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1 **Seasonal variation in mobbing behaviour of passerine birds**

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7

8 **Abstract**

9 When they detect a predator, many birds exhibit mobbing behaviour and produce mobbing
10 calls that quickly draw other prey against the predator. Such antipredator strategy often
11 involves several species and therefore implies heterospecific communication. As fledging and
12 nestling stages could be particularly targeted by predators, a high mobbing intensity is to be
13 expected during the breeding season. While recognizing other species' mobbing calls is
14 critical to setting up this behaviour, to date, we have no information about the perception of
15 these calls with regard to t season. Here, we used playbacks of mobbing calls to study the
16 variation in response of the Great Tit (*Parus major*) and the Blue Tit (*Cyanistes caeruleus*)
17 exposed to the mobbing calls of two heterospecific species, the Eurasian Nuthatch (*Sitta*
18 *europaea*), and the Eurasian Wren (*Troglodytes troglodytes*). To investigate mobbing
19 response seasonality, we conducted playback experiments during spring (breeding season)
20 and autumn (non-breeding season). Contrary to most previous studies, we found that mobbing
21 intensity was greater in autumn than in spring. Additionally, although neither Nuthatch nor
22 Wren is related to the Tit family, we found that both Tit species responded more to the former
23 than the latter species. At the heterospecific communication level, this study demonstrates a
24 previously unsuspected level of complexity in the use of mobbing calls.

25 **Keywords** Bird calls • Interspecific recognition • Interspecific communication • Mobbing •
26 Passerines • Paridae

27

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33 during and/or analysed during the current study are available from the corresponding author
34 following a reasonable request.

35

36

37 **Introduction**

38 The key role of anti-predation defences in predator-prey relationships has been studied for
39 many years, particularly in birds. When birds encounter predators, many species are likely to
40 emit alarm calls. These alarm calls may be used to alert conspecifics of potential danger
41 (Weary and Kramer 1995) or recruit nearby individuals for mobbing defence against the
42 predator (Curio et al. 1978). Mobbing calls typically incite other potential prey to fly towards
43 the caller and the predator. This mobbing behaviour may have several different functions and
44 one of the most important is probably to drive the predator away from the vicinity (Pettifor
45 1990; Flasskamp 1994). The greater the number of mobbers, the greater the chances of
46 driving away a predator (Picman et al. 1988; Krams et al. 2009). However, mobbing entails a
47 real risk to the prey involved, owing to its proximity to the predator (Denson 1979; Curio and
48 Regelmann 1986). Preys adjust the strength of their mobbing behaviour according to the
49 perceived risk associated with the predator's threat level (Billings et al. 2015; Dutour et al.
50 2016; Dutour et al. 2017a). Other factors, including the proximity of the predator (Creswell
51 1993; Kleindorfer et al. 2005), its posture (Hamerstrom 1957; Coss and Ramakrishnan 2000)
52 and its behaviour (Lind et al. 2005; Nolen and Lucas 2009) are also involved in explaining the
53 strength of the mobbing. Among these, seasonality is a probably an important factor to
54 explain mobbing behaviour intensity.

55 Although mobbing can occur in the autumn and winter months, many studies have
56 shown that the mobbing response to predators is higher during the breeding season (Altmann
57 1956; Shedd 1982; Shedd 1983; Krams and Krama 2002). Authors have suggested that the
58 willingness of birds to mob during the breeding season probably stems from at least two
59 factors: (1) birds are territorial at this time and lack the option of easy relocation away from
60 predators on their territories, and (2) birds are likely to have eggs or young more vulnerable to
61 the predator (Shedd 1982). Some studies have also documented a temporal intensification in

62 mobbing behaviour during the breeding cycle. For example, parents increase the strength of
63 this mobbing during the breeding cycle, whereas mobbing is rarely performed during the nest
64 building or egg-laying phase (Montgomerie and Weatherhead 1988; Redondo 1989). Finally,
65 an individual's response intensity to the mobbing playback is a significant predictor of
66 reproductive success (Doran et al. 2005), although one study showed that mobbing calls can
67 increase the rates of nest predation and lower breeding success (Krams et al. 2007). However,
68 Dutour et al. (2017a) observed a reverse pattern when studying responses in birds
69 communities to the Eurasian Pygmy Owl (*Glaucidium passerinum*), with a higher response
70 rate in autumn than during the breeding season. Because the study of Dutour et al. (2017a)
71 focused on a global response from all the species predated by the Pygmy Owl, any
72 comparison between seasons on a species scale would be impossible. In addition, with such
73 an experimental design it is not possible to discriminate between responses emitted towards
74 predators and responses to interspecific mobbing calls. To our knowledge, the mobbing
75 behaviour set up in response to interspecific calls has never been studied across
76 seasons. Hence, there is a need for a pairwise comparison of caller-receiver species to explain
77 their behavioural responses during different seasons.

