

Syntax manipulation changes perception of mobbing call sequences across passerine species

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1 **Syntax manipulation changes perception of mobbing call**
2 **sequences across passerine species**

3

4 Short running title: **Syntax in birds**

5

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18

19 **CONFLICT OF INTEREST**

20 We have no conflict of interest to declare.

21

22

23 **Abstract**

24 Many species approach predators to harass them and drive them away. Both the intensity of
25 this antipredator strategy and its success are positively related to the size of the group that
26 carries out this mobbing. To recruit individuals to the mob, members of prey species produce
27 mobbing calls. In some songbirds – the Japanese tit, *Parus minor*, and the southern pied
28 babbler, *Turdoides bicolor* – mobbing calls are structurally complex and it has been suggested
29 that they convey information by means of compositional syntax, when meaningful items are
30 combined into larger units. These two species combine alert and recruitment calls into an alert
31 and recruitment sequence when attracting conspecifics to cooperate in mobbing a predator.
32 Whether this rudimentary, two-call, compositional structure is used by other bird species in
33 mobbing calls and how it can alter the ability of heterospecifics to adequately recognize
34 mobbing calls is not well understood. Heterospecifics' responses to mobs are critical to the
35 success of the mobbing strategy, so it is of great importance to understand whether and how
36 syntax influences these responses. To address these questions, we conducted two playback
37 experiments. Firstly, we investigated whether the great tit, *Parus major*, extracts different
38 meanings from different individual motifs (i.e., component calls), and from combined motifs
39 in both natural and artificially-reversed order. We found that great tits extract different
40 meanings from the two motifs involved in mobbing calls, and that they also discriminate for
41 motif order reversal in the mobbing calls sequence. Secondly, we investigated whether
42 heterospecifics (the coal tit, *Periparus ater*, and the common chaffinch, *Fringilla coelebs*) are
43 sensitive to syntax alteration of great tit mobbing calls. While chaffinches did not respond to
44 great tit mobbing calls, coal tits were sensitive to mobbing calls sequence reversal although
45 they did not react in the same way as conspecific subjects. Overall, whereas our results
46 indicate that tits are sensitive to call reversal, this is not to say that tits actually use
47 compositional syntax to increase the information content.

48 **KEYWORDS**

49 acoustic communication, call combination, interspecific communication, mobbing, syntax, tits

50

51 **1 | Introduction**

52 During the last decades, accumulating evidence has revealed that animal vocalizations share
53 several features with human language (Collier et al., 2014). Duality of patterning, otherwise
54 known as double articulation (Martinet, 1949), is a property of human language that makes
55 possible a combinatorial structure on two levels: (i) phonological syntax, when meaningless
56 sounds called phonemes (syllable or note) are combined to form meaningful acoustic
57 structures called morphemes (motif) and words; and (ii) compositional syntax, which is the
58 combination of meaningful motifs into a larger structure, whose meaning depends on the
59 motifs involved and the syntactical rules used to put them together (Berwick et al., 2013;
60 Marler, 1998; ten Cate & Okanoya, 2012). The involvement of this property in the acoustic
61 signal enables much more information to be conveyed using a finite set of vocal elements
62 (Berwick et al., 2013). In animals, vocalizations involve a far less complex level of
63 organization than human language. Although more and more evidence for syntax is becoming
64 available for some birds and mammals (Coye et al., 2005; Ouattara et al., 2009), the ability of
65 species to use compositional syntax (or compositionality; see Suzuki et al., 2019) is still
66 debated (Bolhuis et al., 2018; Petkov & Jarvis, 2012; Petkov & Wilson, 2012; Suzuki et al.,
67 2018). More recently, three studies have examined this issue by studying mobbing calls
68 produced by the Japanese tit, *Parus minor*, and the southern pied babbler, *Turdoides bicolor*
69 (Engesser et al., 2016; Suzuki et al., 2016; Suzuki et al., 2017). Mobbing calls are particular
70 forms of alarm signals. They are widespread, especially in passerine birds (Klump & Shalter,
71 1984). They are emitted by animals trying to chase away a predator (Pettifor, 1990). To be
72 efficient, these calls often share particular features allowing listeners to join the mob, features
73 that are thought to be involved in interspecific communication (Dutour et al., 2017a; Hurd
74 1996; Marler 1955). In this situation, where calling birds and receivers have a certain level of
75 shared interest, and communication should be clear and as detailed as required to bring about

76 an appropriate response that involves multiple joint behaviours (Cunha et al., 2017), Griesser
77 et al. (2018) have recently suggested from findings from two avian species that compositional
78 syntax may evolve.

