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RESEARCH PAPER

**Response to allopatric combinatorial calls**

**Great tits (*Parus major*) adequately respond to both allopatric combinatorial mobbing calls and their isolated parts**

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**Abstract**

When mobbing a predator, birds often produce specific mobbing calls that are efficient in recruiting both conspecifics and heterospecifics. Recent studies on Parids have demonstrated that these mobbing calls are in fact a combination of two distinct calls - first, introductory notes eliciting vigilance in the receiver, then broadband frequency notes (“D notes”) triggering approach. Debates on a parallel between human syntax and this form of combination have emerged. The degree to which this combinatoriality is perceived in heterospecific communication may shed light onto the relative complexity of such combinatoriality. In this study, our aim was to determine whether European great tits (*Parus major*) appropriately responded to mobbing calls (and their isolated parts) of an allopatric species, the black-capped chickadee (*Poecile atricapillus*), a North-American species which produces similar

combinatorial mobbing calls. In addition, we tested whether the behavioural response to complete mobbing sequences was different than the simple sum of its two constituents. As we hypothesized, great tits behaved differently when hearing the two isolated calls or the complete mobbing sequence: they produced calls and displayed excitement signs only toward the complete mobbing sequence. Moreover, great tits responded to the introductory and D notes by respectively scanning and approaching, and to the complete sequence by mobbing. Our results altogether support the emerging hypothesis of semantic compositionality in Parids, although the present study does not definitively demonstrate the existence of this cognitive process in the great tit.

Keywords: combinatorial call, heterospecific communication, mobbing, Paridae, *Parus major*, semantic compositionality

## 1 | INTRODUCTION

The vast majority of research in animal communication focuses on intraspecific interactions, while heterospecific exchanges of information are often interpreted as simple by-products of conspecific communication. For example, birds responding to each other alarm calls are more readily seen as by-product mutualism, where the information produced is mostly directed toward conspecifics, and by chance, is also useful to heterospecifics listeners, (Bradbury & Verhencamp, 2011). However, recent studies have begun to unravel complex interactions between different species, especially in bird flocks (Goodale & Kotagama, 2008; Coppinger et al., 2020; Carlson et al., 2020). The gathering of birds of different species, either all year round in tropical environments (Goodale et al., 2015) or during the non-breeding season in temperate environments (Dutour et al., 2019a), is widespread and usually thought to be beneficial for both foraging efficiency and predator defence (Berner & Grubb, 1985). These

49 benefits mainly depend on an increased transfer of information; with vocal communication  
50 being one efficient strategy (Bradbury & Vehrencamp, 2011). Indeed, food calls (Newman &  
51 Caraco, 1989), contact calls (Kondo & Watanabe, 2009) and alarm calls have been thoroughly  
52 described (Caro, 2005). In this latter category, two type of alarm calls are classically opposed.  
53 Flee calls, difficult to localize due to their pure tones (Marler, 1955), are produced when  
54 facing an urgent threat and provoke an escape or a freezing reaction from birds in the vicinity  
55 (Caro, 2005). In opposition, mobbing calls are used when facing an intermediate threat (e.g. a  
56 non-hunting predator, Andrew, 1961), and often made of notes with broadband frequencies,  
57 helping localisation (Marler 1955). Mobbing typically induces the approach of other potential  
58 prey (conspecifics and heterospecifics) and active harassment of the predator (Carlson et al.,  
59 2018; Curio, 1978) and is consequently one great opportunity to study heterospecific  
60 communication (Hurd, 1996; Dutour et al., 2019a; Yu et al., 2019).

61 Studies about the mechanisms underlying heterospecific communication suggest that both  
62 learning and innate processes are in place: associative learning has been evidenced both in the  
63 adult response to mobbing calls and in the ontogeny of mobbing behaviour in fledglings  
64 (Magrath et al., 2015; Potvin et al., 2018; Carlson et al., 2019; Dutour et al., 2019b). This could  
65 well explain higher responsiveness toward sympatric species than toward allopatric ones  
66 (Wheatcroft & Price, 2013). Still, responsiveness towards allopatric species is rather  
67 widespread (Johnson et al., 2003; Fallow et al., 2011; Randler, 2012; Dutour et al., 2017; Yu et  
68 al., 2019) and, although not sufficient in itself, phylogenetic conservation or convergence of  
69 mobbing call characteristics could also well explain such a phenomenon (Stefanski & Falls,  
70 1972; Fallow et al., 2011; Randler, 2012; Wheatcroft & Price, 2015; Dutour et al., 2017).

