, the effect sizes depict a higher  
290 response towards the 3CO treatment than towards any of the three other playbacks (e.g., 3CO  
291 vs 3CR: 3.30, 95%CI: [1.85; 5.89]), while the three other playbacks triggered a similar  
292 response (e.g., 3CR vs 1CO: 1.14, 95%CI: [0.64; 2.05]). Note however that this interaction is  
293 not strongly supported since the model including only the additive effects of number of callers  
294 and emitter species gave a similar BIC (evidence ratio of  $0.69/0.25 = 2.76$ , Table 1D). When  
295 focusing on the intensity of response (Figure 3B), we detected no difference in the number of  
296 birds recruited to the four different playbacks (Table 2D). The number of birds in the mob  
297 never exceeded 7 birds.

298         The best supported model regarding the presence of at least one coal tit included the  
299 emitter species of the playback, but no effect of the number of callers (Figure 3C, Table 1E,  
300 Table 2E). For the crested tit's occurrence, we recorded an interaction between the emitter  
301 species and the number of callers in the playbacks (Figure 3E, Table 1F, Table 2F). Indeed,  
302 our playbacks attracted more often crested tits when there were three coal tits in the playbacks  
303 compared to any of the three other types of playbacks. For both species, the number of birds  
304 recruited when mobbing occurred did not differ between the four types of playbacks (Figure  
305 3D and 3F, Table 2E and 2F).

306



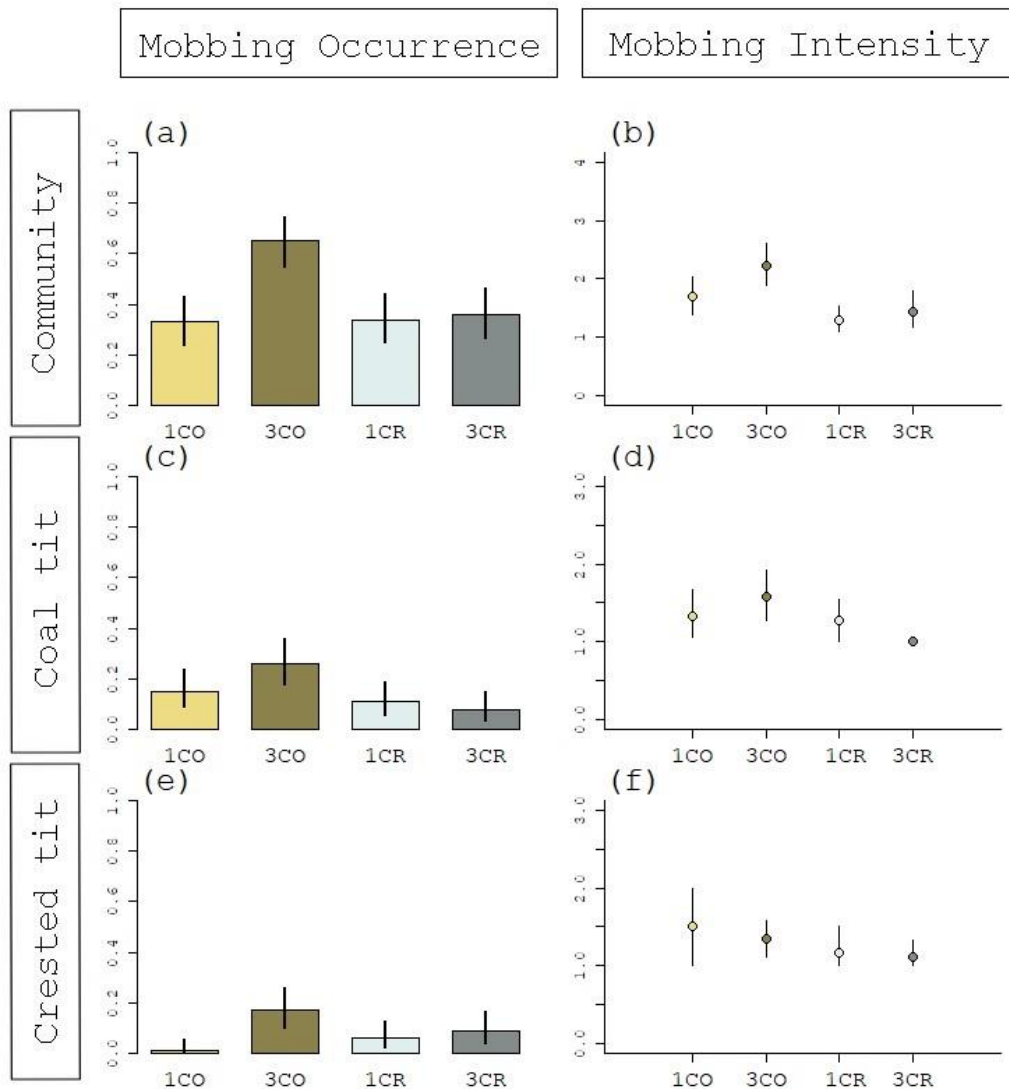
321 **Figure 1.** Number of spots (100 per acoustic treatment) in which at least one bird of each species  
 322 mobbed (i.e., approached and called), when facing each of our four acoustic treatments (3CO: three  
 323 coal tits, 1CO: one coal tit, 3CR: three crested tits, 1CR: one crested tit). Responses to each of the four  
 324 treatments are stacked in sequence on each bar so that the entire bar represents the sum of all  
 325 responses by a given species across treatments. Species taxonomy : blue tit = *Cyanistes caeruleus*,  
 326 carrion crow = *Corvus corone*, crested tit = *Lophophanes cristatus*, coal tit = *Periparus ater*, common  
 327 blackbird = *Turdus merula*, common chaffinch = *Fringilla coelebs*, common chiffchaff =  
 328 *Phylloscopus collybita*, Eurasian nuthatch = *Sitta europaea*, Eurasian wren = *Troglodytes troglodytes*,  
 329 Eurasian blackcap = *Sylvia atricapilla*, European robin = *Erithacus rubecula*, goldcrest = *Regulus*  
 330 *regulus*, great tit = *Parus major*, long-tailed tit = *Aegithalos caudatus*, marsh tit = *Poecile palustris*,  
 331 treecreeper = *Certhia familiaris*, willow tit = *Poecile montanus*.



