Acoustic cues and season affect mobbing responses in a bird community

Short title: cues and context affect heterospecific communication

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ABSTRACT

Heterospecific communication is common for birds when mobbing a predator. However, joining the mob should depend on the number of callers already enrolled, as larger mobs imply lower individual risks for the newcomer. In addition, some 'community informant' species seem more reliable regarding the information transferred in mobbing calls. Birds should therefore rely on both the number of callers and the species identity of the caller(s) when mobbing. Given the large differences in social organization and environment throughout the year in passerine communities, the response to acoustic cues could be impacted by the season. In the present study, we tested the potential interaction between the number of callers, the species identity of the caller (i.e., coal tit or crested tit), and the season on birds' mobbing response using a factorial playback experiment. Overall, we found that soundtracks with three callers triggered more mobbing than soundtracks with one caller and that soundtracks with coal tits' calls triggered more mobbing than soundtracks with crested tits' calls. However, this effect interacted with the season: in spring, only soundtracks with three coal tits triggered a mobbing response. We therefore confirm the hypothesis that birds consider both the species and the number of callers when joining a mobbing chorus. Moreover, our study demonstrates how seasonal context interacts with acoustic cues and illustrates the dynamic properties of heterospecific communication.

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

INTRODUCTION

Clustering around a predator and actively harassing it instead of fleeing is a widespread phenomenon termed ‘mobbing’. Particularly common in birds (Carlson et al. 2018), mobbing essentially triggers the displacement of the predator to another location, both at the short and long time scale (the Move-On Hypothesis, Curio 1978, Flasskamp 1994). Other benefits, such as monitoring the predators and enhancing learning opportunities for offspring, have been proposed (Curio 1978). Costs associated with such behavior are however non-negligible: in addition to the loss of time and energy when responding to an individual calling, the direct confrontation with a predator could result in direct aggression from the predator (Curio and Regelmann 1986, Poian and Yorke 1989, Sordahl 1990). Mobbing efficiency (i.e., the ratio of costs / benefits) can be improved by increasing the number of mobbing individuals (Krams et al. 2010, Wheatcroft and Price 2018). Indeed, larger groups decrease both the individual risk of being targeted by the predator (Hamilton selfish herd or dilution effect, Foster and Treherne 1981), and the overall success of the predator through confusion effect (Carlson et al. 2018). Larger groups also increase the chances of repelling the predator (Hendrichsen et al. 2006) and increase the reliability of the information. Indeed, deceptive mobbing calls can often occur (Goodale et al. 2014, Searcy and Nowicki 2005); hence, larger groups imply lower risks of deception. Such an increase of participants can be achieved both with conspecific and heterospecific individuals, and heterospecific mobs are indeed well documented (e.g., Dutour et al. 2017a, Goodale and Kotagama 2005, Hua et al. 2016). Although heterospecific mobbing responses probably emerged as simple by-product mutualism (Kostan 2002), the relationships between species can be complex. Indeed,

participation in such mobs is often unequal (Dutour et al. 2017b), with some species risking less by following the group at a distance (Magrath et al. 2015). In opposition, other species seem particularly active and trustworthy regarding the information conveyed in the calls (Farine et al. 2015). For such species that are active, reliable, and highly responded to, the term ‘community informant’ has been proposed (Carlson et al. 2020).

The rationale to join mobbing birds should therefore depend on two main cues: (i) the number of birds already mobbing, as a greater number of birds indicates a lower risk for new participants, and (ii) the species identity of the caller(s), since some species convey more reliable and relevant information than others. However, throughout the year, the environment of birds varies greatly, possibly impacting their communication. The social networks, as such as other physiological and environmental factors modify birds’ behavior (Cully and Ligon 1986, Van Duyse et al. 2002). Indeed, some passerines join mixed-species flocks during the winter, yet mostly live in pairs within strongly defended territories during the spring (Broughton et al. 2019, Hinde 1952). Regarding conspecific communication, the increase in territorial aggressiveness in spring (Wingfield and Ramenofsky 1985) may lead to decreased cooperation with conspecifics. We can therefore hypothesize that responses to the cues (i.e., the species identity and the number of callers) should vary according to the social context. Indeed, Dutour and colleagues (2019) detected a higher mobbing response to heterospecifics in winter compared to spring. Such an interaction between context and cues has not been investigated yet, although all have been investigated in isolation on different species (e.g., different responses in different seasons, Dutour et al. 2019; different responses to different number of birds, Igic et al. 2019).

