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1 **The role of associative learning process on the response of**  
2 **fledgling great tits (*Parus major*) to mobbing calls**

3

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11

12 **Abstract**

13 When they detect a predator, many species emit antipredator vocalizations. In some cases,  
14 they emit mobbing calls, which are associated with the caller approaching and harassing the  
15 predator while attracting others to join it. Surprisingly, although mobbing has been widely  
16 reported in adults of numerous species, there has been no test of the role of learning in  
17 mobbing call recognition, especially during ontogeny. Here, we exposed wild great tit (*Parus*  
18 *major*) nestlings to playbacks of an unthreatening, novel sound either associated with  
19 conspecific mobbing calls (experimental treatment) or with another unthreatening novel  
20 sound (control treatment). We then tested them as nestlings and fledglings to see how  
21 responses to the novel sound compared to conspecific mobbing calls. Results revealed that  
22 fledglings in the experimental treatment behaved similarly to conspecific mobbing calls and  
23 the novel sound associated with conspecific mobbing calls. Because mobbing efficiency is  
24 often linked to interspecific communication, associative learning should be used by  
25 heterospecifics as a mobbing calls recognition mechanism. Regardless of treatment during the  
26 nestling phase, fledglings always were sensitive to the playback of conspecific mobbing calls.  
27 However, fledglings from the control group were more likely to approach the loudspeaker  
28 than those from the experimental group when mobbing calls were played, suggesting that  
29 overexposure during the nestling phase altered mobbing learning. Overall, these results  
30 suggest that learning could play a role in the recognition of calls, like heterospecific mobbing  
31 calls, when paired with conspecific mobbing, and that mobbing is perceived as a threatening  
32 stimulus from a very young age.

33

34 **Key words** Alarm call · Associative learning · Birds · Communication · Mobbing

35

## 36 **Introduction**

37

38 In many species of small birds and mammals, two contrasted anti-predator strategies, each  
39 associated to a specific alarm call, can be observed according to predator dangerousness: prey  
40 may flee or mob the predator (Marler 1957). Mobbing behaviour is usually exhibited when  
41 predators do not represent an immediate threat and is characterized by harassment or even  
42 attacks on the predator as well as vocalizations (i.e., mobbing calls) that quickly gather  
43 neighboring conspecifics and other prey species in the mob (Hartley 1950; Curio 1978). Both  
44 the evaluation of the threat associated with the predator and the recognition of mobbing calls,  
45 including heterospecific calls, are required to make mobbing behaviour an efficient anti-  
46 predator strategy.

47 Associative learning is a behavioural modification following reinforcement, based on  
48 associations between two stimuli, responses and events (Shettleworth 1998; Griffin et al.  
49 2015). This process is essential to the development of vocalizations and several behaviours  
50 such as those involved in predator avoidance (Ferrari and Chivers 2011). Animals can learn to  
51 flee after associating an unfamiliar sound (i.e., novel sound) with (i) the appearance of a  
52 model predator (birds: Magrath et al. 2015a; mammals: Shriner 1999; Wheeler et al. 2019) or  
53 (ii) the hearing of alarm calls, without having to see the callers or a predator (Potvin et al.  
54 2018). In mobbing behaviour, there is ample evidence of a process of associative social  
55 learning between conspecific mobbing calls and predators (Curio et al. 1978a; Maloney and  
56 McLean 1995; McLean et al. 1995; Griffin and Galef 2005; McIvor et al. 2018) but in all  
57 cases the training phase was based on visual cues; individuals were trained about predators  
58 through pairing model predator presentations with a training stimulus (i.e., live conspecific  
59 demonstrator engaging in mobbing, mobbing calls paired with mounts of conspecifics, or  
60 mobbing calls alone). However, visual associative learning needs the inexperienced learner to

61 be in the vicinity of the mobbing scene, so that the opportunities for learning while reducing  
62 the risk of threat may be limited, especially for species living in dense vegetation. This  
63 challenge is overcome in the case of acoustic-acoustic association, which may be efficient  
64 even when the tutor and the threat are difficult to observe, possibly resulting in the rapid  
65 spread of mobbing call recognition in natural communities.

