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HAL Authorization

1 **The impact of high temperatures on bird responses to alarm calls**

2

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17

18

19 **Abstract**

20 Given the current pace of climate change, high temperature events will become increasingly
21 frequent in many parts of the world. Predicting how high temperatures will impact the
22 behavior of songbirds - highly sensitive to temperature change due to their tendency to have
23 small size, high metabolic rate and diurnal habits - is therefore crucial and urgent. However,
24 the behavioral impacts of high temperatures on acoustic communication in birds have rarely
25 been studied. Responsiveness to antipredator signals is an important behavior to consider
26 because failure to detect such signals could be lethal. We investigated whether high
27 temperatures affect the behavioral responses of great tits (*Parus major*) to conspecific
28 mobbing calls. We found that the emission of mobbing calls by great tits was affected by the
29 current ambient temperature. Further, we found a significant lag effect of temperature on the
30 approach of great tits to the speaker during the mobbing test. The results suggest that at high
31 temperatures, great tits change their tactic from active defense to less active response. At
32 higher temperatures, great tits produce fewer mobbing vocalizations and invest less time in
33 response to mobbing playback. High temperatures can thus induce behavioral shifts in great
34 tits. In the current context of increasing average temperatures, such effect of temperature on
35 response to vital indicators such as antipredator signals could impact survival when inducing
36 greater risk of depredation.

37 **Keywords** Acoustic communication, climate change, great tit, heat stress, mobbing calls

38 **Significance statement**

39 Anthropogenic climate change is causing heatwaves to increase in number and intensity. High
40 temperatures can reduce the ability of birds to respond to vocalizations. Here, we test if high
41 temperatures affect the ability of great tits (*Parus major*) to respond to conspecific mobbing
42 calls - these calls generally serve to mob a predator and to recruit conspecifics and
43 heterospecifics to join the caller. At higher temperatures, great tits produce fewer mobbing
44 vocalizations and approach the loudspeaker broadcasting mobbing calls less often.

45

46 **Introduction**

47

48 The current pace of climate change is more rapid than has been experienced for the past 65
49 million years (Diffenbaugh and Field 2013; Kemp et al. 2015). Since climate is a major
50 determinant of the natural distribution of species, recent poleward shifts in distribution have
51 already been detected for a number of species from a diverse range of taxa in response to
52 climate change (e.g. Walther et al. 2002; Parmesan and Yohe 2003; Hickling et al. 2006;
53 Pearce-Higgins et al. 2014; Platts et al. 2019). Such rapid changes in temperatures can affect
54 survival or reproduction of organisms and pose a serious threat to the persistence of species,
55 particularly for species that can neither disperse nor adapt fast enough (Bale et al. 2002;
56 Parmesan 2006; Berg et al. 2010; Bellard et al. 2012). In particular, high temperatures can
57 have both lethal and sub-lethal effects on wildlife, resulting in mass mortality in extreme
58 cases (Conradie et al. 2019; McKechnie et al. 2012).

59 Songbird species, due to their small size, high metabolic rate and primarily diurnal
60 habits, can be highly sensitive to changes in temperature (McKechnie and Wolf 2010; du
61 Plessis et al. 2012; Bourne et al. 2020a; Bourne et al. 2020b). To date, most studies have
62 examined the effects of temperature on physiological changes (Dubois et al. 2016; Xie et al.
63 2017), but it can also induce behavioural changes in foraging (du Plessis et al. 2012; Edwards
64 et al. 2015), cognitive performance (Soravia et al. 2021; Blackburn et al. 2022), and acoustic
65 communication (Garson and Hunter 1979; Luther and Danner 2016; Coomes et al. 2019a;
66 Coomes and Derryberry 2021). Recent research found that high temperatures reduce the
67 ability of birds to discriminate between conspecific and heterospecific songs (Coomes et al.
68 2019a), but little is known about the effect of heat on responsiveness to other types of
69 vocalizations. Understanding the effect of temperature on responsiveness to vocal information
70 is important, since vocal signals are a primary form of communication for many bird species

71 (Bradbury and Vehrencamp 1998). Among different contexts of communication,
72 responsiveness to alarm calls is an important behavior to consider because alarm calls are
73 anti-predator signals that contain critical information for avoiding predation (Templeton et al.
74 2005; Magrath et al. 2015). The failure to discriminate the information content of these calls
75 at high temperatures could thus lead to reduced survival.

76 Alarm calls are often classified as flee alarm calls, which are associated with the caller
77 escaping while motivating other individuals to freeze or flee, or mobbing calls, which are
78 associated with the caller approaching and vocalizing or displaying toward the predator while
79 recruiting others to join it (Curio 1978; Magrath et al. 2015). The principal benefit of mobbing
80 is to induce the predator to leave the area (Curio et al. 1978; Pettifor 1990). Thus, mobbing
81 may reduce the immediate predation risk for the mobbers (Pavey and Smyth 1998) and may
82 limit the future risk of attacks (Flasskamp 1994). Although no information is currently
83 available on the energetic costs of mobbing (reviewed in Carlson and Griesser 2022), this
84 behavior may be energetically expensive because it comprises repeated locomotion,
85 movements of multiple body parts simultaneously (e.g. head bobbing, tail flagging) and
86 vocalizations (Smith and Graves 1978; Crofoot 2012). During hot days, birds may be
87 expected to mob less because recent evidence suggests that, similar to humans, animals can
88 experience cognitive decline during heat stress (Coomes and Derryberry 2021; Soravia et al.
89 2021; Blackburn et al. 2022,). This could lead to a lower ability to perceive and respond to
90 stimuli in the surrounding environment, such as cues of predator presence. During heat stress,
91 individuals also have to trade-off the physiological need to offset heat against their investment
92 in other behaviors (Cunningham et al. 2021), and hence may be less likely to invest in
93 particular behaviors such as mobbing.