79 Mobbing calls have been well described in the Paridae (Carlson et al., 2017a; Jung &
80 Freeberg, 2017) and are usually composed of combinations of frequency modulated elements
81 (Hetrick & Sieving, 2011) referred to hereafter as FME, followed by a string of a repeated
82 loud broadband elements (Templeton et al., 2005), referred to hereafter as D notes. As
83 suggested by several authors, such a pattern could well arise from a hierarchized organization
84 following a ‘syntactic-like’ rule (Hailman et al., 1985; Hailman & Ficken, 1986; Lucas &
85 Freeberg, 2007). In the Japanese tit, each motif is also used alone in context other than
86 mobbing. The FME motif is used in vigilance situations and it serves as an alarm signal to
87 which receivers respond by scanning for danger (alert calls), while the D notes are involved
88 within foraging flocks and by nest mates to recruit social partners and elicit an approach of
89 the receivers (recruitment calls) (Suzuki et al., 2016; 2017). When the Japanese tits heard the
90 FME motif combined with the D notes as the compound FME-D, which is also a natural
91 vocalization, they showed both scanning and approach behaviours. However, there was little
92 or no response when the call order was artificially reversed to D-FME (i.e. a sequence with
93 unclear or ambiguous meaning; Bolhuis et al., 2018b; Suzuki et al. 2018). From this, authors
94 suggest that compositional syntax is a mechanism for information transmission, although
95 some authors have argued that Suzuki and colleagues do not provide any evidence for genuine
96 compositionality in these bird vocalizations (Bolhuis et al., 2018a; Bolhuis et al., 2018b). One
97 may ask whether the use of a compositional syntax in mobbing calls is specific to *Parus*
98 *minor* or extends to other Paridae species. Furthermore, using compositional syntax to encode
99 information in mobbing calls with several motifs, including ones involved in social cohesion
100 with conspecifics, could limit the ability of heterospecifics to correctly identify mobbing calls.

101 This is particularly intriguing since mobbing calls can communicate the presence of a predator
102 to heterospecifics as well as conspecifics (Dutour et al., 2016; Dutour et al., 2017a; Hurd,
103 1996), prompting the question whether there is actually a similar underlying compositional
104 structure across bird species, enabling them to decode information in heterospecific mobbing
105 calls (Griesser et al., 2018; Russell & Townsend, 2017). It may also be relevant to ask
106 whether species that do not produce combinatorial calls can nevertheless decode them.

107 The main objectives of the present study were first to test whether the great tit, *Parus*
108 *major*, uses compositional syntax in mobbing calls. The great tit is the closest relative of the
109 Japanese tit (Johansson et al., 2013), and these species have similar calls and similar social
110 structures, and also rely on both conspecifics and heterospecifics during mobbing (Randler &
111 Vollmer, 2013; Suzuki, 2016). We investigated whether receivers extract different meanings
112 from FME or D motif alone, and from combined motifs both natural or artificially-reversed
113 order (i.e., FME-D or D-FME sequences). Secondly, we investigated whether heterospecifics
114 are sensitive to syntax alteration of great tit mobbing calls. In this second experiment, we
115 compared the responses of coal tits, *Periparus ater*, and common chaffinches, *Fringilla*
116 *coelebs*, to playbacks of natural and artificially reversed great tit mobbing calls. We chose
117 coal tits rather than other Paridae species since mobbing calls of this species are particularly
118 complex and composed of multiple motifs (Carlson et al., 2017a; Dutour et al., 2017a), and
119 also because our previous work showed that coal tits are especially prone to respond to
120 heterospecific mobbing calls (Dutour et al., 2017a). We selected the chaffinch as an extra-
121 group member (i.e., non-Paridae species) since it is often found in heterospecific mobs
122 although it is less prone than tits to join heterospecific callers (Dutour et al., 2017a). Since the
123 mobbing calls of the chaffinch were composed of a single “chink” note (Randler & Förschler,
124 2011), we predicted that coal tits would be more sensitive to syntax alteration than
125 chaffinches.

