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1 RESEARCH PAPER

2 **Response to allopatric combinatorial calls**

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

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13

14 **Abstract**

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

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

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

36

37 **1 | INTRODUCTION**

38 The vast majority of research in animal communication focuses on intraspecific interactions,
39 while heterospecific exchanges of information are often interpreted as simple by-products of
40 conspecific communication. For example, birds responding to each other alarm calls are more
41 readily seen as by-product mutualism, where the information produced is mostly directed
42 toward conspecifics, and by chance, is also useful to heterospecifics listeners, Bradbury &
43 Verhencamp, 2011). However, recent studies have begun to unravel complex interactions
44 between different species, especially in bird flocks (Goodale & Kotagama, 2008; Coppinger
45 et al., 2020; Carlson et al., 2020). The gathering of birds of different species, either all year
46 round in tropical environments (Goodale et al., 2015) or during the non-breeding season in
47 temperate environments (Dutour et al., 2019a), is widespread and usually thought to be
48 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

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

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

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

118

119 **2 | METHODS**

120 **2.1 | General organisation**

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

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

133 **2.2 | Preparation of stimuli**

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

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

144 In addition, for both species, D notes length is known to vary with the context (Templeton et
145 al., 2005; Kalb et al., 2019b); we therefore checked that the D notes in our stimuli had the same
146 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).
147 Finally, we verified that no introductory notes used in food or flight related contexts were the

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

151 From these recording files, we designed 40 1 min mobbing sequences of great tits and black-
152 capped chickadees (20 for each species, each obtained from a different sender) using Avisoft-
153 SASLab software. To allow comparison between the responses of black-capped chickadees and
154 great tits, we constructed every mobbing sequence with a similar duty cycle (i.e. the amount of
155 time a signal is present over a specified time, Landsborough et al., 2019) and mobbing call
156 repetition (30 calls per minute, natural range of repetition rate, Suzuki et al., 2016).
157 Consequently, each mobbing call emitted by both species had a similar total introductory note
158 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
159 of notes, since black-capped chickadee's D notes are longer (Figure 1).

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

172 **2.3 | Field tests**

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

175 Each test was performed by two field assistants. One of them was assigned to the playback
176 operation, while the other was kept unaware of the selected stimulus (using headphones with
177 music) and assigned to the behavioural recording of the focal bird. For each test, after detecting
178 an individual using binoculars, the focal bird was observed for at least 1 min, and the pre-test
179 behaviour (usually singing or foraging) was noted. If the animal displayed an alarm behaviour,
180 no test was performed. A loudspeaker was placed 16 meters from the bird (16.79 ± 6.27 m),
181 and at less than 3 meters of a potential roost (bushes/ trees) to allow the approach of the focal
182 bird. The two field assistants were then placed away (minimum of 15 meters to both the bird
183 and the loudspeaker) before playing the stimulus with a remote control. All stimuli were
184 broadcast using a Shopinnov 20 W loudspeaker with an intensity of 79.8 ± 1.9 dB(C)
185 (measured at 1 m from the loudspeaker using Lutron SL-4001, C weighting, slow settings, re:
186 $20 \mu\text{Pa}$).

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

194 **2.4 | Behavioural observations**

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

197 made with their heads from left to right or right to left, approximately a 180° turn; Suzuki et al.,
198 2016); (2) Approach inferred using a dichotomic variable (approaching at least halfway from
199 their starting point) measured with a Leica DISTO D210 telemeter, (3) Mobbing behaviour,
200 recorded when birds approached, scanned and produced mobbing calls (assessed by the person
201 without headphones). This variable was also a dichotomic variable (1 = mobbing, 0 = not
202 mobbing); we therefore had to transform the continuous scanning variable into a dichotomic
203 one. We considered that a bird had scanned if it produced more than the 99% CI of the BCCH-
204 Song Control, hence 5 scans (99% CI: [1.75; 4.2]). (4) The presence of either wing flicking
205 behaviour or tail wagging (both described in Hinde, 1952; Carlson et al., 2017; 2019) was used
206 as a proxy for a higher excitement from the birds, since these behaviours were previously
207 associated with intense mobbing (Hinde, 1952; Andrew, 1961; Carlson, 2017). All observations
208 were made using binoculars and recorded on a voice recorder (Sony ICD-PX370) by the same
209 two trained persons. We limited disturbance for birds with short duration tests, and testing birds
210 only once. Moreover, after our tests, we checked that all birds returned to their pre-test
211 behaviour in less than 5min.

212 **2.5 | Statistical Analysis**

213 All analyses were done in R Studio 1.2.5033 (R core development team 2018). The propensity
214 to mob and the propensity to approach the loudspeaker (both dichotomic variables) were
215 analysed using a logistic regression (binomial distribution and logit link function) with the
216 treatment (the two type of controls, and each type of sound sequences for each species) as an
217 explanatory term. We first performed a contrast analysis to verify that the responsiveness of
218 great tits did not significantly differ between the two control tests (C1 versus C2). We then
219 pooled the two controls and tested whether the responsiveness to each type of sound sequence
220 (I alone, D alone, or I-D) of both species differed from this pooled control tests using a Dunnet-
221 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.