To test these hypotheses, we built a set of playback experiments using a factorial design. We broadcast soundtracks of either one or three coal tits (*Periparus ater*) and one or three crested tits (*Lophophanes cristatus*) to free-ranging birds of both species, and recorded their behavioral response (calling and approaching, the most conspicuous signs of mobbing in birds). Following a recent study (Carlson et al. 2020), coal tits and crested tits contrast in their call reliability (i.e., coal tits vary their calls when facing different threats) and heterospecific attraction when mobbing a predator. To test the effect of the season, we broadcast the same soundtracks in winter and spring. Our experiment therefore aims at determining the relative flexibility of heterospecific relationships and stability of cues throughout birds' seasonal activity. By looking at the mobbing response of both coal and crested tits to each other's calls, as much as the mobbing response of the overall community, we aim at determining how context affects the cues used by birds when investing in mobbing.

MATERIAL AND METHODS

General organization

We aimed at testing the mobbing response of free-ranging birds to different soundtracks, at two different seasons. Playback tests were done in a 10 km² area of coniferous forest in the East of France (46°13'05.0"N 5°41'50.8"E). Densities of coal and crested tits are high in this area, as shown by the long-term ornithological census in the region (both species were detected in 94% of points, spaced at 150 m from each other, LPO AuRA). To circumvent inherent spatial variability, we established 100 spots for the playback tests, following existing trails. Each spot was selected close to a tree allowing birds' approach and concealment of experimenters. All spots were separated by ~ 100 m (mean and standard

deviation X = 110.9 ± 27.2 m) since this distance is sufficient to degrade bird sounds (Morton 1975). In addition, we performed one complementary experiment to verify that the minimum distance of 100 m between test locations is sufficiently large to minimize the risk of pseudo-replication. Specifically, we replicated the experiment and followed the responding birds with binoculars. We found that from one test to the next one, no bird followed us (see details in Supplementary File 1). A similar experiment performed on the great tit shows the same result with a 100 m distance (Salis et al. 2022).

We created a crossover design in which our four different treatments (different emitter species and number of callers, see paragraph Playbacks for details) were broadcast at two seasons (January and May) on each spot. Each spot consequently received eight playback tests. We avoided spatial and temporal autocorrelation by (i) alternating the four treatments at consecutive spots, and (ii) doing the same number of tests of each treatment, each day. The 400 tests in each season were done in a short period (two weeks) to avoid a potential intra-seasonal effect, and each consecutive test spaced by at least five minutes. Post hoc analyses (Sup. File 2) show no effect of order of playback treatment nor of the repeated presentation of playbacks on our results.

Playbacks

We created four treatments: soundtrack with only one coal tit (1CO), three coal tits calling simultaneously (3CO), only one crested tit (1CR), and lastly, three crested tits (3CR). We did not use a negative control (e.g., heterospecific song or background noise) since we were interested in the difference between our treatments. Moreover, background noise has been used in several studies (Dutour et al. 2019, Salis et al. 2022, Suzuki et al. 2016) and

never triggered a response from Parids. We used recordings obtained by A.S. during the previous year in the same area where the experiment took place. The recorded birds mobbed in response to a mobbing chorus of various birds (including coal and crested tits, Dutour et al. 2016). The recordings were done with a ME-67 Sennheiser microphone connected to a K6 basis and a Fostex FR2LE recorder. These recordings were then cleared of any other bird call, their amplitude homogenized at 50% on the entire file with AvisoftSasLab (Avisoft Bioacoustics, Glienicke, Germany), and saved as WAV files. We selected recordings with similar duty cycles (~ 9 seconds for the three birds treatments and ~ 6.5 seconds for the one bird treatment, Landsborough et al. 2020, details in Sup. File. 3) and around the mean (± 1 SD) of previous recordings obtained by our team (coal tit: 82 ± 26 notes per min, N = 30, crested tit: 134 ± 44 notes per min, N = 10). For the treatments with three birds (trio treatments), we superimposed recordings of three different birds calling to simulate a chorus. For each treatment, we built five different soundtracks to circumvent the idiosyncrasy of recorded subjects (Kroodsma 1989).

Test procedure

One test consisted in playing 30 sec of a mobbing call sequence at each spot with a Bose Soundlink Revolve loudspeaker perched on a tripod (H: 1m), put near a tree and at an amplitude of 84.01 ± 2.70 dB (calculated at 1 m with Lutron SL-4001, C weighting, slow settings, re. 20 µPa, Templeton et al., 2016). 30 sec is enough to trigger a mobbing response from nearby birds (previous recordings were obtained with such a stimulation), who can approach and call as a response, sometimes with additional aggressive behavior (e.g., wing

flicking, Salis et al. 2021). A stimulation of only 30 seconds also limited the influence of the first birds to call on the following birds recruited. The two observers positioned themselves at 10 m from the tripod at vantage points before launching the soundtrack with an NW-A45 Sony. Before launching any test, we made sure that no bird was already in the vicinity nor uttering mobbing calls in a distance. We observed the area with binoculars and all birds either calling and/or approaching from the beginning of the test to 15 sec after the end of the soundtrack. One bird was considered as approaching if it came in the 10 m radius around the tripod (Dutour et al. 2017b). Only birds uttering specific and known mobbing calls (see Sup. File 4 for spectrograms) were noted as calling. If a bird displayed the complete sequence of mobbing behavior (i.e., simultaneously calling and approaching the loudspeaker), it was then considered as giving a mobbing response.