71 The acoustic structure of mobbing calls has been described in many passerine species (Ficken  
72 & Popp, 1996) and recent studies suggest that some Parids use a combinatorial call sequence to  
73 encode information in mobbing calls: the association of introductory notes with strong

frequency modulation (here referred as the I notes, Figure 1) and several broadband elements (referred as D notes, following Hailman et al., 1985). Alone, introductory notes are used to warn neighbours about a threat and induce vigilance behaviour; while D calls have a recruitment function (in various contexts such as mating or foraging) and thus trigger an approach of conspecifics (Suzuki et al., 2016). Although the use of a combinatory call sequence in eliciting mobbing behaviour of a conspecific receiver has been evidenced in several passerine birds (Suzuki et al., 2016; Engesser et al., 2016; Dutour et al., 2019c), until now, little has been done to understand to which extent this process also applies to heterospecific mobbing sequences. Yet, such test may bring information on how birds perceive and deal with combinations, and shed light on whether it could be considered semantic compositionality in the human sense (Dutour et al., 2019b). Semantic compositionality (also termed compositional syntax by some authors) occurs when a combination of words has a meaning emerging from its individual parts (each part having its own meaning), and when the order of such parts is important (Engesser & Townsend, 2019; Suzuki et al., 2019; Zuberbühler, 2019). Debates on whether the “I notes followed by D notes” mobbing sequence can approach human compositional syntax have been profuse (Bolhuis et al., 2018a; 2018b; Suzuki et al., 2018). Determining how Parids respond to unknown calls but with similar syntax would improve the current knowledge of birds’ ability to process syntactic rules. Only one study (Suzuki et al., 2017) demonstrated that Japanese tits respond to artificial mobbing sequences made of the concatenation of introductory notes of their own species and D notes of another sympatric Parid species, the willow tit (*Poecile montanus*). By testing birds with allopatric calls, we here have the advantage of ruling out any learning effect, and focus on birds’ ability to generalize from similar acoustic properties.

Several studies have already showed the European great tit’s (*Parus major*) responsiveness to the allopatric black-capped chickadee’s (*Poecile atricapillus*) mobbing call sequence, although the intensity of the responsiveness varied to some extent between studies (Randler, 2012;

Dutour et al., 2017). Acoustic properties of their mobbing calls have been extensively studied (black-capped chickadee: Landsborough et al., 2019, great tit: Kalb et al., 2019b), and both species display a sequence that involves a combination of introductory and D notes in a fixed order (Templeton, 2005; Dutour et al., 2019c, see Figure 1). Therefore, these two species are particularly suitable for testing whether combinatorial heterospecific mobbing calls are decoded in a similar way than intraspecific ones. Here, we first investigated how great tits alter their behavioural responses when exposed to a conspecific mobbing call sequence or its isolated decomposition into introductory or D notes, in order to verify that the combinatory sequence is an indispensable prerequisite to elicit mobbing in the receiver. We measured vigilance effort, willingness to approach (Suzuki, 2017; Dutour et al., 2019c), propensity to mob as well as level of excitement. We then examined whether great tits adopt similar behavioural responses when they are exposed to a black-capped chickadee mobbing call sequences or their isolated decomposition into introductory or D notes. According to previous studies, we should expect that great tits would be sensitive to mobbing call sequences of the black-capped chickadee, but less responsive than to those of conspecifics (Randler, 2012; Dutour et al., 2017; 2019a). We hypothesized that the similarity in call organisation (i.e. introductory notes followed by D notes) between great tit and black-capped chickadee calls would engender similar behaviours (scanning to introductory notes, approaching to D notes, and displaying a complete mobbing behaviour to the complete sequence).

## **2 | METHODS**

### **2.1 | General organisation**

Our aim was to test whether great tits are able to adequately respond to isolated parts of never heard before heterospecific mobbing sequences. We performed a call-to-behaviour experiment, a classical method used to study acoustic communication (Schlenker et al., 2016). More

specifically, we set up 8 different treatments: first, great tits were subjected to stimuli with the complete, natural (I-D) mobbing call sequence of black-capped chickadees (BCCH), then only with the introductory notes or only with the D notes. Second, great tits were subjected to the three same types of sequence (I-D, I alone and D alone) but from other great tits (GRTI). Finally, two different types of controls were broadcast: background noise or the song of the black-capped chickadee, to distinguish the response due to novelty from the actual mobbing response. For each of the eight treatments, we created 20 different stimuli with different callers, and then performed 20 independent tests (i.e. different receiver and emitter for each of the 160 tests performed).

## **2.2 | Preparation of stimuli**

Our stimuli of great tits and black-capped chickadees were designed using recordings obtained from the Xeno-canto online database ([www.xeno-canto.org](http://www.xeno-canto.org)) and the Macaulay Library ([www.macaulaylibrary.org](http://www.macaulaylibrary.org)). For both species, we only used good quality recording files (A or B grades) under the denomination “Alarm call”/“Call”.