126

127 **2 | METHODS**

128 **2.1 | Experimental design**

129 Data was collected during playback experiments conducted at the onset of the breeding season
130 (experiment 1, February/March 2018) and at the end of the breeding season (experiment 2,
131 July/August 2017) on wild passerines inhabiting mixed deciduous-coniferous forests located
132 in south-east France (45°80'N, 4°52'E). In order to examine whether great tit mobbing calls
133 involve compositional syntax (experiment 1), we used five playback types. First, we
134 examined whether each motif alone (FME calls and D calls) induced a distinct behaviour,
135 whether vigilance and recruitment. We then examined whether tits hearing the combined
136 motifs in the natural order (i.e., FME-D calls, the natural mobbing call sequence) display a
137 combination of the behaviours they exhibit when hearing each motif alone, and we tested
138 whether this is also the case when the combined motifs are presented in the reverse order (i.e.,
139 D-FME calls, artificially reversed mobbing call sequence). Finally, we also performed control
140 tests for which the playback contained only background noise (hereafter referred as BN tests).
141 We conducted these tests with 100 adult great tits (20 individuals for each test type); each bird
142 received a single treatment. The goal of experiment 2 was to test whether heterospecific
143 receivers (coal tits and chaffinches) are sensitive to syntax alteration in the same way as
144 intraspecific receivers (great tits). To this end, we investigated how individuals of each
145 species behave when hearing a playback of natural FME-D calls and artificially reversed D-
146 FME calls of great tits. We also replicated these tests with great tits as receivers in order to
147 permit comparisons across species. This second experiment involved 90 different individuals
148 (15 individuals per test and for each species; each individual received a single treatment).

149

150 **2.2 | Field test procedure**

151 Field tests were done following a similar methodology used by Dutour et al. (2017) to
152 investigate the response of passerine birds to allopatric mobbing calls. After a focal bird was
153 located, a loudspeaker was placed 30 meter away from the bird at the bottom of a tree. An
154 experimented ornithologist and a field assistant were positioned opposite each other at
155 vantage points at least 15 meters from the loudspeaker and the focal bird to avoid any
156 disturbance during the test. Before the beginning of the experiment, the baseline behaviour of
157 the focal bird was observed during a pre-trial period lasting at least 1 minute. If the bird was
158 found to show alarm behaviour (i.e., emit mobbing calls, which happened in less than 5% of
159 the cases) the test was abandoned. Otherwise, the playback was started when no other
160 passerine was observed near the focal individual. Then, during 1 min of playbacks, two
161 behavioural variables were recorded so as to infer vigilance effort and recruitment propensity,
162 respectively: (1) the number of horizontal scans (we counted the number of obvious
163 movements that birds made with their heads from left to right or right to left, approximately a
164 180 turn; Suzuki et al., 2016) and (2) an approach within a radius of 15 m of the loudspeaker.
165 Horizontal scanning is a good indicator of perceived danger in birds (Curio et al., 1978) and
166 both behaviours, i.e. scanning and approaching, are common during mobbing events (Carlson
167 et al., 2017b; Dutour et al., 2017a; Suzuki et al., 2016; Suzuki et al., 2017). Moreover, we set
168 the approach distance to 15m since this approach distance was previously found to be a
169 relevant measure of mobbing propensity (see Dutour et al., 2017a for more details). All
170 observations were carried out with binoculars. The concordance of the number of scanning
171 between observers was evaluated in a complementary study (see Supporting Information S1).
172 Since this study revealed a very high concordance despite a systemic bias between observers
173 (see Table S1 Supporting Information S1), only the records done by the experienced
174 ornithologist who participated to the whole study were used for data analyses. All trials were
175 conducted between 6 a.m. and 1 p.m. during calm and dry weather. All focal animals were

176 selected to be separated by more than 100 m to minimize pseudo-replication risk. In addition,
177 we never went back twice to the same forest path, and during the breeding season the tits'
178 territories are separated by 50 m in our study area. Once a test was done, we went on more
179 than 100 m before trying to detect another bird which is calling or foraging. No bird was seen
180 following us. Hence, although birds were not individually ringed, the probability of testing the
181 same individual twice was low, and we are confident that our observations were performed on
182 different individuals. Moreover, playback sequences were evenly distributed across the study
183 period to avoid any temporal confounding effect.

184

185 **2.3 | Playback stimuli and playback materials**

186 We used mobbing calls produced by three great tits previously recorded in response to
187 intraspecific mobbing calls (Dutour et al., 2017a). Calls were recorded with a Fostex FR2LE
188 digital recorder connected to a Sennheiser ME67-K6 microphone (see Dutour et al., 2017a for
189 more details). We also used mobbing calls obtained from the Xeno Canto online database
190 (<http://www.xeno-canto.org>) recorded in different European countries ($n = 6$) located along
191 the species' range in order to encompass the call variation range that a local bird community
192 might experience and to generalize our conclusions. From these recording files, we built 20
193 unique soundtracks of natural mobbing calls (FME-D sequences) using Avisoft-SASLab
194 software (i.e., 20 soundtracks with 1 individual per soundtrack). Recordings were in 16-bit
195 WAV format (44.1 KHz sampling rate). These soundtracks were then used to construct three
196 others, respectively FME calls, D calls, and D-FME calls as follows: FME and D calls were
197 constructed by removing either D or FME calls from each FME-D calls and the D-FME calls
198 were constructed by reversing the order of the motifs in the original FME-D calls of great tits
199 (Figure 1). Within each sound track, calls were repeated at a rate of 26 calls per minute (this
200 calling rate is within the range of the natural repetition rates, unpubl. data). We used a series