66 Mobbing calls are usually characterized by loud and repetitive vocalizations, both  
67 features that should facilitate associative learning, as there is ample opportunity to hear  
68 mobbing calls while observing the threat, with less likelihood of immediate danger (Magrath  
69 et al. 2015b). In birds, such association between a predator and the expression of a mobbing  
70 behaviour could be achieved after young fledge leave their nest. In this case, young fledglings  
71 can learn from their parents and several observations are in agreement with this statement  
72 (Curio et al. 1978b; Griesser and Suzuki 2016). If nestlings however are able to associate  
73 several acoustic signals from their nest cavities (i.e., they are able to associate the mobbing  
74 calls emitted by parents with other vocalizations prevailing on a mobbing scene) they should  
75 also be able to respond to mobbing calls appropriately as soon as they leave the nest. To our  
76 knowledge, this capacity has never been investigated before. Indeed, until now, associative  
77 learning has been examined using the association of several sensory channels, especially  
78 visual and acoustic (e.g. Maloney and McLean 1995; McIvor et al. 2018). However, as  
79 outlined above, young could also associate unknown vocalizations with conspecific mobbing  
80 calls if both are simultaneously emitted in a mobbing scene. Such a mechanism could be  
81 particularly relevant in learning to recognize heterospecific mobbing calls.

82 The great tit (*Parus major*) is a well-suited species to study the ontogeny of mobbing  
83 behaviour in the wild. It is well known for its learning abilities (Exnerová et al. 2006; Cole et  
84 al. 2011; Morand-Ferron et al. 2015) and its tendency to exhibit mobbing behaviour and emit  
85 mobbing calls when confronted with a predator (Lind et al. 2005; Dutour et al. 2016; Carlson

86 et al. 2017a; Kalb et al. 2019). Furthermore, this altricial species provides a good system for  
87 studying whether naïve nestlings are able to associate mobbing calls with unfamiliar stimuli in  
88 the absence of any visual cues from adults or predators in the nest cavity.

89         The goal of this study was to determine whether associative learning might serve as a  
90 mechanism for the development of mobbing calls recognition for free-living animals.  
91 Specifically, we investigated whether experiencing a novel stimulus associated with  
92 conspecific mobbing calls during the nestling period led great tit nestlings to associate this  
93 novel sound with mobbing during the fledgling period. We designed playback experiments in  
94 two groups: (i) an experimental group in which we trained individuals by broadcasting a  
95 novel sound (i.e., associative learning stimulus) with mobbing calls (i.e., functional stimulus)  
96 and (ii) a control group in which the associative learning stimulus was broadcast with another  
97 novel sound (hereafter control stimulus).

98         In line with previous work showing that nestlings cease begging when they hear  
99 playbacks of their parents' alarm calls (Davies et al. 2004; Hollén and Radford 2009; Barati  
100 and McDonald 2017), we predict that at the end of the learning period, only nestlings  
101 belonging to the experimental group should cease begging when they hear the associative  
102 learning stimulus. We also measured responses at the fledgling stage after the playback of the  
103 associative learning stimulus. We predict that the playback of the associative learning  
104 stimulus should elicit a stronger mobbing response from the experimental group compared to  
105 the control group (i.e., increases in scanning, calling and moving) because the experimental  
106 group should associate the unfamiliar sound with mobbing and respond to the unfamiliar  
107 sound as threatening, while the control group should not. Because it was important to ensure  
108 that fledglings were sensitive to mobbing, we also tested whether they responded to the  
109 playback of conspecific mobbing calls.

110

## 111 **Material and methods**

112

### 113 **Study sites and species**

114

115 We chose great tits, a common territorial passerine which breeds in secondary holes and  
116 wooden artificial nest boxes throughout Europe and parts of Asia and North Africa (Perrins  
117 1965). The study was conducted in the Pierre Vérots Foundation, a private natural reserve  
118 located in the south-east France (4°91'E, 45°95'N). The study area covers approximately 150  
119 ha and contains 120 nest boxes separated at minimum by 50 m and mainly occupied by great  
120 tits. This distance corresponds to the minimum distance separating tit territories during the  
121 breeding season in our study area and is far enough to ensure that the playbacks are not heard  
122 by neighbours (at 50 meters, the amplitude levels fluctuate from 33 to 39 dB, obtained from  
123 the loudspeaker, Solo 01dB Metravib, Z weighting, re: 20  $\mu$  m Pa; these levels are lower than  
124 the natural background noise levels in forest areas, fluctuate from 35 to 45 dB in quiet  
125 situations, 52 to 70 dB in noisy situations). The study took place during the breeding season  
126 (April-July 2017). We visited nest boxes at least every two days from the beginning of the  
127 breeding season onwards to determine the laying and hatching dates. When nestlings were 8  
128 days old, they were ringed with a unique combination of color bands for individual  
129 identification. Nestlings spent  $19.3 \pm 1.4$  days in the nest. Nestlings from the same nest all  
130 hatched on the same day and subsequently also fledged on the same day.