Both species produce a mobbing call with an association of introductory and D notes (Fig.1). However, as these notes can also be produced in other context (Freeberg and Lucas, 2002; Kalb et al., 2019b), we controlled several features to ensure that the selected recordings represented mobbing call sequences. To begin, selected recordings were all made of the same introductory and D notes reported in Baker and Becker (2002) and Templeton (2005) for the black-capped chickadee and in Randler (2012) and Kalb et al. (2019a) for the great tit.

In addition, for both species, D notes length is known to vary with the context (Templeton et al., 2005; Kalb et al., 2019b); we therefore checked that the D notes in our stimuli had the same length ( $X = 0.05 \text{ s} \pm 0.01$  for the great tit,  $X = 0.18 \text{ s} \pm 0.02$  for the black-capped chickadee). Finally, we verified that no introductory notes used in food or flight related contexts were the

most frequent in any of our recordings (i.e. the C notes for the black-capped chickadee associated with flight; and the G, H, I and M notes associated with food for the great tit, Freeberg and Lucas, 2002; Kalb et al., 2019b).

From these recording files, we designed 40 1 min mobbing sequences of great tits and black-capped chickadees (20 for each species, each obtained from a different sender) using Avisoft-SASLab software. To allow comparison between the responses of black-capped chickadees and great tits, we constructed every mobbing sequence with a similar duty cycle (i.e. the amount of time a signal is present over a specified time, Landsborough et al., 2019) and mobbing call repetition (30 calls per minute, natural range of repetition rate, Suzuki et al., 2016). Consequently, each mobbing call emitted by both species had a similar total introductory note duration ( $0.31 \text{ s} \pm 0.06$ , mean  $\pm$  SD) and D duration ( $0.50 \text{ s} \pm 0.07$ ), but not the same number of notes, since black-capped chickadee's D notes are longer (Figure 1).

Isolated introductory notes and isolated D notes stimuli for each species (20 stimuli for each treatment, for a total of 80 stimuli) were constructed by replacing the unwanted notes (D notes for the I notes treatment, and I notes for the D notes treatment) by background noise from the original recording, therefore keeping the same duty cycle of each call type as in the original soundtrack, since this acoustic feature seems more important than the number of notes/elements in eliciting mobbing behaviour (Landsborough et al., 2019). We also constructed 20 background noise stimuli extracted from the original recordings (control treatment hereafter referred as C1) and 20 control stimuli using recordings of songs of black-capped chickadees (the two-note “feebee” song, control treatment hereafter referred as C2) from Xeno-canto database, with a rate of 18 song/min (natural rate, calculated from the original recordings). Each of these 160 stimuli were cleared of any other bird calls, background noise was reduced, and amplitude homogenized.

## 2.3 | Field tests



Tests were performed in the east of France at the beginning of the breeding season, in spring (April 2019) in a radius of 25 km around Lyon (45°53'39.3"N 5°03'05.7"E).

Each test was performed by two field assistants. One of them was assigned to the playback operation, while the other was kept unaware of the selected stimulus (using headphones with music) and assigned to the behavioural recording of the focal bird. For each test, after detecting an individual using binoculars, the focal bird was observed for at least 1 min, and the pre-test behaviour (usually singing or foraging) was noted. If the animal displayed an alarm behaviour, no test was performed. A loudspeaker was placed 16 meters from the bird ( $16.79 \pm 6.27$  m), and at less than 3 meters of a potential roost (bushes/ trees) to allow the approach of the focal bird. The two field assistants were then placed away (minimum of 15 meters to both the bird and the loudspeaker) before playing the stimulus with a remote control. All stimuli were broadcast using a Shopinnov 20 W loudspeaker with an intensity of  $79.8 \pm 1.9$  dB(C) (measured at 1 m from the loudspeaker using Lutron SL-4001, C weighting, slow settings, re: 20  $\mu$ Pa).

Tests were carried out between 06:00 and 13:00 h during calm and dry days. To avoid pseudoreplication, all selected focal birds were distant from one another by at least 100 meters (Dutour et al., 2019; Dutour et al., 2020). Two or three different calling males were usually detected within 100 m, we never went on the same path twice, and we made sure that no bird was following us. We are thus confident that each focal bird participated in only one test. Moreover, each of the 8 treatments were tested each day in a different order to avoid autocorrelation among the responses of focal birds.