332

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





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

352 **Table 1.** Hurdle models selection tables. For each response variable (number of responding  
 353 birds at the community level, number of responding coal tits, number of responding crested  
 354 tits), we first constructed a full Hurdle model with the effect of the emitter species, the effect  
 355 of the number of callers as well as their interactive effect in both parts of the model (see  
 356 material and method for details). We compare this full model to models without the  
 357 interaction in both the occurrence part and the intensity part of the model. We provide the  
 358 Bayesian Information Criterion (BIC) and the weighted BIC (wBIC) to represent the relative  
 359 support of each model. With wBIC we can calculate evidence ratio between two models (e.g.,  
 360 the first model is  $0.83 / 0.10 \approx 8.3$  times more supported than the second model).

361

362

	Occurrence (Presence of mobbers)	Intensity (Number of mobbers)	BIC	wBIC
<b>WINTER</b>				
<b>A. Community</b>	<b>Emitter Species + Number of callers</b>	<b>Emitter Species + Number of callers</b>	1449,73	0,83
	Emitter Species x Number of callers	Emitter Species + Number of callers	1453,87	0,10
	Emitter Species + Number of callers	Emitter Species x Number of callers	1454,99	0,06
	Emitter Species x Number of callers	Emitter Species x Number of callers	1459,13	0,008
<b>B. Coal tit</b>	<b>Emitter Species + Number of callers</b>	<b>Emitter Species + Number of callers</b>	758,07	0,81
	Emitter Species + Number of callers	Emitter Species x Number of callers	762,03	0,11
	Emitter Species x Number of callers	Emitter Species + Number of callers	762,99	0,07
	Emitter Species x Number of callers	Emitter Species x Number of callers	766,95	0,01
<b>C. Crested tit</b>	<b>Emitter Species + Number of callers</b>	<b>Emitter Species + Number of callers</b>	731,95	0,51
	Emitter Species x Number of callers	Emitter Species + Number of callers	732,30	0,43
	Emitter Species + Number of callers	Emitter Species x Number of callers	737,25	0,04
	Emitter Species x Number of callers	Emitter Species x Number of callers	737,61	0,03