131

### 132 **Experimental procedures: presentation of stimuli**

133

134 The aim of our experiment was to assess whether chicks were able to associate a novel  
135 stimulus with conspecific mobbing calls. In 120 nest boxes, 31 were unoccupied, 14 occupied

136 by the blue tit (*Cyanistes caeruleus*) and one was occupied by the willow tit (*Poecile*  
137 *montanus*). Each of the remaining 74 nest boxes occupied by great tits was randomly assigned  
138 to one of the two treatments (balanced for laying date to ensure equal representation of both  
139 treatment groups over the breeding season). In the first treatment (38 nests), the associative  
140 learning stimulus was associated with conspecific mobbing calls (hereafter experimental  
141 group) while in the second treatment (36 nests) the associative learning stimulus was  
142 associated with unfamiliar stimulus (control sequence, hereafter control group). Behavioural  
143 tests were conducted both during the development of nestlings and the fledging day.  
144 Playbacks were always broadcasted once adults were silent and away from the nest (at least  
145 15 m) or from the focal fledgling (at least 5 m). If parents responded to playback during tests,  
146 we stopped the playback and restarted at least 30min after, but such cases were rare (~5% of  
147 total tests).

148

#### 149 **Choice of experimental stimuli and playback materials**

150

151 Three kinds of stimuli were used during playback experiments. First, we used mobbing calls  
152 produced by four great tits in response to the Eurasian pygmy owl (*Glaucidium passerinum*)  
153 and to conspecific mobbing calls. Calls were recorded with a Fostex FR2LE digital recorder  
154 connected to a Sennheiser ME67-K6P microphone. We also used mobbing calls produced by  
155 ten great tits obtained from the Xeno Canto online database (<http://www.xeno-canto.org>) (see  
156 online supplement, Appendix 1). For the associative learning and the unfamiliar stimulus, we  
157 used two musical instrument sounds (clarinet and trumpet sequences) obtained from an online  
158 sound bank (<http://www.universal-soundbank.com>) to ensure the stimuli used had no  
159 biological value and were unfamiliar. In order to ensure that control sounds were unfamiliar,  
160 we first conducted a pilot study to assess the response of adult great tits ( $n = 9$ ). None of them



161 approached and mobbed the loudspeaker. We matched the frequency characteristics and  
162 temporal structure of the associative learning and the unfamiliar stimulus to obtain stimuli of  
163 the same duration and the same frequency bandwidth using Avisoft-SASLab Pro. For the  
164 experimental treatment, we built playbacks containing the associative learning stimulus (i.e.,  
165 clarinet) with mobbing calls. For the control treatment, the associative learning stimulus was  
166 associated with the unfamiliar stimulus (i.e., trumpet) (spectrograms of mobbing calls,  
167 associative learning stimulus and unfamiliar stimulus are available in supplementary material  
168 Appendix 2 Fig. A2). Each playback track consisted of 10 seconds of associative learning  
169 stimulus followed by 10 seconds of the mobbing calls or the unfamiliar signal, and this  
170 sequence was repeated three times in order to reach one-minute in total, time used in a recent  
171 study conducted on nestling passerines in response to calls (Wheatcroft 2015). In order to  
172 avoid habituation to playbacks, we constructed 21 one-minute playback samples for each  
173 group and each sample was used only once (i.e., as nestlings spent  $19.3 \pm 1.4$  days in the nest,  
174 we used one stimulus by day) (Hurlbert 1984; Kroodsma et al. 2001). Because we used  
175 mobbing calls produced by 14 great tits in total to construct 21 playback sequences, some  
176 soundtracks are therefore only imperfectly independent from other ones, but the risk of  
177 pseudoreplication was clearly minimized. We also built two additional 30-second playback  
178 samples containing associative learning stimulus or mobbing calls to test the response of  
179 nestlings and fledglings. We decided to keep the test duration shorter than was usual in  
180 previous studies conducted on adults' great tit (including our own Dutour et al. 2017b; see  
181 also Suzuki et al. 2012) in order to limit the risk of interference from parents during tests. The  
182 average amplitude used for these playbacks was obtained with a sound level meter placed 1 m  
183 from the loudspeaker ( $83.9 \pm 3.51$  dB, mean  $\pm$  SD, Solo 01dB Metravib, Z weighting, re:  $20 \mu$   
184 m Pa). We broadcast sound tracks using a Shopinnov 20 W loudspeaker (frequency response  
185 100 Hz -15 kHz).