201 of five to eight D motifs to construct playback (mean \pm SE = 7.11 ± 0.06 ; Figure 1). Each
202 track D notes were placed 82 ± 40 ms before FME (no difference from the time between FME
203 and D notes in the natural sequence; $t = 1.789$, $p > 0.05$). The number of D notes could relate
204 to the perceived level of threat (Templeton et al., 2005) which could artificially bring about
205 variation in the response of focal birds. With this mind, all playback sequences were arranged
206 to adjust the ratio of the D notes over the FME notes in a mobbing call sequence, making this
207 ratio slightly lower in our study (range: 5/8 - 8/11) than in Suzuki et al., (2016, range: 7/10 -
208 10/13, see Figure 1 in both manuscripts for comparison). We also constructed 20 control
209 soundtracks using the parts where no birds were calling in the same recordings as natural
210 mobbing calls (BN). In order to avoid pseudoreplication (Kroodsma et al., 2001), we played
211 back each soundtrack only once using a Shopinnov 20 W loudspeaker (the probability of
212 testing an individual twice was low, see above). The average amplitude used for these
213 playbacks was obtained with a sound level meter placed 1 m from the loudspeaker (~ 83 dB,
214 Solo 01dB Metravib, Z weighting, re: $20 \mu\text{m Pa}$).

215

216 **2.4 | Statistical analyses**

217 In the analysis of experiment 1, we used generalized linear mixed models (GLMMs) treating
218 the individual records from which were constructed all subsequent soundtracks (i.e. the test
219 types FME calls, D calls, FME-D calls, D-FME calls and control) as a random effect. The test
220 type was introduced as an explanatory term and the observation duration (i.e., the time during
221 which we could observe the bird) as an adjustment covariate in the fixed part of the model.
222 All analyses performed on the number of scans were performed using a log link function and
223 a generalized Poisson distribution (Proc GLIMMIX; SAS institute inc, 2012) to circumvent
224 the overdispersion of count data relative to a Poisson distribution (see Joe & Zhu, 2005 for
225 justification). For the approaching behaviour, the individual binary response (i.e., approaching

226 versus not approaching) was introduced as the dependent variable using a logit link and a
227 binomial distribution for the error term. For both response variables, the effect of explanatory
228 terms was examined using a non-sequential F test, and subsequently removed from the model
229 if non-significant. Although the random effect was never found significant (results not
230 shown), it was always kept in the model if possible (see below). Multiple comparisons
231 between test types were performed on least square mean estimates using a Dunnett-Hsu
232 correction in the case of pairwise comparisons against the control situation (i.e. BN test) or the
233 Sidak correction otherwise. Finally, for each test type, we used a Wilcoxon test to determine
234 whether scanning behaviour differed between approaching individuals and those staying
235 away, or conversely whether each approach was associated with scanning. Tests were not
236 performed for the FME and the BN playbacks, given the lack of approaching birds in these
237 sequences (see Results).

238 We proceeded in a similar way for the analyses of experiment 2. We first verified that
239 the mobbing call sequence reversal resulted in the same behavioural pattern for conspecific
240 receivers as observed in experiment 1. More specifically, we compared the number of scans
241 and propensity to approach using generalized linear mixed models including the test type and
242 the period (the onset of the breeding season i.e., experiment 1, or the end of the breeding
243 season, i.e., experiment 2) as explanatory terms in the fixed part of the model and the
244 individual from whom the recording came as a random effect.

245 We then compared the responses (scan and approach) of the three species to the great
246 tits mobbing calls presented in the natural order (i.e., FME-D calls) and reversed sequence
247 (i.e., D-FME calls). For this purpose, the receiver species (great tit, coal tit and chaffinch), the
248 test type (FME-D and D-FME calls), and their interactive effect were introduced as
249 explanatory terms in the fixed part of the model and the individual from which the recording
250 came as a random effect. We then performed contrast analyses to test whether each