## **2.4 | Behavioural observations**

During 1 min of playback, four types of behavioural states were assessed, (1) Vigilance effort as indicated by the number of horizontal scans displayed (the number of movements that birds

made with their heads from left to right or right to left, approximately a 180° turn; Suzuki et al., 2016); (2) Approach inferred using a dichotomic variable (approaching at least halfway from their starting point) measured with a Leica DISTO D210 telemeter, (3) Mobbing behaviour, recorded when birds approached, scanned and produced mobbing calls (assessed by the person without headphones). This variable was also a dichotomic variable (1 = mobbing, 0 = not mobbing); we therefore had to transform the continuous scanning variable into a dichotomic one. We considered that a bird had scanned if it produced more than the 99% CI of the BCCH-Song Control, hence 5 scans (99% CI: [1.75; 4.2]). (4) The presence of either wing flicking behaviour or tail wagging (both described in Hinde, 1952; Carlson et al., 2017; 2019) was used as a proxy for a higher excitement from the birds, since these behaviours were previously associated with intense mobbing (Hinde, 1952; Andrew, 1961; Carlson, 2017). All observations were made using binoculars and recorded on a voice recorder (Sony ICD-PX370) by the same two trained persons. We limited disturbance for birds with short duration tests, and testing birds only once. Moreover, after our tests, we checked that all birds returned to their pre-test behaviour in less than 5min.

## **2.5 | Statistical Analysis**

All analyses were done in R Studio 1.2.5033 (R core development team 2018). The propensity to mob and the propensity to approach the loudspeaker (both dichotomic variables) were analysed using a logistic regression (binomial distribution and logit link function) with the treatment (the two type of controls, and each type of sound sequences for each species) as an explanatory term. We first performed a contrast analysis to verify that the responsiveness of great tits did not significantly differ between the two control tests (C1 versus C2). We then pooled the two controls and tested whether the responsiveness to each type of sound sequence (I alone, D alone, or I-D) of both species differed from this pooled control tests using a Dunnett-Hsu correction. A partial analysis (discarding both control tests) was performed to compare the

222 response of tits to the three types of sound sequences (I alone, D alone, or I-D) according to the  
223 emitter species. More specifically we examined the interaction between both factors to test  
224 whether the responsiveness variation among the sound sequences differed according to the  
225 issuing species. We used odds ratio (OR) for post-hoc comparisons (*odds.ratio*, package  
226 *questionr*). For the approach variable, we first made sure that the complete (I-D) and D alone  
227 sequences engendered a similar response, then pooled these two treatments before comparing  
228 them to responses elicited by sequences with only with introductory notes.

229 The number of scans displayed by focal birds during tests was analysed using a generalized  
230 linear model (negative binomial error distribution and log-link function, *glm.nb*, package  
231 MASS, since an overdispersion of 2.09 was detected with a Poisson error distribution) and the  
232 actual time seeing the bird in the one minute observation as offset. We followed the same  
233 framework than for mobbing and approach behaviour; except that further comparisons between  
234 the types of sound sequences and emitter species were performed using contrasts analyses  
235 (functions *emmeans* and *multcomp::cld*, packages *emmeans* and *multcompView*).

236 When reporting the comparisons of interest in the results section, we relate to the different  
237 treatments with first the emitter species in the stimuli (BCCH for black capped chickadees  
238 stimuli, GRTI for those with great tits' calls), then with the parts of the call sequence present  
239 ('Complete' if both Introductory notes and D notes were kept, 'I' for stimuli for which the D  
240 notes were discarded, and 'D' for stimuli in which the introductory notes were removed).

241 Finally, since the occurrence of signs of higher excitement was low (19 out of 160 tests), we  
242 used a Fisher exact test to compare the proportion of individuals that displayed signs of higher  
243 excitement through the different sound treatments and the pooled controls; then calculated the  
244 odds ratio for the highest responses.

### 3 | RESULTS

#### 3.1 | How do great tits respond to the complete conspecific mobbing sequence and its isolated parts?

If a complete mobbing sequence is a prerequisite for eliciting mobbing in receiver, great tits should display a mobbing response (approach, scan and call) towards stimuli with complete mobbing call sequence (Introductory notes + D notes), but should only scan to introductory notes and approach to D notes.

Our results show that birds mobbed more often toward the conspecific complete mobbing sequences than toward the controls (pooled controls vs. GRTI-Complete:  $OR = 0.01$ , 95 %  $CI$  [0.0006; 0.19],  $p = .002$ ; Figure 2). For treatments with only introductory notes or D notes, mobbing response was infrequent and did not differ from controls (all  $p > .05$ ). In addition, only the complete mobbing sequences triggered excitement in birds (Fisher exact test,  $p < .001$ , Controls vs GRTI-Complete:  $OR = 0.03$ , 95% $CI$  [0.004, 0.27],  $p = .002$ ).

Great tits scanned more toward any call than the controls (all  $p < .001$ ; Figure 3), and scanned more toward Control 2 (black-capped chickadee song) than Control 1 (background noise; C1 vs C2:  $z = 2.73$ ,  $p = .006$ ). As expected, introductory notes stimuli triggered as much scanning behaviour as complete call sequences (GRTI-I vs GRTI-Complete:  $z = 1.27$ ,  $p = .20$ ). Unexpectedly however, birds also scanned as much toward isolated D notes stimuli as toward stimuli with introductory notes (GRTI-D vs pooled GRTI-I /GRTI- Complete:  $z = 0.76$ ,  $p = .45$ ).