186

## 187 **Behavioural responses of nestlings**

188

189 Begging calls suppression is described as a good measure of whether nestlings interpret  
190 sounds as cues of danger (Magrath et al. 2010). To determine whether playback treatment  
191 (i.e., associative learning stimulus with unfamiliar stimulus or associative learning stimulus  
192 with mobbing calls) influenced nestling calling activity, every day, between 7am and 1pm,  
193 and between hatching day and fledging day, we measured nestling production of begging calls  
194 within the nest box during 30 seconds (begging call = 1, no begging call = 0) before and after  
195 broadcasting the treatment, 1 minute being time by which passerine nestlings' behaviour  
196 return to normal (Wheatcroft 2015). To measure this behaviour, one observer was placed ~  
197 50 cm from each nest to listen to the calls of the nestlings, which were clearly heard at short  
198 distance. Although there were multiple observers ( $n = 8$ ) to measure begging call propensity,  
199 we did not detect an observer effect (GLMM:  $P > 0.05$ ). Additionally, at the end of the  
200 nestling phase, between 19 days post hatch and fledging day, begging call propensity was  
201 measured before and after playback of the associative learning stimulus. To create as natural a  
202 situation as possible, the loudspeaker was placed on the top of the nest box for all trials. The  
203 average amplitude used for the playback was obtained with a sound level meter placed in the  
204 nest boxes ( $67.98 \pm 0.94$  dB, mean  $\pm$  SD, Solo 01dB Metravib Z weighting, re:  $20 \mu$  m Pa).

205

## 206 **Behavioural responses of fledglings**

207

208 To test whether associative learning is involved in the development of mobbing calls  
209 recognition, we studied fledglings' responses to the playback of either the associative learning  
210 stimulus alone (control:  $n = 30$  from 22 nests; experimental:  $n = 31$  from 19 nests) or the

211 conspecific mobbing calls (control:  $n = 19$  from 14 nests; experimental:  $n = 26$  from 16 nests).  
212 Tests were performed during the day of fledging (except 4 tests conducted the second day  
213 after fledging corresponding to 3.8% of total tests). Each test was conducted by two field  
214 assistants. One was assigned to the soundtrack preparation and playback operation, while the  
215 other was kept unaware of the selected soundtrack (although they could hear it) and assigned  
216 to the observation of the focal bird. In all experiments and before the playback, the identity of  
217 the focal fledgling was determined using the unique leg color bands fitted to each fledgling  
218 using binoculars. Neither of the two field assistants knew whether the fledgling was in the  
219 control or experimental group. Once a focal fledgling was identified, the loudspeaker used to  
220 broadcast the acoustic stimulus was placed  $\sim 20$  m from the fledgling at the base of a tree at  
221 1.5 meter high. All observations were done using binoculars. Observations were made  $\sim 10$  m  
222 from the loudspeaker and the focal fledgling, a distance from which the tits' behaviour was not  
223 disturbed. Trials were conducted mostly around 12am (range 8am - 5pm) to ensure good light,  
224 in calm and dry weather. Playbacks were started when no bird was visible close to the speaker  
225 and no bird was calling. To test fledglings' responses, we recorded the following behavioural  
226 variables during the 30 s of playbacks: (i) number of horizontal scans (i.e., the number of  
227 movements that birds made with their heads from left to right or right to left), (ii) calling (i.e.,  
228 producing any mobbing vocalizations; call propensity: mobbing vocalization = 1; no mobbing  
229 vocalization = 0), (iii) approaching the loudspeaker (i.e., we recorded whether birds  
230 approached within 15 m of the loudspeaker during playback; see Dutour et al. 2017b for more  
231 details), and (iv) fleeing (i.e., we recorded whether birds moved away more than 10 m from  
232 their initial position). We measured these behaviours because they are good indicators of  
233 perceived danger in birds (Curio et al. 1978a) and are common during mobbing events  
234 (Suzuki et al. 2016; Carlson et al. 2017a; Carlson et al. 2017b; Dutour et al. 2017b; Suzuki et

235 al. 2017). There was 10-minute gap between playback of the associative learning stimulus and  
236 playback of mobbing calls.