SPRING				
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D. Community	<b>Emitter Species x Number of callers</b>	<b>Emitter Species + Number of callers</b>	972,10	0,69
	Emitter Species + Number of callers	Emitter Species + Number of callers	974,11	0,25
	Emitter Species x Number of callers	Emitter Species x Number of callers	977,92	0,04
	Emitter Species + Number of callers	Emitter Species x Number of callers	979,92	0,01
E. Coal tit	<b>Emitter Species + Number of callers</b>	<b>Emitter Species + Number of callers</b>	480,37	0,61
	Emitter Species + Number of callers	Emitter Species x Number of callers	482,59	0,2
	Emitter Species x Number of callers	Emitter Species + Number of callers	483,37	0,14
	Emitter Species x Number of callers	Emitter Species x Number of callers	485,6	0,05
F. Crested tit	<b>Emitter Species x Number of callers</b>	<b>Emitter Species + Number of callers</b>	289,76	0,55
	Emitter Species + Number of callers	Emitter Species + Number of callers	290,42	0,4
	Emitter Species x Number of callers	Emitter Species x Number of callers	295,66	0,03
	Emitter Species + Number of callers	Emitter Species x Number of callers	296,33	0,02

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369 **Table 2.** Outputs of the models selected in bold in Table 1. Each Hurdle model is a two-stage  
 370 model, the first one examining the effect of explanatory terms on the occurrence of response  
 371 (mobbing occurrence) and the second one examining the effect of explanatory terms on the  
 372 positive counts (mobbing intensity), see material and method for details. We provide the  
 373 estimates with their standard error (the intercept is the 1CO treatment), the z value and the  
 374 associated p-value. The detailed outputs of the three other models in Table 1 are added as  
 375 supplementary material 5.

WINTER				
<b>A. Community</b>				
<b>Occurrence</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	-0,94	0,17	-5,51	< 0,0001
Emitter Species	1,19	0,23	5,23	< 0,0001
Number of Callers	0,69	0,16	4,34	< 0,0001
<b>Intensity</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	0,98	0,11	8,81	< 0,0001
Emitter Species	-0,58	0,16	-3,67	0,0002
Number of Callers	-0,33	0,11	-3,06	0,0002
<b>B. Coal tit</b>				
<b>Occurrence</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	0,53	0,16	3,32	0,001
Emitter Species	1,28	0,26	4,96	< 0,0001
Number of Callers	0,63	0,18	3,57	0,0003
<b>Intensity</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	0,40	0,11	3,47	0,001
Emitter Species	-0,44	0,23	-1,87	0,06
Number of Callers	-0,31	0,15	-2,03	0,04
<b>C. Crested tit</b>				
<b>Occurrence</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	0,53	0,15	3,55	0,0004
Emitter Species	1,03	0,24	4,33	< 0,0001
Number of Callers	0,51	0,17	3,06	0,002
<b>Intensity</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	0,35	0,12	3,04	0,002
Emitter Species	-0,48	0,24	-2,01	0,04
Number of Callers	-0,28	0,15	-1,80	0,07