Finally, for the approach behaviour, birds responded more often to both the complete and isolated D notes stimuli than to the controls (all  $p < .05$ ; Figure 4). They also approached complete mobbing sequences and isolated D notes sequences more often (GRTI-D vs GRTI-Complete:  $OR = 0.50$ , 95%  $CI$ : [0.12; 1.89],  $p = .31$ ) and approached isolated introductory notes

269 stimuli less often than stimuli with D notes (GRTI- I vs pooled GRTI-D/ GRTI-Complete:  $OR$   
270  $= 0.20$ , 95%  $CI$ :  $[0.06; 0.63]$ ,  $p = .008$ ).

### 271 **3.2 | Does responsiveness to different types of call sequences vary according to** 272 **sender species?**

273 If great tits decrypt allopatric mobbing calls in the same way as conspecific calls, we should  
274 not detect interaction between treatment and emitter species whatever the behavioural response.  
275 As for conspecific calls, introductory notes should trigger vigilance, D notes trigger approach,  
276 and the complete sequence (I-D) trigger mobbing and excitement signs.

277 For mobbing behaviour, no interaction between the emitter species and the type of call was  
278 detected (GLM, Species\*Test:  $\chi^2 = 1.07$ ,  $df = 2$ ,  $p = .58$ ; Figure 2), but great tits mobbed  
279 conspecific more than allopatric calls (GLM, Species effect:  $\chi^2 = 4.68$ ,  $df = 1$ ,  $p = .03$ ). Great  
280 tits mobbed only towards the complete allopatric mobbing call sequences (Controls vs BCCH-  
281 Complete:  $OR = 0.04$ , 95 %  $CI$   $[0.002; 0.89]$ ,  $p = .04$ ), and only this sequence triggered  
282 excitement in birds (Controls vs BCCH- Complete:  $OR = 0.10$ , 95% $CI$   $[0.01, 0.99]$ ,  $p = .049$ ).

283 For the scanning behaviour, no difference between allopatric and conspecific calls was detected  
284 (GLM, Test\*Species effect:  $\chi^2 = 0.23$ ,  $df = 2$ ,  $p = .89$ , Species effect:  $\chi^2 = 2.11$ ,  $df = 1$ ,  $p = .14$ ,  
285  $n = 120$ ; Figure 3). Specifically, great tits scanned as much black-capped chickadee's complete  
286 mobbing sequences than black-capped chickadee's isolated introductory notes stimuli (BCCH-  
287 Complete vs BCCH-I:  $z = 1.27$ ,  $p = .20$ ), but also scanned as much black-capped chickadee's  
288 isolated D notes stimuli as toward calls containing introductory notes (BCCH-D vs pooled  
289 BCCH-I / BCCH- Complete:  $z = 0.76$ ,  $p = .45$ ).

290 As was the case for mobbing behaviour, great tits approached black-capped chickadees calls  
291 less than great tits calls (GLM, Test\*Species effect:  $\chi^2 = 0.33$ ,  $df = 2$ ,  $p = .85$ , Species effect:  $\chi^2$   
292  $= 15.82$ ,  $df = 1$ ,  $p < .001$ ,  $n = 120$ ; Figure 4). Great tits approached black-capped chickadee's

complete call sequences and black-capped chickadee's isolated D notes stimuli more than controls (both  $p < .05$ ). They also approached complete mobbing sequences as much as isolated D notes sequences (BCCH-D vs BCCH-Complete:  $OR = 0.78$ , 95%  $CI$ : [0.19; 3.15],  $p = .72$ ). The slight increase of approach toward sequences with D notes compared to isolated introductory notes sequences was not statistically significant (BCCH-I vs pooled BCCH-D / BCCH- Complete:  $OR = 0.29$ , 95%  $CI$ : [0.04; 1.25],  $p = .13$ ). Still, the effects sizes are similar between species' calls (0.20 vs 0.29, confidence intervals largely overlapping, Cumming et al., 2007), indicating that great tits altered their behaviour the same way (i.e. approached) to both species' calls.

## 4 | DISCUSSION

Overall, less birds responded to the allopatric calls than to the conspecific calls. Yet, we found that whatever the emitter species (conspecific or allopatric), Great tits mobbed (scanned, approached and called but also displayed signs of excitement) when the sequence was complete (introductory notes + D notes). Moreover, isolated introductory notes triggered vigilance while isolated D notes triggered approach. Unexpectedly, Great tits scanned also when hearing isolated D notes of both great tits and black capped chickadees.