Statistical analyses

All statistical analyses were done with R studio (R v.3.6.1, R core team 2022). We estimated the mobbing response of the community to the soundtracks with two variables: first, we analyzed whether the soundtrack triggered a mobbing response from at least one bird (dichotomic variable: presence = 1, absence = 0). Secondly, the intensity of the mobbing was estimated with the number of individuals that mobbed, since larger mobs are more efficient in deterring the predator (Templeton et al. 2005, Woods 2018). To this aim, we ran generalized linear mixed models (function *glmer*, package *lme4*). When the response variable was the occurrence of mobbing, we used a binomial distribution (logit link function), while for mobbing intensity, we used a Poisson distribution (log link function, no overdispersion

detected). We first built a complete model with the three explicative variables: the number of callers (singleton versus trio), the emitter species (coal vs crested tit), the season (spring versus winter), and their interactions. The playbacks ID (five different playbacks in each treatment) and the spot location (100 points) were introduced as random effects. The significance of each explanatory term introduced in the full model was examined using a likelihood ratio test (implemented in the function *anova*), and non-significant terms were then successively discarded to obtain the final model. To examine more specifically how birds' response varies according to the treatment within each season, we also ran partial analyses separately for each season. Post-hoc comparisons were computed with estimated marginal means with a Sidak correction for multiple testing (package *emmeans*, functions *emmeans* and m*ultcomp::cld*) and on the response scale to obtain effect sizes of the differences.

Secondly, we specifically focused on the mobbing response of coal and crested tits to each other's calls. We therefore ran separate analyses for each species on the occurrence of response (i.e., presence/absence of at least one coal or one crested tit mobbing). Given the low proportion of spots for which both species responded to our soundtracks, it was not possible to analyze the response intensity (i.e., the number of mobbing birds). We therefore only used a GLMM logistic regression (i.e., a binomial distribution for the error term and a logit link, points, and playbacks' ID as random variables) to analyze the influence of treatments on the occurrence of response. As with the community response, we first ran a complete model with the season, the emitter species, the number of callers, and their interactive effects, then ran partial analyses separately for each season. Since the presence of coal tits and crested tits was recorded for each test, we were able to test the relative association of these two species. We

therefore ran Spearman correlation tests (*cor.test*, giving the Φ coefficient of correlation for dichotomic data) to test whether spots in which coal tits mobbed were also points in which crested tits mobbed.

RESULTS

Overall analyses

The occurrence of response (i.e., the elicitation of at least one mobbing bird) was driven by a complex three-way interactive effect between the season, the number of callers, and the emitter species (Table 1). In contrast, the response intensity (i.e., when mobbing occurred, the number of mobbing birds) was affected by an additive effect of all the three explanatory variables (the emitter species, the number of callers and the season): more birds responded in winter than in spring, more to coal tits than crested tits, and more to trios than to singletons (Table 1, Figure 2c and 2d).

When analyzing the response of coal tits or crested tits alone, a three-way interaction was detected for the occurrence of mobbing in both species (Table 1), indicating therefore that the differences between treatments substantially vary between the two seasons (winter and spring). To investigate properly the differences between our four playback treatments, we ran separate analyses for each season.

Table 2. Complete models exploring the relative effect of season, number of callers (NB) and emitter species on mobbing responses. Generalized Linear Mixed Models using a binomial distribution to treat the dependent were done to analyze the mobbing propensity within the community, or more specifically within coal tits and crested tits (binomial distribution). GLMM using a Poisson distribution were done to analyze the number of mobbing birds when mobbing occurred (only for the community). The emitter species are either the coal or the crested tit, the number of callers in the soundtrack is either one (singleton) or three (trio), and the season is either spring or winter. All degrees of freedom = 1. Significant p-values (*P*) are in bold.