251 heterospecific receiver specie (i.e. coal tit and chaffinch) responded differently than the
252 conspecific one (i.e. great tit) to the mobbing calls sequence reversion. Multiple comparisons
253 between test types were subsequently performed on least square mean estimates using a Sidak
254 correction. Concerning the approach behaviour, none of the coal tits approached when
255 exposed to one of the two test types (i.e., D-FME calls; $n = 15$) resulting in a sparse data
256 structure. For this reason, likelihood optimization in the presence of a random effect is made
257 impracticable and all tests based on the standard deviation associated to the estimates are
258 made unreliable. We therefore used a GLM instead of a GLMM to analyse the approaching
259 behaviour, and we used likelihood ratio tests instead of the F test to assess the significance of
260 explanatory terms introduced in the model as well as the significance of contrast analyses.
261 Partial analyses for each heterospecific receiver species were then performed, and in the case
262 of the coal tits, the difference between both test types was examined used a Fisher exact test.
263 We also completed these analyses by Wilcoxon tests to determine for each species whether
264 scanning differed between approaching individuals and those staying away or conversely
265 whether each approach was associated with scanning within each test type (i.e., FME-D and D-
266 FME calls). These tests were not performed for coal tits in response to D-FME calls since no
267 individual approached during the test, and nor for chaffinches since almost none of them
268 approached during the test (see Results).

269

270 **2.5 | Ethical note**

271 This work was approved by the Prefecture de l'Ain (DDPP01-15-230) and by the ethical rules
272 set by University Lyon 1 in accordance with the current laws in France.

273

274 **3 | Results**

275 **3.1 | Experiment 1: compositional syntax in great tit mobbing calls**

276 Overall, our analyses indicate that the scanning behaviour varied significantly according to
277 the test type (respectively for the effects of the test type and the observation duration:
278 $F_{4,23} = 14.9, p < 0.0001$; $F_{1,85} = 5.65, p < 0.0197$; see Figure 2a). Pairwise comparisons
279 between each test type and the BN control reveal a significantly higher number of scans for the
280 FME calls and FME-D calls tests (respectively for FME, D, FME-D calls and D-FME: $t = 5.28, p <$
281 0.0001 ; $t = 0.38, p = 0.98$; $t = 3.96, p = 0.0021$; $t = -0.14, p = 0.99$). There was also no
282 significant difference between FME-D calls and FME calls ($t = 1.80, p = 0.59$) and pairwise
283 comparisons confirm that both FME and FME-D calls triggered significantly more scans than D
284 calls and D-FME ones (all $p < 0.01$). The probability of approaching varied significantly
285 between the test types (respectively for the effects of the test type and the observation
286 duration: $F_{4,23} = 4.17, p = 0.011$; $F_{1,85} = 0.94, p = 0.33$; see Figure 2b). Pairwise
287 comparisons between each test type and the BN control reveal a significantly higher approach
288 propensity for the D and FME-D calls tests (respectively for FME, D, FME-D calls and D-FME: $t =$
289 $-0.01, p > 0.99$; $t = 3.05, p = 0.0154$; $t = 2.54, p = 0.0464$; $t = 1.99, p = 0.136$). Moreover,
290 there was no significant difference between D calls and FME-D calls tests ($t = 0.96; p = 0.88$)
291 and pairwise comparisons indicate that both D calls and FME-D calls significantly increased the
292 approach propensity when compared to FME calls but not when compared to D-FME calls (D
293 calls *versus* FME calls : $t = 3.16, p = 0.022$; FME-D calls *versus* FME calls : $t = 2.64, p = 0.071$;
294 D calls *versus* D-FME calls : $t = 1.87, p = 0.32$; FME-D calls *versus* D-FME calls : $t = 0.96, p =$
295 0.88). Finally, regardless of the test type, scanning did not differ between approaching
296 individuals and those staying away (Wilcoxon tests respectively for the D, FME-D, D-FME
297 calls: $W = 49.5, p = 0.78$; $W = 25.5, p = 0.07$; $W = 37, p = 0.52$; test not performed for the
298 FME and the BN playbacks given the lack of approaching birds in these sequences).

299

300 **3.2 | Experiment 2: effect of syntax alteration on heterospecific perception**