### 4.1 | Response to conspecific calls: a new argument towards semantic compositionality?

Only the combinatorial mobbing sequence (i.e. I-D) triggered mobbing behaviour in Great tits, while isolated introductory notes triggered scanning and D sequences induced an approach to the loudspeaker. This result is in adequacy with the emerging hypothesis of semantic compositionality in Parids (Engesser and Townsend, 2019; Suzuki et al., 2019; Zuberbühler, 2019). To be true, this hypothesis must meet several criteria: (i) A different order should trigger a different response, which has been demonstrated for conspecific calls in the

317 Japanese tit (Suzuki et al., 2016), but also recently for the great tit toward the black-capped  
318 chickadee calls (Dutour et al., 2020). (ii) The whole sequence should not only be the sum of its  
319 different parts, but have a new emergent meaning, which is the main result of our study. Here,  
320 great tits not only scanned and approached, but also produced mobbing calls and displayed  
321 signs of excitement such as wing-flicking and tail wagging. This suggests that they extract a  
322 semantic content in I-D call sequences different from the simple sum of introductory and D call  
323 sequences: the meaning of the complete call is related to the parts (Engesser & Townsend,  
324 2019), but is not simply the sum of these parts. Finally, (iii) the two parts, when isolated, should  
325 still be meaning-bearing units. This latter has been confirmed in Suzuki et al. (2016) and Dutour  
326 et al. (2019c) but is only partly corroborated in the present study. Indeed, for the scanning  
327 behaviour, no difference was found between isolated introductory and D calls. Yet, the isolated  
328 part meaning criterion is of primary importance to consider the great tits' coding system as  
329 semantic and not only phonological compositionality (i.e. when elements are combined but  
330 meaningless on their own, like in birdsong, Marler, 1998). If great tits do also scan the  
331 environment when hearing isolated D calls, the vigilance meaning of introductory notes may  
332 not be specific, consequently weakening the compositionality hypothesis.

333 Several non-mutually exclusive explanations may be proposed: (i) Scanning, interpreted as a  
334 vigilance behaviour, may be caused by many environmental and internal parameters. For  
335 instance, high stress levels may increase vigilance and scanning behaviour. Nonetheless,  
336 individuals are known to deal differently with stress (Koolhaas et al., 1999) and both a freezing  
337 and a highly active individual can have high levels of stress hormones, although behavioural  
338 measures such as scanning would be different (Careau et al., 2008). Consequently, we can  
339 hypothesize that individuals with different coping styles (i.e. how individuals react to stress)  
340 would give opposite results in scanning behaviour, and therefore that scanning behaviour is not  
341 a relevant variable in these contexts. (ii) Protocol choices such as the distance to the focal bird

may impact bird behaviour. Since mobbing calls are meant to indicate a potential threat in the vicinity, the willingness to scan the environment may be strongly dependent on the proximity to this potential threat (Seppänen et al., 2007). While Suzuki and colleagues (2016) were at ~ 5 meters from the birds, the present study tested birds at ~ 16m. We can hypothesize that distance is used by great tits as a proxy for urgency: a more distant sound would engender increased scanning for any sound, while closer sounds would trigger more urgent response such as direct physical movement (i.e. approaching or fleeing away). Nonetheless, the control (black-capped chickadee song) we used provoked less scanning than any of the conspecific calls. Even if distance was probably implicated, this parameter cannot explain the absence of difference between all conspecific treatments. Finally, we cannot rule out the hypothesis that previous work may have been biased by observer's expectations (Rosenthal & Fode, 1963; Holman et al., 2015), as we are the first study for which the main observer did not hear the broadcast treatment. Nevertheless, our own protocol could also be improved. For example, video recording the great tits to confirm the reliability of our observations was not possible but will be prioritized in future experiments.

## **4.2 | Responding to allopatric calls: less response from great tits, but similar in kind.**

A second important result in our study is that great tits always responded more to conspecifics than to heterospecifics. This result is congruent with various studies using heterospecific call sequences, and particularly Randler (2012) that found a lower response of great tits to black-capped chickadees calls, but not with Dutour et al. (2020) who did not detect differences in approach when comparing conspecific and heterospecific calls in the great tit. This low level of response could be explained by the choice we made when preparing our stimuli. Indeed, we chose to control by the duty cycle to compare the two species: whatever the length of introductory and D notes, great tits all heard calls of the same length for both great