SPRING				
<b>D. Community</b>				
<b>Occurrence</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	0,05	0,16	0,29	0,77
Emitter Species	0,59	0,22	2,76	0,006
Number of Callers	0,97	0,22	4,43	< 0,0001
Emitter Species: Number of Callers	-0,90	0,30	-2,97	0,003
<b>Intensity</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	-0,08	0,44	-0,19	0,85
Emitter Species	-2,30	2,76	-0,83	0,41
Number of Callers	-0,55	0,36	-1,54	0,12
<b>E. Coal tit</b>				
<b>Occurrence</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	1,36	0,18	7,74	< 0,0001
Emitter Species	0,90	0,30	3,02	0,003
Number of Callers	0,23	0,20	1,13	0,26
<b>Intensity</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	-0,40	0,36	-1,11	0,27
Emitter Species	-0,97	0,63	-1,53	0,13
Number of Callers	-0,13	0,31	-0,41	0,69
<b>F. Crested tit</b>				
<b>Occurrence</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	3,09	0,52	5,95	< 0,0001
Emitter Species	-0,56	0,59	-0,95	0,34
Number of Callers	2,13	0,74	2,90	0,004
Emitter Species: Number of Callers	-1,82	0,83	-2,19	0,03
<b>Intensity</b>				
	<b>Estimate</b>	<b>SE</b>	<b>z</b>	<b>p</b>
(Intercept)	-0,06	0,48	-0,12	0,90
Emitter Species	-1,30	0,88	-1,048	0,14
Number of Callers	0,51	0,61	0,84	0,40

376 **DISCUSSION**

377           In winter, coal tits' soundtracks triggered more mobbing response from conspecifics  
378 and heterospecifics than crested tits' soundtracks; and soundtracks with three callers triggered  
379 more mobbing response from the bird community than soundtracks with only one caller.  
380 However, when replicating the experiment in spring, we found a lower general response but  
381 also differences between playbacks, with increased responses only toward the 3 coal tits'  
382 playbacks. This interaction between context and acoustic cues demonstrates the flexible  
383 nature of heterospecific communication.

384

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

386           Birds **often modulate** their mobbing responses depending on the threat they perceive.  
387 For example, different predators are mobbed with different levels of intensity (Curio et al.  
388 1983, Templeton et al. 2005). Individuals can also change their mobbing response depending  
389 on the distance of the threat, the movement of the predator, or other cues surrounding the  
390 predator (Book & Freeberg 2015, Carlson et al. 2017). In this study, we recorded a higher  
391 mobbing response towards soundtracks with three individuals than towards soundtracks with  
392 only one individual calling. This result is congruent with the hypothesis that birds will use  
393 acoustic cues to gain information on the threat. Indeed, a larger number of birds may indicate  
394 a more significant predator, as larger mobs are produced in front of more important predators  
395 (Dutour et al. 2017b, Sandoval & Wilson 2012). In addition, joining a group instead of a lone  
396 caller increases the dilution effect, hence reducing risk for the newcomer (Sridhar et al. 2009).

397 Alternatively, the increased response to the playbacks with more birds may be unrelated to an  
398 assessment of risk by birds, but rather be a simple mechanical threshold reached when the call  
399 is more salient to receivers (by reaching a specific threshold and/or being easier to detect).  
400 One solution to test the risk assessment hypothesis could be to create a similar experiment but  
401 based only on visual cues. The idea would be to test the mobbing response of birds in front of  
402 a predator model accompanied with either one or three models of conspecifics. This kind of  
403 experiment should be done in large aviaries for which we can control what visual cues the  
404 birds receive. If the focal bird approach and mob more a when a group is already present, then  
405 the risk hypothesis would be more supported.

406         The mechanisms implicated in the differentiation between playbacks of one and three  
407 callers can be various. In natural settings, birds can consider the number of spatially different  
408 acoustic sources (Bradbury and Vehrencamp 2011). In our study, we launched the  
409 soundtracks with only one loudspeaker whatever the treatment to suppress this effect.  
410 Therefore, in our tests, the acoustic criteria that remain available are the duty cycle (i.e., the  
411 proportion of the calling sequence when the signal is present), and the count of calling  
412 individual through individual signatures. Our experiment does not add any insights on which  
413 criteria was used by birds. Based on the current literature, the duty cycle is probably one  
414 major coding strategy for increased risk in Parids (Landsborough et al. 2020, Salis et al.  
415 2022), and Parids modify their response to unknown non-Parids calls with different duty  
416 cycles (Dutour et al. 2022). Yet, great tits can also recognize caller identity, as they increased  
417 their mobbing response toward soundtracks made with calls of several individuals compared  
418 to soundtracks with only one individual calling (Dutour et al. 2021). In this latter experiment,