	Community				Coal tits		Crested tits	
	Occurrence of mobbing		Number of mobbers		Occurrence of mobbing		Occurrence of mobbing	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Species	29,85	**< 0,001**	36,84	**< 0,001**	32,37	**< 0,001**	14,87	**< 0,001**
NB	27,22	**< 0,001**	23,86	**< 0,001**	11,87	**< 0,001**	11,67	**< 0,001**
Season	24,26	**< 0,001**	74,06	**< 0,001**	17,08	**< 0,001**	28,92	**< 0,001**
Species : NB	1,43	0,23	0,07	0,79	0,16	0,69	1,47	0,22
Species : Season	3,1	0,08	0,1	0,75	0,9	0,34	1,07	0,3
NB : Season	0,42	0,52	0,84	0,36	2,15	0,14	0,007	0,93
Species : NB : Season	7,03	**0,008**	0,36	0,55	3,93	**0,047**	8,61	**0,003**

Partial analyses during the winter season

In winter, eleven different species were attracted to our soundtracks (Figure 1A), with a maximum diversity of six species at one test. The two main species, outside coal and crested tits, were the Goldcrest *(Regulus regulus*, present in 39% of our tests) and the Marsh tit (*Poecile palustris*, 23%). The presence of at least one bird mobbing, irrespective of the species (i.e., community response, Figure 2A) was dependent on the number of callers in the playback and the caller species (Table 2A). Indeed, birds mobbed more often the coal tit

soundtracks compared to the crested tit soundtracks, and more to soundtracks with three birds rather than only one bird calling.

When isolating the response of coal tits, we also detected an additive effect of number of callers and emitter species (Table 2B), resulting in a lower response toward singletons of crested tits, intermediate scores toward trios of crested tits and singletons of coal tits, and the highest occurrence of response toward soundtracks with three coal tits (Figure 3C). In contrast, the crested tit responded to a similar level to the soundtracks with three coal tits, three crested tits, and only one coal tit, showing a reduced response only when hearing one crested tit calling (Figure 3B, Table 2C). The association of the coal tit and crested tit during mobbing tests was high ($\Phi = 0.48$, $S = 55122727$, $P < 0.001$). Indeed, in 61% of spots in which a crested tit was mobbing, a coal tit was also mobbing, and 66% on the coal tit side.

Partial analyses during the spring season

In spring, we detected a lower mobbing propensity: the occurrence of response to any treatment did not reach 25%, compared to almost 50% in winter. 15 different species were attracted to our soundtracks (Figure 1B), with a maximum diversity of five species at one test. The two most common species that responded were the Goldcrest (present in 24/% of our tests) and the Common Chaffinch (*Fringilla coelebs*, 18%). The occurrence of at least one bird mobbing was impacted by an interaction between the number of callers in the playbacks and the emitter species (Table 2A). Indeed, birds responded more often to trios of coal tits compared to any of the three other treatments (Figure 2B).

When looking at the response of coal tits, the interaction term did not reach statistical significance (Table 2B), although effect sizes between treatments followed the same pattern (Figure 3C). As with the overall community response, the response of the crested tit was impacted by an interaction between the number of callers and the emitter species (Table 2C), resulting in a stronger difference between singletons of coal tits and trios of coal tits (Odds Ratio = 3.07, Standard Error = 1.05, P = 0.02) than between singletons of crested tits and trios of crested tits (OR = 0.44, SE = 0.55, P = 0.96, Figure 3D). The association between coal tits' presence and crested tits' presence was no longer present (Φ = 0.03, S = 10381583, P = 0.59): in only 18% of spots in which the crested tit mobbed and in 10% of spots in which the coal tit responded, the other species was present.

Table 1. Effect of the number of callers and the emitter species on the propensity and intensity of mobbing in two seasons. Generalized Linear Mixed Models using a binomial distribution to treat the dependent were done to analyze the mobbing propensity within the community, or more specifically within coal tits and crested tits (binomial distribution). The emitter species are either the coal or the crested tit, while the number of callers in the soundtrack is either one (singleton) or three (trio). Non-significant effects were successively removed from the full model presented here (in bold, the factors kept in the final model). All degrees of freedom = 1. P = p-value.

Species of interest	Season	Explanatory variables	χ^2	*P*
a. Community	Winter	**Emitter species**	24.22	< 0.001
		Number of callers	16.13	< 0.001
		Emitter species * Number of callers	1.09	0.29
	Spring	**Emitter species**	7.15	0.007
		Number of callers	10.48	0.001
		Emitter species * Number of callers	7.04	0.008
b. Coal tit	Winter	**Emitter species**	24.80	< 0.001
		Number of callers	12.31	< 0.001
		Emitter species * Number of callers	1.04	0.31
	Spring	**Emitter species**	8.15	0.004
		Number of callers	1.22	0.27
		Emitter species * Number of callers	2.94	0.09
c. Crested tit	Winter	**Emitter species**	15.86	< 0.001
		Number of callers	7.92	0.004
		Emitter species * Number of callers	5.32	0.02
	Spring	**Emitter species**	0.82	0.36
		Number of callers	4.32	0.04
		Emitter species * Number of callers	4.90	0.03