237

### 238 **Data analysis**

239

240 Analyses were done using SAS 9.4 (SAS Institute Inc., Cary, NC, U.S.A.) and R v.2.15.1  
241 softwares (The R Foundation for Statistical Computing, Vienna, Austria, [http://www.r-](http://www.r-project.org)  
242 [project.org](http://www.r-project.org)). We first examined whether begging call propensity varied between treatment  
243 groups during the nestling period. For this purpose, we analyzed call propensity recorded each  
244 day before broadcasting the treatment using a logistic linear mixed model (LLMM) for which  
245 the call propensity was treated as a repeated dependent binary variable. To this aim, nest was  
246 considered as a random effect and the correlation between successive observations recorded at  
247 the same nest was specified using an autoregressive covariance structure. The treatment  
248 group, the time elapsed since hatch (i.e., nestlings age) as well as their interactive effect, were  
249 introduced as fixed effects. The significance of each fixed effect was tested using a non-  
250 sequential F test and the Kenward-Roger method was used to approximate the denominator  
251 degrees of freedom (SAS 9.4). Non-significant terms were successively dropped to obtain the  
252 final model. We used a similar model framework to compare the propensity of nestlings to  
253 stop begging after the onset of the broadcasting treatment according to the treatment group  
254 and the time elapsed since hatching. For this purpose, all observations for which nestlings  
255 were not calling before the onset of the playback treatment were discarded from the analysis.  
256 We used a Fisher exact test to test whether the begging calls propensity just after the playback  
257 of the associative learning stimulus only when nestlings were between 19 days post hatch and  
258 fledging day varied according to the group (experimental or control).

259 To investigate the behavioural responses of fledglings, we first examined whether the  
260 number of horizontal scans varied between treatment groups and playback during the  
261 fledgling period ( $n = 106$ ). For this purpose, we ran generalized linear mixed models  
262 (GLMM) which included the treatment group, the playback (associative learning stimulus or  
263 mobbing calls) and their interactive effect as a fixed terms and nest as a random term. We  
264 used a negative binomial error distribution and log-link function for this analysis (*glmer.nb* in  
265 the package *lme4*; Bates et al. 2014). To investigate the call propensity, we used a binomial  
266 error distribution and logit-link function (*glmer* in the package *lme4*; Bates et al., 2014)  
267 (calling response = 1; no calling response = 0). As above, nests were included in the model as  
268 a random effect. The treatment group, the playback and their interactive effect were  
269 introduced as fixed effects. For both scanning and call propensity, we further conducted  
270 pairwise comparisons (*glht* in the package *multcomp*). Finally, because approaching and  
271 fleeing behaviours (two behaviours linked to movements) were opposed to immobility  
272 behaviour (see online supplement Appendix 3, Fig. A3), all approaching and fleeing  
273 individuals were regrouped within a unique category (hereafter moving individuals) and  
274 compared to the individuals who stayed still. To compare the propensity of fledglings to move  
275 vs individuals who stayed still according to treatment group and playback, we used a binomial  
276 error distribution and logit-link function. We then focused our analysis on moving individuals  
277 only (i.e., fleeing and approaching individuals;  $n = 23$ ). Because only a small number of  
278 fledglings moved, Fisher's exact test was used to investigate the variation in mobbing  
279 propensity (i.e., approach) according to the treatment group in response to the mobbing call  
280 playbacks ( $n = 17$ ). Because only one of the control fledglings moved when exposed to the  
281 playback of the associative learning stimulus, we discarded this group and we used a Fisher's  
282 exact test to investigate the variation in mobbing propensity of individuals from the  
283 experimental group between the two playbacks ( $n = 16$ ).

284

285 **Data availability** The datasets generated during the current study are available from the  
286 corresponding author on request.