301 As experiments on heterospecific responses to the syntax alteration of great tit mobbing calls
302 were done at the end of the breeding period while experiment 1 was performed at the onset of
303 the breeding season, we first controlled that great tits response to the alteration of conspecific
304 mobbing calls does not vary during the breeding season. Our results indicate that, whatever
305 the study period (i.e. at the onset or at the end of the breeding season), great tits approached
306 the loudspeaker with the same propensity in response to FME-D calls or D-FME calls (period
307 effect: $F_{1,8} = 0.82$; $p = 0.39$; test type effect: $F_{1,8} = 1.44$; $p = 0.26$; interactive effect:
308 $F_{1,8} = 0.01$; $p = 0.94$; see Figure 3a). However, if the study period also did not alter the
309 effect of the mobbing call inversion on their scanning behaviour, great tits exhibited a higher
310 vigilance effort at the end of the breeding season than at the onset (period effect: $F_{1,8} =$
311 5.45 ; $p = 0.0478$; test type effect: $F_{1,8} = 32.27$; $p = 0.0005$; interactive effect: $F_{1,8} =$
312 0.01 ; $p = 0.93$; see Figure 3b). Moreover, as in the case of experiment 1, scanning did not
313 differ between approaching individuals and those staying away (Wilcoxon test respectively
314 for the FME-D and the D-FME calls: $n = 15$, $W = 29$; $p = 0.86$; $n = 15$, $W = 25$; $p = 0.77$).
315 These results indicate that the intensity of the subjects' reaction to FME-D calls compared to
316 D-FME calls remained unchanged before and after the breeding season for conspecifics, and
317 offers stable ground for interspecific comparison.

318 Comparing the response to the inversion of great tit mobbing call sequence among
319 receiver species, our results reveal a significant interactive effect of the receiver species and
320 the test type on the number of scans displayed during the test (receiver species effect:
321 $F_{2,16} = 2.32$; $p = 0.131$; test type effect: $F_{1,8} = 9.36$; $p = 0.0156$; interaction term: $F_{2,16} =$
322 4.73 ; $p = 0.0243$). As revealed by the contrast analyses, only the difference of the number of
323 scans between the two test types exhibited by chaffinches significantly varied from the one
324 exhibited by the great tits (respectively for chaffinches *versus* great tits and coal tits *versus*
325 great tits : $F_{1,16} = 7.55$; $p = 0.0143$; $F_{1,16} = 0.01$; $p = 0.93$). The difference of approach

326 propensity between the two test types also varied significantly according to the receiver
327 species (receiver species effect: $\chi_2^2 = 20; p < 0.0001$; test type effect: $\chi_1^2 = 2.98; p =$
328 0.084 ; interaction term: $\chi_2^2 = 6.31; p = 0.042$). However, only the difference of approach
329 propensity between the two test types exhibited by the coal tits significantly varied from the
330 one exhibited by the great tits as revealed by the contrast analyses (respectively for
331 chaffinches *versus* great tits and coal tits *versus* great tits: $\chi_1^2 = 0.82; p = 0.36$; $\chi_1^2 =$
332 $4.16; p = 0.0413$). Partial analyses indicate that chaffinches did not scan the surroundings
333 differently according to the order of the mobbing call sequence presented ($F_{1,16} = 0.60; p =$
334 0.45). Chaffinches also rarely approached the loudspeaker, regardless of the sequence order
335 (Figure 3c). In contrast, the coal tits displayed both increased vigilance and a higher
336 propensity to approach the loudspeaker when hearing the FME-D calls than when hearing the
337 D-FME calls (for the number of scans: $F_{1,16} = 9.08; p = 0.0082$; for the approach propensity
338 : Fisher exact test $p = 0.042$, see Figure 3b). Finally, unlike the great tits, coal tits
339 approaching the loudspeaker also scanned significantly more intensely (14.2 ± 3.9) than those
340 staying away (8.1 ± 5.2) when hearing the great tit mobbing calls in the natural order
341 (Wilcoxon test: $n = 15; W = 8; p = 0.042$; test not performed for the D-FME calls given the
342 lack of approaching birds in this sequence).

343

344 **4 | DISCUSSION**

345 We found that great tits behave distinctively when hearing respectively the FME motifs and
346 the D ones. They scan the environment when hearing the former, and approach the sound
347 source when hearing the latter. As previously seen in the Japanese tits (Suzuki et al., 2016;
348 Suzuki et al., 2017), these results indicate that these two motifs also convey distinct meanings
349 to the great tit. One corresponds to an alarm call (i.e., the FME motif) which elicits increased
350 vigilance from the receiver, while the other corresponds to a recruitment call (i.e., the D