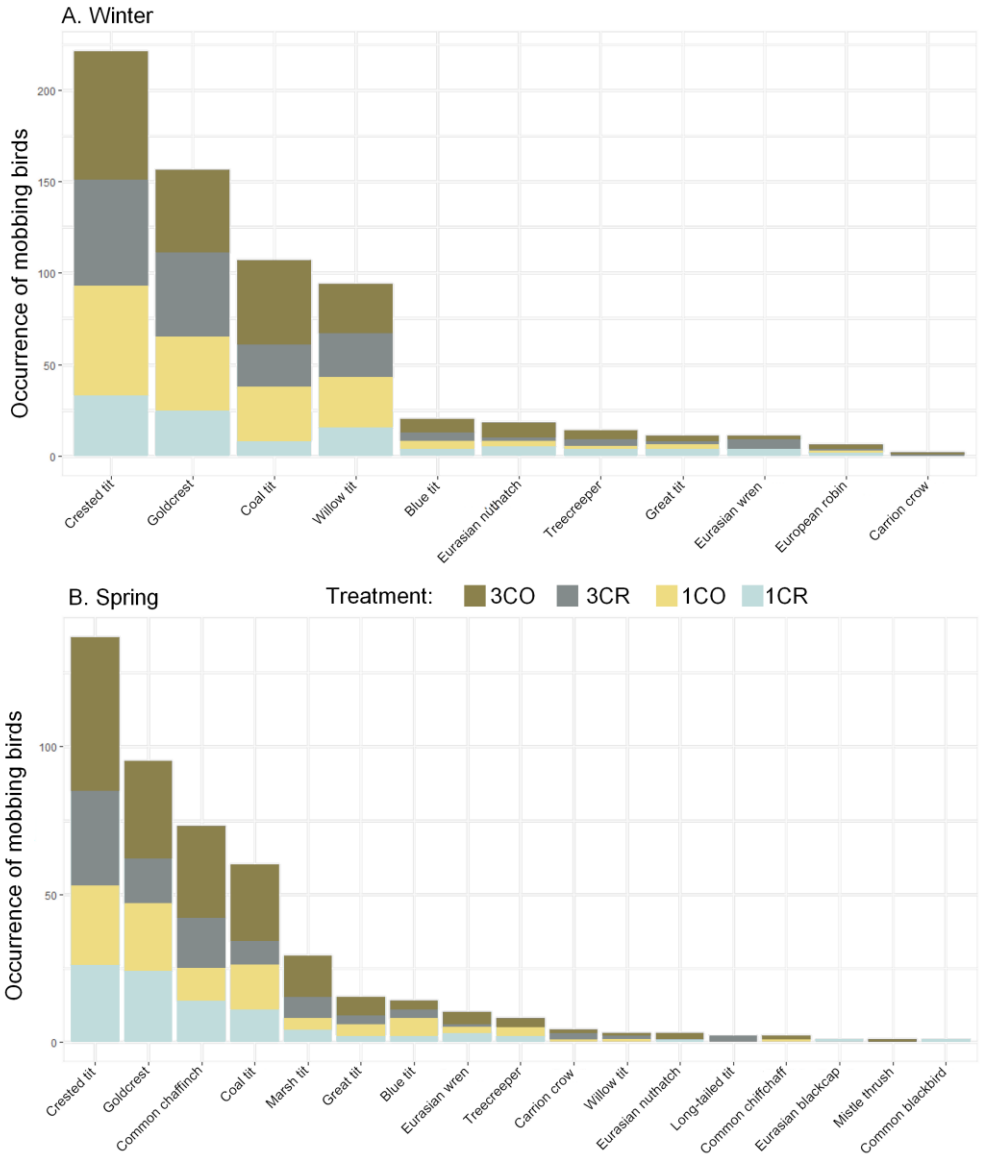

Figure 1. Number of points (100 per acoustic treatment) in which at least one bird of each species mobbed (i.e., approached and called), when facing each of our four acoustic treatments (3CO: three coal tits, 1CO: one coal tit, 3CR: three crested tits, 1CR: one crested tit). Species taxonomy : Blue tit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