tits and black-capped chickadees calls. As D notes of black-capped chickadees are longer, the playbacks for this species contained only 2-3 D notes per mobbing call but 6-8 D notes for great tits. Yet, in Parids, D notes are probably used to code for the level of threat (Templeton, 2005; Kalb et al., 2019b), and this information is also considered in heterospecific communication (Templeton & Greene, 2007; Randler & Förschler, 2011; Randler, 2012). Still, recent work aiming at disentangling the effect of number of notes and duty cycle found that the latter was of greater importance for the birds' response (Landsborough et al., 2019); our choice was therefore in adequacy with current knowledge on the subject. Either way, the impact of duty cycle or number of D notes indicates that gradual factors may be as important as semantic compositionality in the decoding processes of the great tits. An additional explanation for this increased response toward conspecific calls may be that great tits vary their investment depending on the reliability of the information (Magrath et al., 2015). There is a trade-off between the risk of not responding (potential death) and the energy lost in investing in false mobbing calls. The first option leading to more important negative consequences than the second, responding to not wholly reliable cues could be selected (the "Better safe than sorry" hypothesis, Haftorn, 2000). Still, birds can take into account the quality of the sender (Goodale & Kotagama, 2008; Magrath et al., 2009). Conspecific calls being more reliable than unknown calls, a lower number of birds responding is therefore expected and is congruent with results in other species (Johnson et al., 2003; Dutour et al., 2017).

Even if their response was lower than to conspecifics calls, great tits approached to D notes and scanned to introductory notes of the black-capped chickadee. Moreover, more birds mobbed to complete allopatric mobbing sequence than to either of the two controls. Both the introductory and D notes share some key characteristics (sharp modulation of frequency for the first, broadband frequency resulting in a harsh sound for the latter, Fig 1). Therefore, great tits can respond to allopatric calls that are relatively similar to their own. A misinterpretation due

to the notes' similarity may explain these results. Nevertheless, humans easily distinguish these different sounds and it seems thus unlikely that birds, known for their fine acoustic discrimination abilities (Bloomfield et al., 2008; Fishbein et al., 2020), performed worse than humans. More likely is the generalization of the introductory and D notes, implying that tits were able to differentiate the two close stimuli, but focused on their similarity when responding (Ghirlanda & Enquist, 2003). Indeed, generalization has recently been proposed as a mechanism explaining heterospecific acoustic communication (Fallow et al., 2011; 2013). The ability to generalize a syntactic rule makes sense since some birds can generalize the underlying structure of a sound (differentiating new *XYX* sounds from new *XXY* sounds, Spierings & ten Cate, 2016). We can therefore hypothesize that, when hearing I-D mobbing calls, great tits generalize from their own call structure and expect to find a predator nearby. By responding to allopatric I-D calls by mobbing, isolated introductory notes by scanning, and D notes by approaching, great tits give us another argument toward the compositionality theory. Consequently, as they respond to heterospecific and conspecific calls in the same manner, we can hypothesize that great tits probably attribute some general meaning of alert to introductory notes and recruitment to D notes, but also a general mobbing meaning to I-D sequences, which states that the concatenation of introductory and D notes may be seen as true semantic compositionality. Nonetheless, although our results seem to corroborate that hypothesis, they do not directly prove the neural processes implied in these responses. Our work is therefore one encouraging first step towards a stronger understanding of syntactic-like processes in the Paridae. We advocate for cautious replicates in other species and trans-disciplinary collaborations such as with neurology to clarify this subject.

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## FIGURES

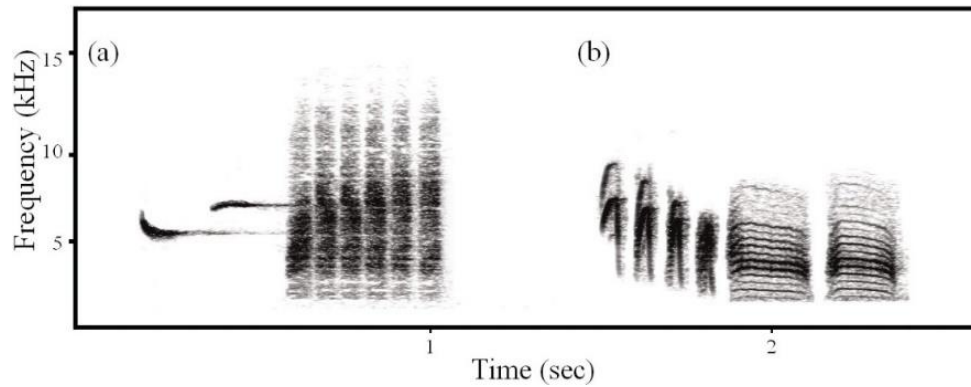


FIGURE 1: Spectrograms of typical mobbing call of (a) great tits (*Parus major*), and (b) black-capped chickadees (*Poecile atricapillus*). X-axis is Time (seconds) and Y-axis is frequency (kHz).

For both species, the mobbing call is made of the combination of a few introductory notes followed by several broadband frequency notes (D notes). Made with Avisoft SASLab: FFTLength 512; Bandwidth 324 Hz; Resolution 96 Hz.