245 3 | RESULTS

246 3.1 | How do great tits respond to the complete conspecific mobbing sequence 247 and its isolated parts?

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

252 Our results show that birds mobbed more often toward the conspecific complete mobbing
253 sequences than toward the controls (pooled controls vs. GRTI-Complete: $OR = 0.01$, 95 % CI
254 $[0.0006; 0.19]$, $p = .002$; Figure 2). For treatments with only introductory notes or D notes,
255 mobbing response was infrequent and did not differ from controls (all $p > .05$). In addition, only
256 the complete mobbing sequences triggered excitement in birds (Fisher exact test, $p < .001$,
257 Controls vs GRTI-Complete: $OR = 0.03$, 95% $CI [0.004, 0.27]$, $p = .002$).

258 Great tits scanned more toward any call than the controls (all $p < .001$; Figure 3), and scanned
259 more toward Control 2 (black-capped chickadee song) than Control 1 (background noise; C1
260 vs C2: $z = 2.73$, $p = .006$). As expected, introductory notes stimuli triggered as much scanning
261 behaviour as complete call sequences (GRTI-I vs GRTI-Complete: $z = 1.27$, $p = .20$).
262 Unexpectedly however, birds also scanned as much toward isolated D notes stimuli as toward
263 stimuli with introductory notes (GRTI-D vs pooled GRTI-I /GRTI- Complete: $z = 0.76$, $p =$
264 $.45$).

265 Finally, for the approach behaviour, birds responded more often to both the complete and
266 isolated D notes stimuli than to the controls (all $p < .05$; Figure 4). They also approached
267 complete mobbing sequences and isolated D notes sequences more often (GRTI-D vs GRTI-
268 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: χ^2
292 = 15.82, $df = 1$, $p < .001$, $n = 120$; Figure 4). Great tits approached black-capped chickadee's

293 complete call sequences and black-capped chickadee's isolated D notes stimuli more than
294 controls (both $p < .05$). They also approached complete mobbing sequences as much as isolated
295 D notes sequences (BCCH-D vs BCCH-Complete: $OR = 0.78$, 95% CI : [0.19; 3.15], $p = .72$).
296 The slight increase of approach toward sequences with D notes compared to isolated
297 introductory notes sequences was not statistically significant (BCCH-I vs pooled BCCH-D /
298 BCCH- Complete: $OR = 0.29$, 95% CI : [0.04; 1.25], $p = .13$). Still, the effects sizes are similar
299 between species' calls (0.20 vs 0.29, confidence intervals largely overlapping, Cumming et al.,
300 2007), indicating that great tits altered their behaviour the same way (i.e. approached) to both
301 species' calls.

302 4 | DISCUSSION

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

309 **4.1 | Response to conspecific calls: a new argument towards semantic** 310 **compositionality?**

311 Only the combinatorial mobbing sequence (i.e. I-D) triggered mobbing behaviour in
312 Great tits, while isolated introductory notes triggered scanning and D sequences induced an
313 approach to the loudspeaker. This result is in adequacy with the emerging hypothesis of
314 semantic compositionality in Parids (Engesser and Townsend, 2019; Suzuki et al., 2019;
315 Zuberbühler, 2019). To be true, this hypothesis must meet several criteria: (i) A different order
316 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

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

357 **4.2 | Responding to allopatric calls: less response from great tits, but similar** 358 **in kind.**

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

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

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

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

414

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420 Use of Animals in Research and with The European Code of Conduct for Research Integrity.
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422 of procedures of the UMR5023; but did not need any special permit. We have no conflict of
423 interest to declare. Data used for statistical analysis as such as GPS points of all tests can be
424 made available upon request.

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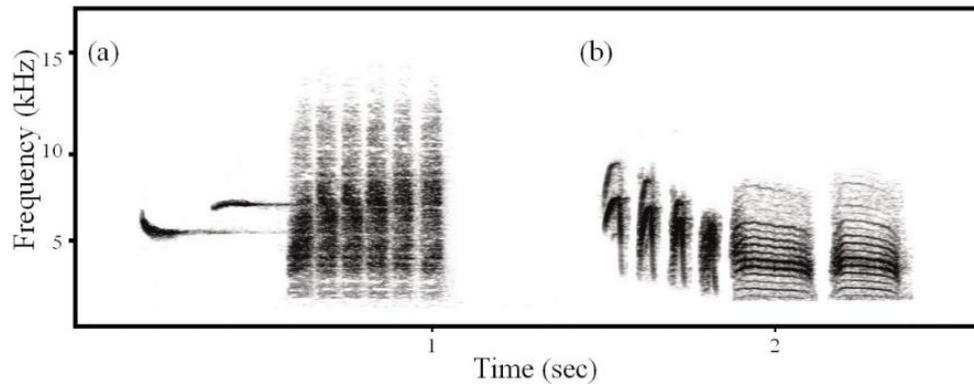
620 **FIGURES**