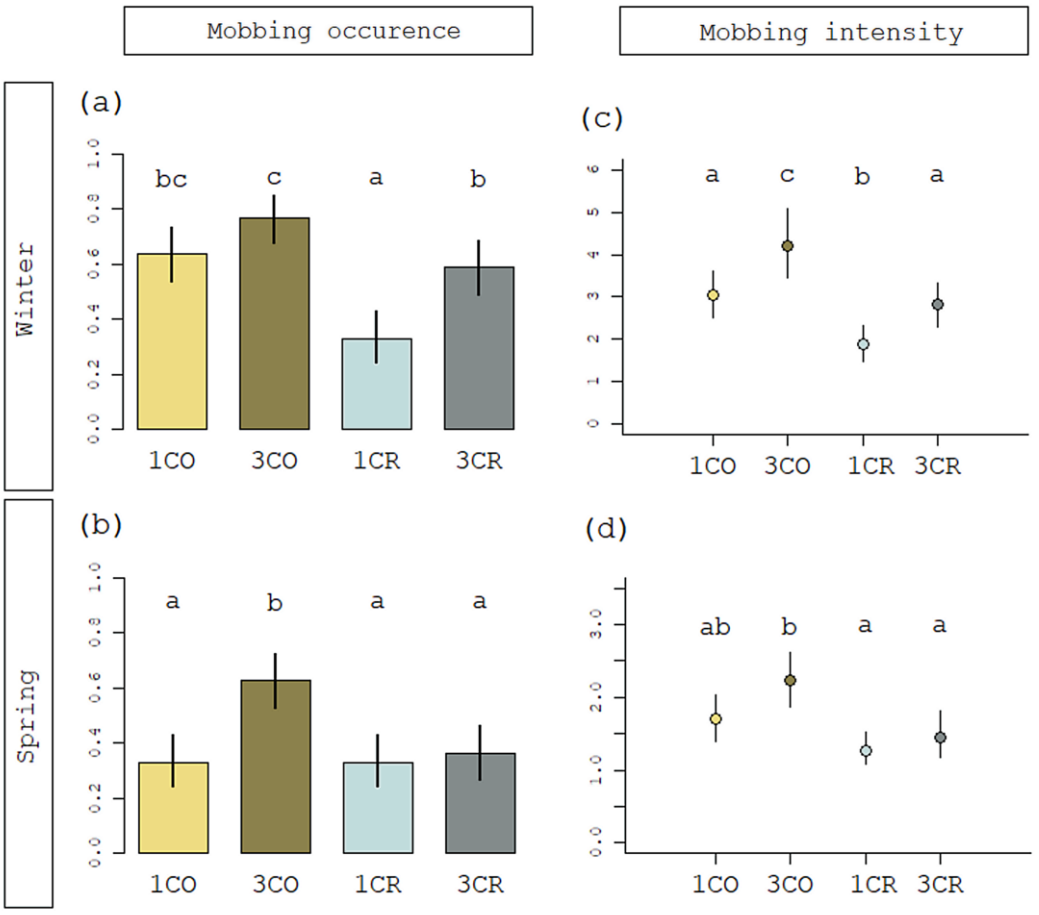

Figure 2. Mobbing response of the bird community to our four different mobbing soundtracks (1CO: one coal tit, 3CO: three coal tits, 1CR: one crested tit, 3CR: three crested tits). Similar letters indicate that no statistically significant differences were found between the treatments ($\alpha = 0.05$). Error bars are 95% confidence intervals. Graphs on the left represent mobbing occurrence: the proportion of spots in which at least one bird mobbed (i.e., approach and called, $N = 100$ per treatment). Graphs on the right represent mobbing intensity: the number of birds that responded when there was a mobbing response (sample sizes are the proportion of the graphs on the left). The upper graphs are the response of birds in winter and the lower in spring.