78 Like other members of the Paridae family, the great tit (*Parus major*) and the blue tit
79 (*Cyanistes caeruleus*) are highly vigilant and aggressive during mobbing events: they form
80 mixed-species flocks and mob together (Dutour et al. 2017a). These interspecific flocks can
81 constitute facilitators of mobbing (Goodale and Kotagama 2005; Nolen and Lucas 2009).
82 Here, we address one previously unexamined aspect of the mobbing behaviour of passerine
83 birds. We examine to what extent responses to interspecific mobbing calls vary according to
84 the season. We investigate the variation in response of the Great Tit and the Blue Tit exposed
85 to the mobbing calls of the Eurasian Nuthatch (*Sitta europaea*) and the Eurasian Wren

86 (*Troglodytes troglodytes*). We predict that the mobbing response should be more intense
87 during the autumn than during spring.

88

89 **Methods**

90 **Species and sites studied**

91 The study was conducted in large mixed deciduous-coniferous forests near Lyon in the
92 Rhône-Alpes region (France; 45°80'N, 4°52'E). To ensure the independence of experimental
93 testing (no bird was tested twice during our study), playback sites were separated by more
94 than 100 m and we never came back a second time to the same place. In addition, we avoided
95 any temporal effect during our experiments by evenly distributing the playbacks of the
96 different species across the study period. All tests were conducted in the breeding season
97 (April-Jun 2016) and in the autumn (September-October 2016). Tests involved 140 different
98 individuals (the detailed number of tests conducted for each combination is presented in Table
99 1).

100

101 **Playback Experiments**

102 Once a target bird was identified, we placed the loudspeaker used to broadcast the acoustic
103 signal 30 m away from the bird at the base of a tree. We performed our playback experiments
104 only when no other passerines were observed near the targeted individual, to be sure that the
105 response of the tested bird was due to our playback rather than to the behaviour of other
106 passerines. All tests, where an untargeted bird started to mob before the targeted bird, were
107 discarded from the dataset. Once the loudspeaker was positioned, two observers with
108 binoculars stood opposite each other at vantage points 15 m away from the loudspeaker to
109 observe bird response during the test. All tests were divided into a 1 min baseline of silence,
110 followed by 1 min of signal playback. We found no evidence that our presence disturbed the

111 behaviour of the target bird before the playback emission. During the playback, we considered
112 that the target bird responded positively to our test if it approached within a 15m radius of the
113 loudspeaker (see Dutour et al. 2017b for more details).

114

115 **Choice of experimental stimuli and playback materials**

116 The mobbing calls produced by Wren and Nuthatch in response to a pygmy owl or uploaded
117 from Xeno Canto (XC file hereafter) online database were played with a Shopinnov 20W
118 loudspeaker (frequency response 100Hz-15kHz). To limit pseudo replication (Hurlbert 1984;
119 Kroodsma 2001), we used mobbing calls from 5 different individuals for the Wren
120 (XC252499) and we used two soundtracks recorded in two populations for the Nuthatch
121 (Germany XC252502 and Sweden XC28224).

122

123 **Statistical analysis**

124 Analyses were done using R v.2.15.1 software (R Development Core Team 2012). We used
125 generalised linear mixed models (GLMM) to investigate the variation in mobbing propensity
126 (i.e. speaker approach) among the receiver species (i.e. Great Tit or Blue Tit) and according to
127 the mobbing stimuli broadcast (i.e. mobbing calls of Nuthatch and Wren) and the season
128 (breeding season and autumn). More specifically, the individual binary response (mobbing
129 response = 1; no mobbing response = 0) was introduced as dependent variable using a logit
130 link and a binomial distribution for the error term, and the season, the receiver species, the
131 mobbing stimuli and their interactive effects were introduced as explanatory terms in the fixed
132 part of the model. As different playback soundtracks were used for each receiver species,
133 soundtracks were introduced in the model as random effects. We also performed a model for
134 each receiver species to investigate the variation in mobbing propensity according to the
135 season and the mobbing stimuli.