287

## 288 **Results**

289

### 290 **Behavioural responses of nestlings**

291

292 The calling behaviour before the broadcasting treatment did not significantly vary in function  
293 to the time elapsed since hatching up to fledging but it was significantly higher for the  
294 experimental group than the control group ( $n = 1420$ , treatment effect:  $F_{1,341} = 4.17$ ;  $P = 0.042$   
295 ; time effect:  $F_{1,426} = 0.66$ ;  $P = 0.417$ ; interaction:  $F_{1,425} = 0.40$ ;  $P = 0.529$ ). The propensity to  
296 stop calling after the onset of the broadcasting treatment significantly increased in function to  
297 the time elapsed since hatching but did not vary between treatment groups although call  
298 suppression tended to increase with time slightly more for the control group than for the  
299 experimental group ( $n = 353$ , treatment effect:  $F_{1,156} = 0.11$ ;  $P = 0.745$  ; time effect:  $F_{1,176} =$   
300  $46.19$ ;  $p < 0.0001$ ; interaction:  $F_{1,170} = 3.69$ ;  $P = 0.057$ ). We did not detect a treatment group  
301 effect on the nestlings responses to the playback of the associative learning stimulus ( $n = 11$ ;  
302  $P = 0.608$ ).

303

### 304 **Behavioural responses of fledglings**

305

306 Scanning was significantly affected by the interaction between the stimuli that were broadcast  
307 (associative learning stimulus or mobbing calls) and the treatment group (experimental and  
308 control) (Table 1; Fig. 1). In response to mobbing calls playbacks, the rate of horizontal scans

309 did not differ between the two groups ( $P = 0.99$ ; Fig. 1). It was higher during playback of  
310 mobbing calls than during playback of the associative learning stimulus for the control group  
311 ( $P = 0.004$ ; Fig. 1) while it did not differ for the experimental group ( $P = 0.99$ ; Fig. 1).  
312 Similar variations were found for call propensity as indicated by a significant interaction  
313 effect between group and playback (Table 1; Fig. 2), although these variations were not  
314 statistically different between both groups in response to the associative learning stimulus  
315 playback ( $P = 0.95$ ; proportion of calling: associative learning = 22.5%; control = 6.7%).  
316 Furthermore, there was a significant effect of playback on the probability of moving (i.e.,  
317 approaching and flight behaviours), whereas group had no significant effect (Table 1; Fig. 3).  
318 In response to mobbing calls, fledglings were more likely to move than in response to the  
319 associative learning stimulus playback. Results indicate that (i) in response to the mobbing  
320 call playbacks, individuals from the control group were more prone to approach the  
321 loudspeaker than experimental individuals ( $n = 17$ ; Fisher test:  $P = 0.049$ ; Fig. 3) (ii)  
322 approaching behaviour of individuals from the experimental group did not differ between the  
323 two playbacks ( $n = 16$ ; Fisher test:  $P = 0.999$ ; Fig. 3).

324

## 325 **Discussion**

326

327 We have investigated whether nestlings submitted to a novel stimulus associated with  
328 mobbing calls enabled them to recognize this stimulus as an indicator of threat proximity  
329 when becoming fledglings. This experiment, involving classical conditioning, showed that  
330 fledglings learned to associate a novel stimuli with mobbing calls and exhibited vigilance  
331 behaviours in response to the novel stimuli whereas they do not as nestlings.

332

### 333 **Effect of the associative learning during the nestling phase**

334

335 Several studies have shown that nestlings become silent when they hear playbacks of their  
336 parents' alarm calls (Davies et al. 2004; Platzen and Magrath 2004; Madden et al. 2005; Haff  
337 and Magrath 2012; Barati and McDonald 2017). However, most of these studies have  
338 compared alarm calls to background noise or sympatric species stimuli (i.e., stimuli known).  
339 In the present study, nestlings suppressed calling when submitted to associative learning  
340 stimulus equally to mobbing call playbacks, suggesting that novelty (i.e., a stimulus never  
341 heard before) alone may be used as a signal of danger (Schaller and Emlen 1961; Curio et al.  
342 1978b). We found that, contrary to young nestlings, older nestlings reduced begging calls in  
343 response to the associative learning stimulus and mobbing calls, suggesting that older  
344 nestlings are less prone to recognition errors than younger ones (Davies and Brooke 1988;  
345 Davies et al. 2004). This pattern of gradual acquisition is in accordance with previous studies  
346 conducted on nestling great tits (Rydén 1978). We did not detect a group effect on nestling'  
347 responses to playbacks of the associative learning stimulus at the end of the learning period,  
348 but the low sample size may have reduced our ability to detect a significant pattern. A detailed  
349 study of nestlings' behaviour would be insightful to actually address this question (e.g., if they  
350 crouched down inside their nest cavity, suppressed their movements, increase their heart rate  
351 and electromyographic activity after parental alarm calls; Rydén 1978; Ryden 1980; Suzuki  
352 2011). Finally, another interesting aspect is related to the sound degradation. As we used hole  
353 nesters, a sound degradation may occur that a sound will appear different within and outside  
354 the nest box. However, quite low-frequency sounds have been used in this study, with  
355 probably low alteration, and the sounds were broadcast using a loudspeaker placed on the top  
356 of the nest box for all trials, with the only obstacle being the wall thickness of the nest box.  
357 Future work could investigate which sound characteristics of the parent calls could be