419 the duty cycles of the different treatments were strictly equal. This result was however not  
420 replicated when testing the response to different number of heterospecifics (chaffinches  
421 *Fringilla coelebs*, Dutour and Randler 2021). In our experiments, we believe that the  
422 overlapping of the calls in the three birds treatments avoid the risk of interpreting these  
423 treatments as only one bird calling intensely. Further experiments exploring the response of  
424 each species to conspecific and heterospecific calls with controlled duty cycle may enlighten  
425 whether individual recognition can also be used in heterospecific communication.

426

427         A mobbing response occurred more often when broadcasting coal tits' mobbing calls  
428 compared to crested tits' calls, but also more birds responded to it. Unexpectedly, even  
429 crested tits responded more to coal tits' mobbing calls than to calls from their own species.  
430 Coal tits therefore appear to be listened to and heavily responded to, leading to larger (and  
431 possibly more efficient) mobs. This is in line with the hypothesis that species from the same  
432 community show different levels of reliability (Magrath et al. 2015). The notion of “a  
433 community informant” was developed for Parids in Carlson et al. (2020). They investigated  
434 whether the birds possessed a reliable way of encoding predator information, and if several  
435 heterospecifics relied on these calls. They showed that the great tit (*Parus major*) best fitted  
436 the definition of community informant. The coal tit approached the definition, with only one  
437 caveat: the dunnock (*Prunella modularis*) did not respond to it. As the authors suggested, the  
438 lack of response from one species does not mean that other species from the community do  
439 not respond to it (Carlson et al. 2020). Indeed, in our study, 14 species responded to coal tits'  
440 soundtracks. In contrast, the crested tit did not meet any of the criteria set by Carlson and



441 colleagues. Coal tits appear therefore to be one important species regarding predator  
442 information in the community, and this is congruent with their increased sensibility to  
443 predation by pygmy owls (*Glaucidium passerinum*) in winter (Suhonen et al. 1993).

444

#### 445 **Replicating the experiment in spring: A lower general response**

446 In winter, Parids living in temperate regions often flock with heterospecifics,  
447 sometimes leading to impressive mobs (up to 20 birds in the present experiment). In  
448 opposition, during the reproductive period (May-July), Parids nest and defend their territory  
449 with intensity (Hinde 1952). For this reason, we first explored the mobbing response of birds  
450 in winter, as this is the season in which interactions and cooperative mobbing with  
451 heterospecifics makes more sense. However, we replicated the experiment in spring to  
452 explore whether seasonal context of the experiment could impact our results. We did not test  
453 the same birds and cannot control the changes in environment and community between the  
454 first tests in winter and the replicate in spring. For these reasons, we did not statistically  
455 compare the two seasons, but will nonetheless discuss the differences found between the  
456 original experiment and the replication.

457 In spring, the number of birds mobbing to the four different types of playbacks was  
458 lower than in winter and did not differ between playback types. We here propose that in  
459 spring, when all birds defend their territory, the number of birds that can respond is restricted  
460 to the neighbors. Moreover, in spring, aggressiveness toward conspecifics is high and may  
461 therefore reduce the number of potential birds responding to mobbing calls. This

462 aggressiveness may also explain why not so many birds responded to conspecific mobbing  
463 calls in spring (coal tits to coal tits and crested tits to crested tits).