136

137 **Results**

138 Our analyses showed that the season, the receiver species and mobbing stimuli have a
139 significant additive effect on the proportion of individuals which exhibited mobbing
140 behaviour (Table 2; Fig. 1). Blue Tits responded more strongly than Great Tits ($p = 0.033$). In
141 Great Tits, both mobbing stimuli and season had a significant additive effects on the
142 proportion of individuals that exhibited mobbing behaviour (season effect: $\chi_1^2 = 3.527$, $p =$
143 0.060 ; mobbing stimuli effect: $\chi_1^2 = 5.10$; $p = 0.024$). Great Tits mobbed 1.8 times more
144 during autumn than they did during the breeding season. In response to Nuthatch calls, Great
145 Tits were more likely to approach within 15 m of the loudspeaker than in response to Wren
146 calls. Concerning the Blue Tits, we obtained the same result (season effect: $\chi_1^2 = 5.36$, $p =$
147 0.021 ; mobbing stimuli effect: $\chi_1^2 = 5.12$, $p = 0.023$): individuals mobbed 1.7 times more
148 during the autumn than they did during the breeding season and were more prone to respond
149 to Nuthatch calls than to Wren calls.

150

151 **Discussion**

152 Our playback experiments indicated that mobbing intensity was significantly greater in
153 autumn than in the breeding season, whatever the receiver species or mobbing stimuli used
154 and despite the fact that we may have tested juveniles (3-4 months old) with lesser experience
155 on mixed-flocks and potentially showing weaker response. This result does not agree with
156 most of the previous studies, which suggested increased mobbing activity during the breeding
157 season (e.g., Altmann 1956; Shedd 1982; Shedd 1983; Krams and Krama 2002). However,
158 those studies examined mobbing behaviour in response to conspecific mobbing calls or to
159 predator playbacks but not against interspecific mobbing calls (but see Tremblay and St Clair
160 2009). Nonetheless, these results confirm, on the species scale, the results obtained in a

161 previous study conducted on the community scale (Dutour et al. 2017a). Increased mobbing
162 activity during autumn could be explained by a seasonal variation in predator diet, as
163 predation pressure on passerine birds is probably different across seasons (Dutour et al.
164 2017a). In the case where birds make up a large share of the predator's diet year round,
165 vigorously attacking them at any time may make evolutionary sense (Cully and Ligon 1986;
166 Nijman 2004; Chiver et al. 2017; Dutour et al. 2017a). In our case, a higher predation pressure
167 in autumn could then explain more intense mobbing behaviours at this time. In addition,
168 contrary to the breeding season, where mobbing behaviour is constrained by territorial
169 boundaries (Betts et al. 2005), during the non-breeding season mobbing could occur in areas
170 outside the territory, increasing opportunities to respond to mobbing calls. Alternatively,
171 higher mobbing intensity during autumn could be explained by migratory patterns. If the
172 birds tested are migratory birds, they have less opportunity to meet local predators, possibly
173 leading Tits to respond to the mobbing calls of resident species in order to gather information
174 (Nocera et al. 2008). Ultimately, increased mobbing activity during autumn could be related
175 to variations in sensitivity of the receiver (Lucas et al. 2002; Lucas et al. 2007). During the
176 breeding season, Tits spend time with their conspecifics (mate and nestlings), whereas they
177 form mixed-species flocks during the non-breeding season. We could suggest that species are
178 more sensitive (i) to conspecific mobbing calls during the breeding season and (ii) to
179 heterospecific mobbing calls during the non breeding season. During the breeding season, a
180 targeted individual has an interest in responding to conspecific mobbing calls because the
181 probability that mobbing calls are emitted by its mate are high, even though this strategy
182 presumes individual recognition (Kennedy et al. 2009; Wheatcroft and Price 2008; McDonald
183 2012). Furthermore, for conspecifics, mobbing could play important indirect roles during the
184 breeding season. For example, da Cunha et al. (2017) suggest that males may use mobbing to
185 display their phenotypic quality to females. In this case, predator mobbing could be seen as a

186 way to influence sexual selection. Conversely, during the autumn and winter months, some
187 passerine birds conduct the majority of their daily activities with mixed-species flocks
188 (Ekman 1989). As birds often respond “by contagion” to the reactions of other birds, it is
189 possible that during this period a higher number of prey species increase the propensity of
190 birds to react and thus increase the strength of the mobbing, as shown by Sieving et al. (2004).
191 Thus, in the non-breeding season, all these factors together can trigger a strong response from
192 passerines to the mobbing calls of other species.