358 perceived by offspring in their nest according to their nestling conditions (hole nesters vs  
359 open nesters).

360

### 361 **Mobbing calls recognition and associative learning in fledglings**

362

363 Fledglings exhibited a higher rate of scanning when hearing the associative learning stimulus  
364 but only if it was associated with mobbing calls during the nestling phase. A similar trend was  
365 also observed for calling activity and the propensity to move. Together, these results indicate  
366 that individuals associated the artificial sound with conspecific mobbing calls without having  
367 to see the mobbing scene. Scanning rate is a good proxy of vigilance effort (Lendrem 1983;  
368 Huang et al. 2012; Creel et al. 2014) suggesting that chicks actually perceived the associative  
369 learning stimulus as an indicator of threat proximity only if it was associated with mobbing  
370 calls during the learning phase. Whether fledglings associated the artificial stimulus as the  
371 source of threat itself or as heterospecific mobbing calls (indicating the presence of a threat)  
372 and whether the ontogeny of mobbing behaviour only relies on learning processes, remain  
373 open questions. Positive correlation between the rate of response development and the  
374 magnitude of exposure to heterospecific alarm calls suggest a learning process. For instance,  
375 infant vervet monkeys (*Cercopithecus aethiops pygerythrus*) develop responses to superb  
376 starling (*Lamprotornis superbus*) mobbing calls more quickly on territories where these birds  
377 are common, suggesting that these young have more opportunities to learn about the calls than  
378 young on territories where starlings are less common (Hauser 1988). Concerning adults, they  
379 can associate novel sounds with a chorus of conspecific and heterospecific aerial alarm calls  
380 (Potvin et al. 2018). One may thus expect that a learning process where individuals associate  
381 the threat and/or heterospecific mobbing calls with the conspecific mobbing calls can operate  
382 in the wild. Such mechanisms could make the set of recognized heterospecific mobbing calls

383 adjusted to the local composition of prey communities, which is also congruent with field  
384 studies reporting local variations of the rate of responses towards heterospecific mobbing calls  
385 (Wheatcroft and Price 2013).

386 In addition to such associative learning processes, our study also reveals that  
387 fledglings responded to conspecific mobbing calls despite the treatment they experienced.  
388 Indeed, in both groups, hearing conspecific mobbing calls resulted in increased vigilance, a  
389 higher proneness to call as well as to move. Since all these tests were performed on fledging  
390 day, we can safely assume that no fledgling could have had the opportunity to observe a  
391 mobbing scene before the tests. Our results therefore indicate that fledglings do not need to  
392 observe mobbing events to respond to mobbing calls, suggesting that conspecific mobbing  
393 calls are inherently perceived as indicating a threat. However, two hypotheses, not mutually  
394 exclusive, could explain the responses to mobbing calls: the response (1) is at least partly  
395 innate, this result has been found in adult great tits in response to allopatric mobbing calls  
396 (Randler 2012, Dutour et al. 2017b), or (2) is due to the impregnation of acoustic signals  
397 heard during the nestling phase. Mobbing calls are composed of frequency modulated  
398 elements, which are involved in vigilance, and D notes involved in foraging flocks or to  
399 recruit partners during the breeding season, to which receivers respond by approaching the  
400 caller (Dutour et al. 2019). In the present study, tests were performed during fledgling when  
401 great tits form family groups and often use D notes to maintain group cohesion (Dutour, pers.  
402 observation). The responses of fledglings could be related to the context (i.e., presence of  
403 family members in the vicinity), or could be due to sensitivity to the D notes. Furthermore,  
404 contrary to fledglings belonging to the control group, those belonging to the experimental  
405 group were more prone to flee than approach the loudspeaker. It could be from the playbacks  
406 which were always presented to fledglings in the same order (i.e., associative learning sound,  
407 then mobbing calls), creating biases that differed between treatments. Indeed, this could be a