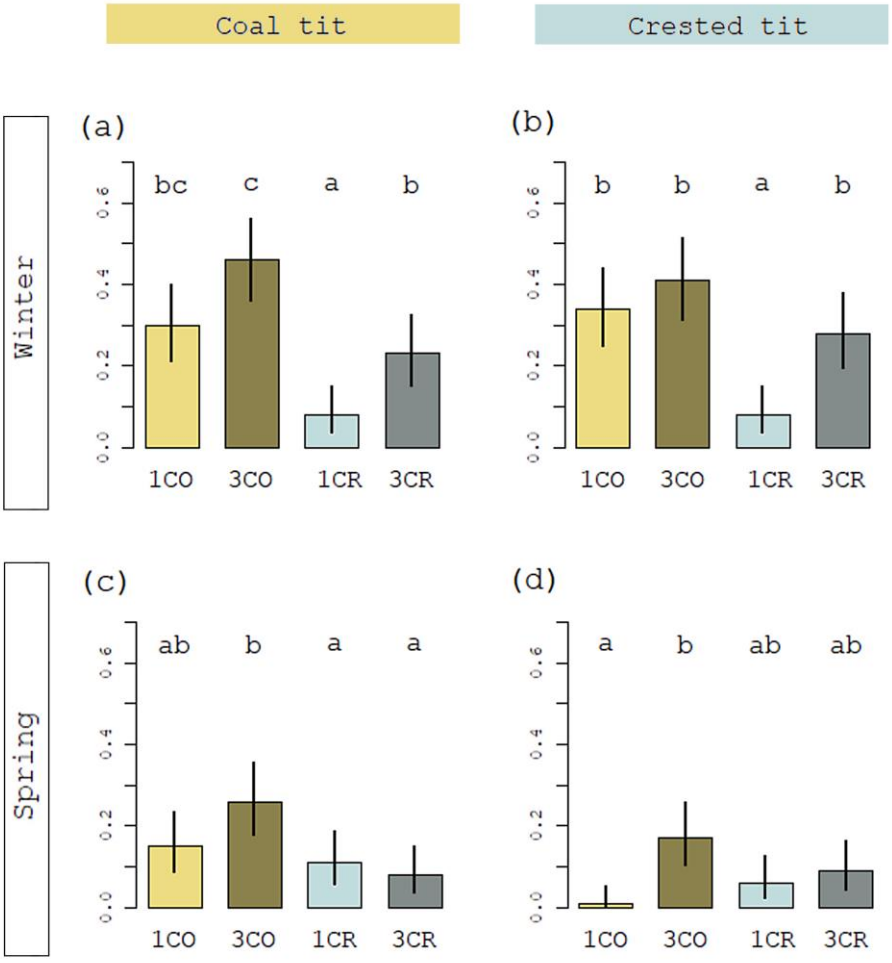

Figure 3. Proportions of points in which either a coal tit (left) or a crested tit (right) mobbed in response to our four different soundtracks (n = 100 for each treatment, 1CO: one coal tit, 3CO: three coal tits, 1CR: one crested tit, 3CR: three crested tits). The upper graphs are the mobbing response of birds in winter and the lower in spring. Similar letters indicate that no statistically significant differences were found between the treatments (α = 0.05). Error bars are 95% confidence intervals.

DISCUSSION

Overall, coal tits' soundtracks triggered more mobbing response from conspecifics and heterospecifics than crested tits' soundtracks; and soundtracks with three callers triggered more mobbing response from the bird community than soundtracks with only one caller. Taken in isolation, the effects of emitter species, number of callers, and season are in line with previous studies investigating the subject. However, in addition to the lower general response in spring, the season also impacted differently the interactive effect of the emitter species and the number of callers. This interaction between context and cues demonstrates the flexible nature of heterospecific communication.

Birds rely on both the number of callers and the species identity when investing in mobbing

In both seasons, the mobbing response towards soundtracks with three individuals calling triggered higher responses than soundtracks with only one individual calling. These results are in line with our hypothesis: a greater number of birds mobbing a predator represents a lower risk for a potential mobber, as it probably represents (i) a lower risk of attack from the predator (confusion and dilution effect, Sridhar et al. 2009), (ii) an increased transfer of reliable and relevant information (Magrath et al. 2015). One previous study found similar results with the Australian magpie (*Gymnorhina tibicen,* Igic et al. 2019), but with flee calls. Magpies flew and scanned more in response to soundtracks with more individuals. Birds can consider several cues to assess the number of birds calling. First, the Beacon effect increases the active space when several birds call in a natural situation (Buck and Buck 1966). Nevertheless, in the present study, by broadcasting singletons and trios soundtracks at the

same amplitude, we suppressed this effect. Birds can also consider the number of spatially different acoustic sources (Bradbury and Vehrencamp 2011). In our study, we launched the soundtracks with only one loudspeaker whatever the treatment to suppress this effect. Therefore, in our tests, the only cues that remain are the duty cycle (i.e., the proportion of the calling sequence when the signal is present) and the caller identity. The duty cycle is probably one major coding strategy for increased risk in Parids (Landsborough et al. 2020). However, in a recent study, great tits (*Parus major*) increased their mobbing response toward soundtracks made with calls of several individuals compared to soundtracks with only one individual calling (Dutour et al. 2021). In this latter experiment, the duty cycles of the different treatments were strictly equal. This likely suggests that both cues (duty cycle and caller identity) can be used by Parids when assessing the number of calling individuals.

A mobbing response occurred more often when broadcasting coal tits' mobbing calls compared to crested tits' calls, but also more birds responded to it. Unexpectedly, even crested tits responded more to coal tits' mobbing calls than to calls from their own species. Coal tits therefore appear to be listened to and heavily responded to, leading to larger (and possibly more efficient) mobs. This is in line with the hypothesis that species from the same community show different levels of reliability (Magrath et al. 2015). The notion of "community informant" was developed for Parids in Carlson et al. (2020). They investigated whether the birds possessed a reliable way of encoding predator information, and if several heterospecifics relied on these calls. They showed that the great tit (*Parus major*) best fitted the definition of community informant. The coal tit approached the definition, with only one caveat: the dunnock (*Prunella modularis*) did not respond to it. As the authors suggested, the

lack of response from one species does not mean that other species from the community do not respond to it (Carlson et al. 2020). Indeed, in our study, 14 species responded to coal tits' soundtracks. In opposition, the crested tit did not meet any of the criteria set by Carlson and colleagues. Coal tits therefore appear to be one important species regarding predator information in the community, while crested tits do not.