193 Our results indicated that Great and Blue Tits responded more strongly to the calls of
194 Nuthatch and much less to those of Wren. The similarity in response of Blue Tits and Great
195 Tits to both Nuthatch and Wren calls suggests that they may use these signals in an analogous
196 manner. Nuthatch is a passerine that may occur in mixed flocks with Tits during the non-
197 breeding season (Hinde 1952), whereas the Eurasian Wren is a species with which they rarely
198 co-exist. Thus, Tits may have opportunities to learn to associate the heterospecific mobbing
199 calls of Nuthatches with predatory threats, and this may contribute to the rapid spread of anti-
200 predator behaviour within a bird community (Wheatcroft and Price 2013; Magrath et al. 2015;
201 Suzuki 2016). Our results go beyond simple learning, as they suggest that previous exposure
202 and learning maintain heterospecific responses (Wheatcroft and Price 2013), in addition to
203 innate processes (Randler 2012; Dutour et al. 2017b). To test the role of learning between
204 species, we could have tested juveniles with less experience of mixed-flocks in Autumn.
205 Juveniles should respond less than adults. Other hypotheses could be advanced to explain an
206 increasing mobbing response to Nuthatch: Tits are very similar in size to Nuthatches, occupy
207 many of the same habitats, and are therefore attacked by most of the same predators.
208 Furthermore, it has been found that the White-Breasted Nuthatch (*Sitta carolinensis*), a close
209 relative of the Eurasian Nuthatch, has (i) a greater ability to detect the predator playback
210 (Lucas et al. 2002; Lucas et al. 2007) and (ii) a greater tendency to mob before other species

211 (Nolen and Lucas 2009). In our case, Eurasian Nuthatch may have played a key role in the
212 initiation of mobbing behaviour and that can be beneficial in responding to its mobbing calls.
213 Tits make complex antipredator responses depending on the mobber's identity and their
214 ecological relations. Recognizing other species' mobbing calls is critical for the efficiency of
215 the antipredator behaviour. Previous studies suggest that Red-Breasted Nuthatches (*Sitta*
216 *canadensis*) discriminate between subtle differences in Black-Capped Chickadees (*Poecile*
217 *atricapillus*) alarm calls that contain information about the size of potential predators
218 (Templeton and Greene 2005; Templeton and Greene 2007). A next step is to study how
219 passerine birds encode information about predator threat in their mobbing calls (see Carlson et
220 al. 2017 for Paridae) and how this information is used by heterospecifics.

221 We have demonstrated that season influenced decision making in Tits. Overall,
222 mobbing is a complex antipredator strategy, and many parameters, such as prevalence in
223 flocks, similarity of mobbing calls or learning process among species sharing the same
224 habitat, may influence the expression of this behaviour. Further research identifying mobbing
225 and non-mobbing species would provide information on species interdependence and avian
226 community organization.

227

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335

Figure Captions

336

337 **Fig. 1** Percentage of trials in which Great Tits and Blue Tits approached within 15 m of the
338 loudspeaker during the presentations of mobbing calls of a Wren (grey) and a Nuthatch
339 (black) in the breeding season and in autumn.

340

341 **Table 1** Details of the number of tests conducted for each combination in this study ($n = 140$)

		Playbacks			
		Nuthatch		Wren	
		Breeding season	Autumn	Breeding season	Autumn
Tested species	Blue Tit	15	21	15	15
	Great Tit	15	21	18	20

342

343 **Table 2** Generalised linear mixed model type II Wald Chi-square results

Explanatory terms in the fixed part of the models	χ^2	p
season	9.65 ^a	0.002
receiver species	4.521 ^a	0.033
mobbing stimuli	9.236 ^a	0.002
season*receiver species	0.229 ^a	0.632
season*mobbing stimuli	0.036 ^a	0.849
receiver species*mobbing stimuli	0.011 ^a	0.915
season*receiver species*mobbing stimuli	0.593 ^a	0.441

344 ^a $df = 1$