408 carry-over from the experimental group hearing the unfamiliar sound, which is threatening to  
409 them, before mobbing calls, while the control group heard a non-threatening sound and then  
410 the mobbing calls. The situation seemed more dangerous for the experimental group if the two  
411 cues had an additive effect. However, this result suggests that reinforcement with mobbing  
412 calls during the nestling phase altered mobbing learning. Such impairment could be either due  
413 to call overexposure, as previously shown in vocalization learning (Tchernichovski et al.  
414 1999; Brainard and Doupe 2013), or because of the absence of a threat associated with the  
415 mobbing call during exposure. An alternative explanation is that maybe fleeing is the adaptive  
416 response to mobbing calls for young juveniles. This should be addressed in further studies. It  
417 would be feasible in relatively resident birds like great tits where dispersal distances are small.  
418 Flee would not be an impairment when expressed by a young, inexperienced, and physically  
419 clumsy individual compared with more experienced, agile and older juveniles (~ 120 days  
420 post fledging) (Kullberg & Lind, 2002) or adults. In that case, being exposed to additional  
421 mobbing via playbacks may have sped up the development of this response.

422

## 423 **Conclusion**

424 This study shows that nestling great tits do not discriminate between two different acoustic  
425 signals but demonstrates that they associate mobbing calls with a novel sound when exiting  
426 the nest cavity as fledglings. Nevertheless, fledglings did not respond with typical mobbing  
427 behaviour (i.e., approach and harass), which likely require experience of parental visual  
428 response (i.e., cultural transmission) (Kullberg and Lind 2002). The present findings raise  
429 questions about how nestlings extract information about the nature of predators and how  
430 finely they can discriminate between different acoustic stimuli.

431

432 **References**

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596

### 597 **Compliance with ethical standards**

598 **Conflict of interest** The authors declare that they have no conflict of interest.

599

600 **Ethics approval** Our work was carried out under permission from the Prefecture du Rhône  
601 (Ref 2015-13), Prefecture de l’Ain (DDPP01-15-230) and with the approval of the ethics  
602 committee at Lyon 1 University, France (permit number: 2017012410184917). All authors are  
603 accredited for performing experiments with living animals (French diploma “Experimentation  
604 animale” first level for researchers). After ringing, all nestlings were readily accepted back by  
605 their parents.

606 **Human and animal rights** This article does not contain any studies with human participants  
607 performed by any of the authors.

608

609 **Table 1**

610 Generalized linear mixed models (GLMM) results for playback (associative learning stimulus  
 611 or mobbing calls) and group (experimental or control) as predictors of variation in fledglings  
 612 response behaviours (scanning, calling, approaching + fleeing). The “\*” character indicates  
 613 the interaction between the explanatory terms. Significant P values are indicated in bold.

Behaviours	Fixed effects	df	$\chi^2$	<i>P</i>
scanning	playback	1	5.8243	<b>0.0158</b>
	group	1	6.1785	<b>0.0129</b>
	playback*group	1	5.4487	<b>0.0196</b>
calling	playback	1	0.9227	0.3368
	group	1	0.0247	0.8752
	playback*group	1	4.8979	<b>0.0269</b>
approaching + fleeing	playback	1	8.9545	<b>0.0028</b>
	group	1	1.6161	0.2036
	playback*group	1	0.8797	0.3483

614

615

616

## FIGURE CAPTIONS

617

618 **Fig. 1** Number of horizontal scans made by experimental and control fledglings during the  
619 playbacks of associative learning stimulus and mobbing calls (mean  $\pm$  SE)

620

621 **Fig. 2** Experimental and control fledglings' probability of calling during playbacks of  
622 associative learning stimulus and mobbing calls

623

624 **Fig. 3** Response of experimental and control fledglings to playbacks of associative learning  
625 stimulus (white) and mobbing calls (grey)

626