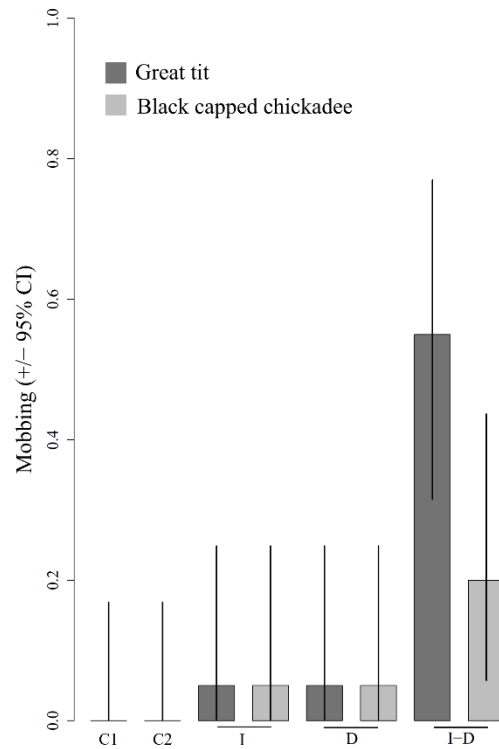


FIGURE 2: Proportion of individuals that mobbed (approached, scanned the environment, and produced mobbing calls) when hearing the different treatments. C1 & C2 represent the two controls (C1= background noise, C2 = black-capped chickadee song). Colours represent the emitter species. N = 20 for each treatment.

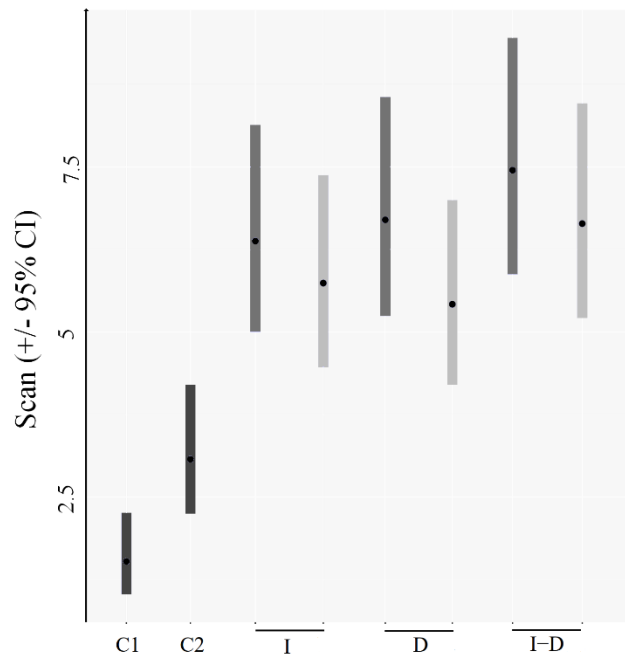


FIGURE 3: Estimates (mean number of scans produced by great tits in 1 min) and 95% CI extracted from our model (negative binomial error distribution with the time we saw the bird as an offset), according to the call sequence and the emitter species. Colours indicates the emitter species. C1 & C2 represent the two controls (C1= background noise, C2 = black-capped chickadee song). N = 20 for each treatment.

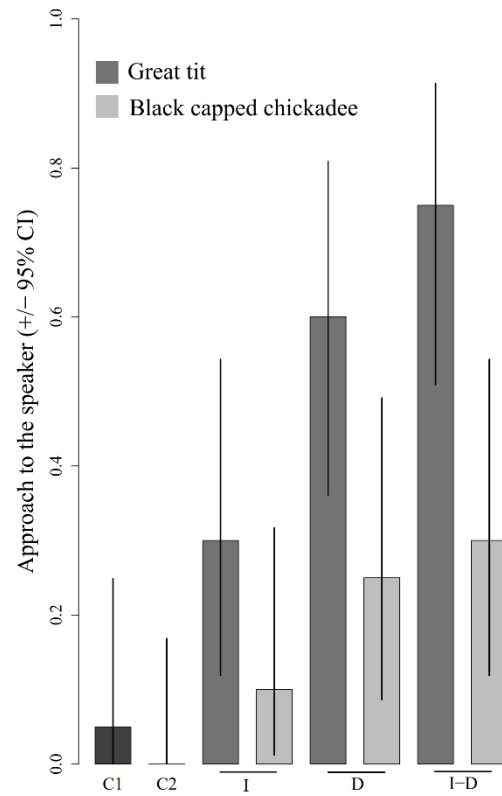


FIGURE 4: Proportion of individuals approaching the speaker given the emitter species and the call sequence. C1 & C2 represent the two controls (C1= background noise, C2= black-capped chickadee song). Colours represent the emitter species. N = 20 for each treatment.