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

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

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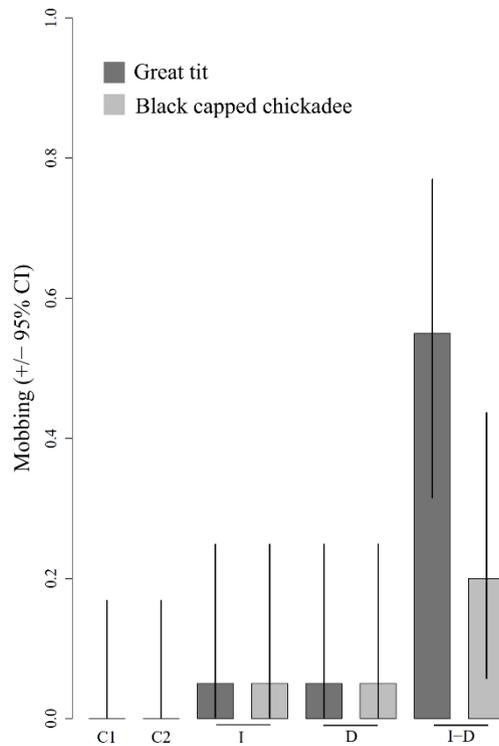
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656 FIGURE 2: Proportion of individuals that mobbed (approached, scanned the environment, and

657 produced mobbing calls) when hearing the different treatments. C1 & C2 represent the two

658 controls (C1= background noise, C2 = black-capped chickadee song). Colours represent the

659 emitter species. N = 20 for each treatment.

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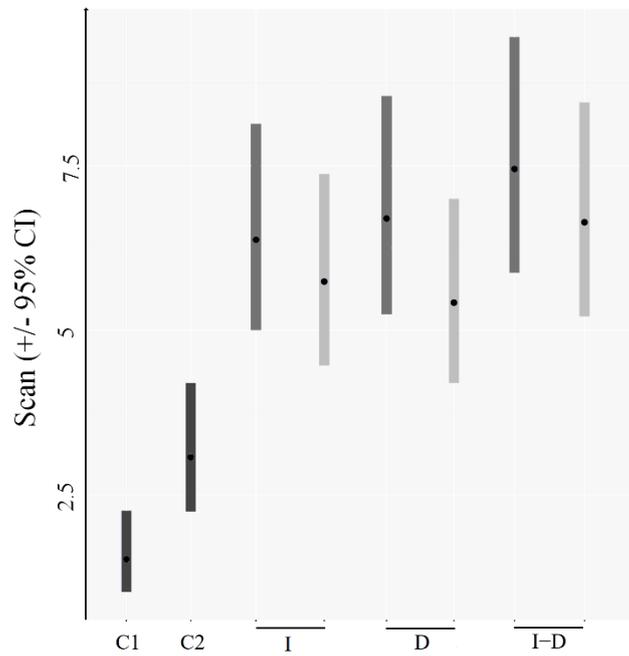


FIGURE 3: Estimates (mean number of scans produced by great tits in 1 min) and 95% CI extracted from our model (negative binomial error distribution with the time we saw the bird as an offset), according to the call sequence and the emitter species. Colours indicates the emitter species. C1 & C2 represent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

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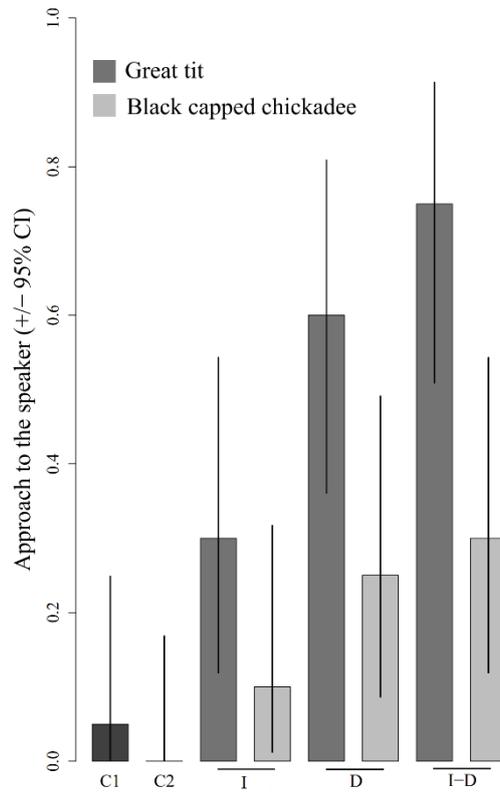
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693 FIGURE 4: Proportion of individuals approaching the speaker given the emitter species and the
694 call sequence. C1 & C2 represent the two controls (C1= background noise, C2= black-capped
695 chickadee song). Colours represent the emitter species.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

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