A different response in Spring: cues interact with context

In winter, Parids living in temperate regions often flock with heterospecifics, sometimes leading to impressive mobs (up to 20 birds in the present experiment). This flock organization is consistent with the fact that, in winter, the mobbing response of coal and crested tits were correlated, as they often flock together. In opposition, during the reproductive period (May-July), Parids nest and defend their territory with intensity (Hinde 1952). Spring territoriality may explain one of our results: we detected a lower number of birds mobbing to the different soundtracks in spring. We here propose that in spring, when all birds defend their territory, the number of birds that can respond is limited to the neighbors and therefore quite stable. Moreover, in spring, aggressivity toward conspecifics is high and may therefore reduce the number of potential birds responding to mobbing calls. This aggressivity may also explain why not so many birds responded to conspecific mobbing calls in spring (coal tits to coal tits and crested tits to crested tits). Secondly, our results depict an apparent decrease in mobbing occurrence in spring compared to winter. This difference must be taken with cautiousness, as the community and the density of the population may vary with the seasons: a decrease in mobbing response may simply be related to fewer individuals in the territory. An order effect due to tests in winter being done before the tests in spring is unlikely

given the absence of order effect in our experiment at a short time scale. In addition, in spring, we were able to hear coal tits singing at the 100 spots studied. We are therefore confident that, in spring, each spot could have recorded one coal tit's mobbing response. This suggests that at least for the coal tit, the response to conspecific and heterospecific mobbing calls decreases in spring. This result is consistent with Dutour et al. (2019) who detected in Parids a higher mobbing response toward heterospecific calls in winter compared to summer. The proximal reasons for such a decrease can be various. Increased territoriality and aggression in spring may very well limit cooperative communication, since the mobbing calls may resemble intra-specific aggression/territoriality calls, leading to a lower relevance for heterospecifics. Other factors such as decreased predator pressure in spring (Dutour et al. 2017b) could also result in a lower investment in mobbing in spring. The ratio cost/benefits in responding to distanced mobbing calls is therefore probably flexible through different times of the year. Given that most of these factors are intercorrelated, determining which one is responsible for the difference in mobbing is unfeasible in natural conditions.

Almost no response to crested mobbing calls in spring

In addition to a general lower mobbing response in spring, all birds (the general community response, but also the isolated analysis of coal tits and crested tits) responded similarly to singletons or trios of crested tits, while this difference was strong in winter with a higher response towards trios. Put in other words, the effect of species identity and the number of callers were additive in winter but interactive in spring. This suggests that the crested tit is not considered as informative in spring, even when mobbing in groups, and unexpectedly, even to conspecifics. Three explanations can be proposed. Firstly, a group of

three crested tits in spring may be too rare to bear meaning, as they are in pairs and defending their nest. However, this hypothesis does not stand as this is also the case for the coal tit, but that the difference between one and three callers still stands in spring for this species. Alternatively, the contact with crested tits may be reduced in spring, hence decreasing learning opportunities for heterospecifics. However, crested tits stay on the same territory throughout the year (Ekman 1979). We consequently do not think that a lower presence of crested tits can explain this lack of mobbing response to both singletons and trios of crested tits soundtracks. We rather suggest that this lack of mobbing response may emerge from reduced reliability of the calls. To be efficient, an acoustic signal needs to be easily distinguishable from other signals (Bradbury and Vehrencamp 2011). The song and mobbing calls of the crested tits are extremely similar (Cramp and Perrins 1993, Hailman 1989). As crested tits produce both songs and mobbing calls in spring, we can hypothesize that the global vocal production of crested tits therefore becomes less reliable from an external individual, hence leading to a decreased response to such calls. In contrast, the coal tit appears to be reliable and responded to in both seasons. This result is in adequacy with Jiang et al. (2020) who also found that between seasons differences in playback responses did not affect the nuclear status of some particular species (in their case, David's Fulvetta *Alcippe davidi*).

To conclude, individuals from different species rely on several acoustic cues when responding to conspecific or heterospecific mobbing calls. Both the number of callers and the species calling are salient to the receivers, and those cues are not used in the same way throughout the year. These results emphasize the importance of seasons in studies investigating the complexity of heterospecific communication.

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