351 motif) which elicits approach behaviour from the receiver. In response to the naturally
352 ordered mobbing call sequence (i.e., FME-D calls), great tits exhibited both increased
353 vigilance (with a high proportion of scanning) and a rapid approach ($n = 19$; mean \pm SE =
354 30.22 ± 3.38 seconds) toward the sound source, potentially to support the simulated caller
355 opposing the putative threat, indicating that tits extracted both meanings from the naturally-
356 ordered combination of the two motifs. To confirm that the mobbing sequence constitutes a
357 combination of two individual calls, a second step is to construct combinations by artificially
358 merging both calls (with the calls originating from the same individual) and show that natural
359 and artificial versions elicit the same response. Both the nature and the intensity of the
360 responses we observed in the present study are similar to those obtained for the Japanese tit
361 (Suzuki et al., 2016) and for the pied babbler (Engesser et al., 2016). However, while in the
362 Japanese tits both the vigilance effort and the propensity to approach vanish when tits hear the
363 mobbing call sequence in the reversed order (Suzuki et al., 2016; Suzuki et al., 2017), the
364 results are different in the case of the great tit. The vigilance effort vanishes but the propensity
365 to approach did not change when the combination order was reversed. Although the
366 percentage of trials in which great tits approached the loudspeaker during the D-FME calls is
367 reduced by 14% compared to the FME-D calls, this difference is low when compared to the
368 one reported by Suzuki et al. (2016) on the Japanese tits (i.e. 41.2% of reduction). Since we
369 observed similar responses in both experiments, which were performed in two breeding
370 seasons, this behavioural pattern is reproducible. Our results therefore suggest that great tits
371 are sensitive to the ordered combination of the two motifs. However, as noted by several
372 authors (Berwick et al., 2013; ten Cate & Okanoya, 2012), this is not to say that tits actually
373 exploit compositional syntax to convey more information. To our knowledge, great tits never
374 use reversed mobbing calls sequences in the wild, and several hypotheses could explain a
375 sequence order reversal effect without invoking compositional syntax usage. First, these

376 results could be explained by the occurrence of a perception bias (Grafe, 1996; Klump &
377 Gerhardt, 1992) when the sequence order is reversed. Indeed, D notes, which are large
378 frequency bandwidths enhancing location, may operate as auditory masking on the FME notes
379 (frequency modulations resistant to degradation; Brown & Handford, 1996; Marler, 1955)
380 given the relative short delay between both sequences. Thus tits could no longer perceive the
381 FME notes when they are artificially placed after the D notes. Such a phenomenon could well
382 explain why great tits reduced vigilance behaviour when hearing the artificially reversed
383 sequence of mobbing calls. This hypothesis could be tested directly by replacing D notes by a
384 distinct high-bandwidth note (e.g., a burst of loud white noise). Auditory masking by D notes
385 could also be the reason why great tits do not produce D-FME calls and, therefore, explain
386 why the ordering rule is the way it is. Mobbing call responsiveness (and/or interpretation)
387 may also depend on the social context, for instance according to the presence of the receiver's
388 mate in the vicinity (Suzuki et al., 2016) or the seasonal activity (Dutour et al., 2017b; Dutour
389 et al., 2019; Lucas et al., 2007). In the Japanese tit, the sequence reversal effect was examined
390 in flock members during the non-breeding season (Suzuki et al., 2016) while in the present
391 study tests were conducted on great tits at the onset and at the end of the breeding season.
392 Since the sensitivity to recruitment calls may vary between these two social contexts, further
393 work is required to examine this point.

394 Chaffinches were barely sensitive to great tit mobbing calls although this species is
395 regularly observed in heterospecific mobbing groups (Dutour et al., 2016). Moreover, we
396 recently found a very low responsiveness of chaffinches to heterospecific mobbing calls when
397 compared to their own mobbing calls (Dutour et al., 2017a; see also Randler & Vollmer,
398 2013). We suggested that such a lack of response could have a causal explanation (the strong
399 dissimilarity between mobbing calls of the chaffinch and other species), and a functional
400 explanation (the exploitation of a distinct ecological niche). The second hypothesis cannot

401 explain our results because chaffinches and great tits usually share the same ecological niche.
402 It is therefore likely that chaffinches are sensitive only to their own species, although the
403 absence of a background noise test in experiment 2 cannot allow us to safely conclude on this
404 point.