464         Additionally, not only did fewer individuals respond in spring than in winter, but in  
465 spring, the proportion of locations with any response was lower than in winter. This  
466 difference must be taken with cautiousness, as the community and the density of the  
467 populations may vary with the seasons: a decrease in mobbing response may simply be  
468 related to fewer individuals in the territory. An order effect due to tests in winter being done  
469 before the tests in spring is unlikely given the absence of order effect in our experiment at a  
470 short time scale (see Sup. Mat. 2 For details). In addition, in spring, we were able to hear coal  
471 tits singing at the 100 spots studied. We are therefore confident that, in spring, each spot could  
472 have recorded one coal tit's mobbing response. This suggests that at least for the coal tit, the  
473 response to conspecific and heterospecific mobbing calls decreases in spring. This result is  
474 consistent with Dutour et al. (2019) who detected in Parids a higher mobbing response toward  
475 heterospecific calls in winter compared to summer. The proximal reasons for such a decrease  
476 can be various. Increased territoriality and aggression in spring may very well limit  
477 cooperative communication, since the mobbing calls may resemble intra-specific  
478 aggression/territoriality calls, leading to a lower relevance for heterospecifics. Other factors  
479 such as decreased predator pressure in spring (Dutour et al. 2017b) could also result in a lower  
480 investment in mobbing in spring. The ratio cost/benefits in responding to distanced mobbing  
481 calls is therefore probably flexible through different times of the year. Given that most of  
482 these factors are intercorrelated, determining which one is responsible for the difference in  
483 mobbing is unfeasible in natural conditions.

484           **Replicating the experiment in spring: Almost no response to crested mobbing**  
485 **calls**

486           In addition to a general lower mobbing response in spring, the differences between  
487 treatments were also impacted by the season. Indeed, while we selected similar models for the  
488 community, coal tits', and crested tits' response in winter (additive effect of number of caller  
489 and emitter species), we found support for different models in spring. A general tendency was  
490 detected, with only the playbacks with three coal tits triggering more response than the three  
491 other playbacks. This suggests that the crested tit is not considered as informative in spring,  
492 even when mobbing in groups, and unexpectedly, even to conspecifics. Several explanations  
493 can be proposed. First, a group of three crested tits in spring may be too rare to bear meaning,  
494 as they are in pairs and defending their nest. However, this hypothesis does not stand as this is  
495 also the case for the coal tit, but that the difference between one and three callers still stands  
496 in spring for this species. Alternatively, the contact with crested tits may be reduced in spring  
497 if crested tits densities are lower during this season, hence decreasing learning opportunities  
498 for heterospecifics. However, crested tits stay on the same territory throughout the year  
499 (Ekman 1979) making this hypothesis unlikely despite the fact that our experiments do not  
500 allow us to formally rule out it. We rather suggest that this lack of mobbing response may  
501 emerge from reduced reliability of the calls. To be efficient, an acoustic signal needs to be  
502 easily distinguishable from other signals (Bradbury and Vehrencamp 2011). The song and  
503 mobbing calls of the crested tits are extremely similar (Cramp and Perrins 1993, Hailman  
504 1989). As crested tits produce both songs and mobbing calls in spring, we can hypothesize  
505 that the global vocal production of crested tits therefore becomes less reliable from an

506 external individual, hence leading to a decreased response to such calls. In contrast, the coal  
507 tit appears to be reliable and responded to in both seasons. This result is consistent with Jiang  
508 et al. (2020) who also found that between seasons differences in playback responses did not  
509 affect the nuclear status of some particular species (in their case, David's fulvetta *Alcippe*  
510 *davidi*). The difference between the response of the bird community to coal tits' playbacks  
511 compared to crested tits' playbacks may also be due to a higher aggressiveness from crested  
512 tits. Crested tits are known to be more aggressive during spring (Campbell 1958), and crested  
513 tits, larger than coal tits, have higher rank dominance status (Suhonen et al. 1993). We have,  
514 however, little data on whether the heterospecific aggressiveness is higher than coal tits'  
515 aggressiveness since dominance status is not necessarily linked to increased aggressiveness  
516 (Wilson 1992). Finally, difference in nest predation may impact the reliability of the  
517 information produced, but to our knowledge, nest predators are similar between Parid species  
518 (Cramp and Perrins 1993).

519       To conclude, birds from a community respond differently to acoustic situations with  
520 varying emitter species and number of callers. The number of callers may be recognized  
521 either with caller identity and/or changes in duty cycles. Those acoustic cues are not  
522 responded to in the same way throughout the year, possibly because of changes in  
523 territoriality and reliance on heterospecific calls. These results emphasize the importance of  
524 seasons in studies investigating the complexity of heterospecific communication.

525

526

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