405 Conversely, coal tits were not significantly less responsive than conspecific subjects to
406 the naturally-ordered great tit mobbing call sequence (i.e., FME-D calls) regardless of the
407 behaviour being measured (i.e., vigilance or approach). However, their behaviours differ from
408 that of conspecific great tit subjects since approaching coal tits were also more vigilant than
409 those staying away, whereas approaching great tits were not significantly more vigilant than
410 their counterparts staying away. Furthermore, and above all, when the mobbing call sequence
411 order was reversed, coal tits not only reduced their vigilance effort but also no longer
412 approached the loudspeaker. If these results indicate that coal tits are sensitive to great tit
413 mobbing call sequence reversal, they also suggest that coal tits do not extract the same
414 meaning from the mobbing calls sequence as great tits do. In particular, their responsiveness
415 seems more binary or less versatile than that of great tits. This could indicate that some
416 information (i.e., social information) is present in great tit mobbing calls, inducing conspecific
417 responses, whereas coal tits do not pay attention to it. If auditory masking can explain great tit
418 responses to D-FME calls, we hypothesized that wouldn't the same hold true for coal tits. Coal
419 tits could be indeed more sensitive to FME notes when they are artificially placed after the D
420 notes compared to great tits, because their mobbing calls are more complex (Carlson et al.,
421 2017a), composed of combinations of many different calls; and they are more high pitched
422 (unpublished data). One other hypothesis could be used to explain the behaviour of coal tits. It
423 is possible that coal tits acquire the meaning of FME, D and FME-D calls via associative
424 learning (i.e., coal tits learn to associate these calls emitted by great tits with a vigilance
425 situation, a foraging flock or mobbing; e.g., Potvin et al., 2018) because these signals can be

426 heard repeatedly in the field. In contrast, coal tits cannot have acquired any meaning for D-
427 FME sequences as they are never heard. This may explain their lack of reaction to these
428 stimuli. This hypothesis would also be consistent with the ‘correlation’ between scanning and
429 approach in coal tits (i.e., the binary response depending on whether the birds have been
430 sufficiently exposed to great tits to associate these calls with a danger, or not). Although coal
431 tits are sensitive to great tits mobbing call sequence reversal, our results did not provide
432 evidence for compositional processing. Additional playbacks to verify coal tits’ and
433 chaffinches’ reactions to FME and D notes, as well as to artificial stimuli starting with an
434 FME- or a D- motif (but finishing with another motif that is normally not used in combination
435 with these motifs) would be most valuable to disentangle this question.

436 Our results also suggest that the combination order of the repetitive loud and broadband
437 notes (i.e., the D motif) preceded by the frequency modulation notes (i.e., the FME motif)
438 within the mobbing call sequence is of prime importance to elicit a response in the receiver. In
439 this respect, it is particularly striking that, in the few bird species for which the effect of
440 compositional syntax has been investigated, all studies reported that natural mobbing call
441 sequences follow this combination ordering (Engesser et al., 2016; Suzuki et al., 2016; Suzuki
442 et al., 2017; Templeton et al., 2005). Furthermore, as suggested by the present study and
443 recent studies on the Japanese tit (Suzuki et al., 2017), it seems that this rule is more
444 important than the acoustic similarity of each motif between species to enable heterospecific
445 response. Nevertheless, whether this rule applies more broadly to bird communities remains
446 to be established and further studies on a larger set of bird species will be necessary. To this
447 aim, comparisons across allopatric species should be especially informative. Furthermore, as
448 birds may not only eavesdrop on heterospecific communication to extract information about
449 predator threats but also about food resources (Magrath et al., 2015), future work is needed to

450 clarify how each motif alone (i.e., alert calls and recruitment calls) is understood by
451 heterospecifics.

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573

574 **SUPPORTING INFORMATION**

575 Additional supporting information may be found online in the Supporting Information section
576 at the end of the article.

577

FIGURE CAPTIONS

578 **FIGURE 1** Spectrograms of calls played to great tit, coal tit and chaffinch: **a** FME-D
579 mobbing call of the great tit showing call with introductory frequency modulated elements
580 (FME) (similar to chickadee A or B elements) and subsequent D notes (D) and **b** D-FME call
581 is a reversed combination of FME and D calls. These calls were produced with Avisoft
582 SASLab©

583

584 **FIGURE 2** Responses of great tits to playbacks of FME, FME-D, D-FME, D and control
585 (BN) test types. **a** Number of scans made by tits during playback (generalized linear mixed
586 model: $F_{4,23} = 14.9, p < 0.0001$). Horizontal line: median value; box ends: upper and lower
587 quartiles; whiskers: variation range of values. **b** Percentage of trials in which tits approached
588 the loudspeaker (generalized linear mixed model: $F_{4,23} = 4.17, p = 0.011$). Sample size: $n =$
589 100 individuals. Each individual was exposed to only one per test type, giving $n = 20$ per test
590 type

591

592 **FIGURE 3** Number of horizontal scans and percentage of trials in which **a** great tits, **b** coal
593 tits and **c** chaffinches approached the loudspeaker during the presentations of the playbacks of
594 FME-D and artificially reversed D-FME motifs of mobbing signals. Horizontal line: median
595 value; box ends: upper and lower quartiles; whiskers: variation range of values. Sample size:
596 $n = 90$ individuals ($n = 30$ per species and 15 per test type)