94 In this study, we investigated whether high temperatures affect the ability of great tits
95 (*Parus major*) to respond to conspecific mobbing calls (Fig. 1a). Great tits are known to mob

96 a range of predators (Lind et al. 2005; Dutour et al. 2016; Kalb and Randler 2019), and to
97 respond to conspecific and heterospecific mobbing calls (Randler and Vollmer 2013; Dutour
98 et al. 2019). We predicted that great tit responses would be lower during hot days,
99 approaching the speaker less in terms of distance when hearing mobbing calls, and emitting
100 fewer mobbing calls. Previous studies have suggested that temperature affects the frequency
101 of avian song both via the immediate effects of current temperature (e.g. Gottlander 1987) or
102 by carry-over effects of prolonged high temperature events (time lag effect, e.g. Garson and
103 Hunter 1979). Thus, both temperature states are important considerations when studying the
104 potential effect of high temperatures on avian communication. Finally, Strauss et al. (2020)
105 suggested that temperature might have a non-linear effect on singing, with a reduced number
106 of songs under both cold and warm conditions, mainly because of the higher energetic
107 demands leading to a trade-off between foraging and vocalizing. However, Strauss et al.
108 (2020) did not find non-linear patterns in their data, perhaps because the temperature during
109 their behavioral experiments never exceeded 20°C. We therefore expanded on these
110 experiments by investigating the non-linear relationship between temperature and great tit
111 behavior in response to mobbing calls over a larger range of temperatures.

112

113 **Material and methods**

114

115 **General methods**

116

117 This study measured the response to mobbing calls of great tits at air temperatures ranging
118 from 18°C to 36°C. The great tit's thermoneutral zone range is 15–30 °C (Broggi et al. 2005;
119 Mathot et al. 2016). The maximum temperature of 36°C is considered a high temperature in
120 the region where this study was conducted (see <https://www.meteo-sain-bel.fr/>). Data were

121 collected during playback tests conducted on wild great tits inhabiting mixed deciduous-
122 coniferous forests located near Lyon (45.818992°N, 4.517753°E; France). All tests were
123 conducted between 24 June and 4 September 2020, during a typical dry summer period
124 (except two additional control tests conducted in early October; see hereafter). Since the focal
125 birds were unbanded, we kept a minimum distance of at least 200 meters between
126 experimental sites to minimize the chance of testing the same individuals more than once (as
127 in Dutour et al. 2017; Kalb and Randler 2019). As a control, songs of common chaffinch
128 (*Fringilla coelebs*) were played back to great tits (Fig. 1b, Kalb and Randler 2019).
129 Chaffinches are widespread throughout the study area and great tits were assumed to be
130 familiar with chaffinch song. A total of 92 great tit individuals were exposed to audio
131 playback tests (mobbing calls: 60 individuals, control: 32 individuals). The playbacks
132 (mobbing calls or control) were evenly distributed across the study period to avoid a temporal
133 effect on the tests (see Online Resource 1).

134

135 **Call collection and stimuli preparation**

136

137 Mobbing calls used in the study were recorded from great tits responding to mobbing calls of
138 conspecifics (Dutour et al. 2017; Kalb et al. 2019) or were obtained from the Xeno-Canto
139 online database (<http://www.xeno-canto.org/>) with search criteria specifying the type of
140 vocalization as “alarm call” (we reduced our selection to sound files that we could make sure
141 were associated with a mobbing event, and most of these mobbing calls have already been
142 used in previous mobbing studies; e.g. Dutour et al. 2021; Salis et al. 2021), quality “A” (i.e.
143 highest recording quality), and without other bird species audible in the recording. We used
144 mobbing calls of great tits that were composed of combinations of frequency-modulated
145 elements followed by a string of a repeated loud broadband elements (FME-D call; Dutour et

146 al. 2019). From these recording files, 40 unique soundtracks of mobbing calls were built using
147 Avisoft-SASLab software (i.e. with one calling individual per soundtrack). Chaffinch songs
148 were obtained from the Xeno-Canto online database with search criteria specifying the type of
149 vocalization as “song”, quality “A”, and without other bird species in the recording. From
150 these recording files, 32 unique soundtracks of chaffinch songs were compiled (one calling
151 individual per soundtrack). The song of chaffinch consists of two or three trill-like phrases,
152 followed by an end phrase of more complex and dissimilar notes (Nottebohm 1968). On each
153 soundtrack, low frequency noise has been systematically removed (below 1 kHz, Kalb and
154 Randler 2019) and natural calling rates have been used for each species: great tit mobbing
155 calls were repeated at a rate of 26 calls/min (Dutour et al. 2019), and chaffinch songs at a rate
156 of 8 songs/min (rates observed in previous records; unpublished data). On average, the
157 duration of a great tit mobbing call was 0.88 sec and the duration of a chaffinch song was 2.5
158 sec (Fig. 1). Consequently, focal great tits heard 23 sec of great tit mobbing call per minute
159 compared to 20 sec of chaffinch song. Each sound file consisted of one minute of playback
160 and was saved in Waveform audio file format.

161

162 **Playback experiment**

163

164 All playback tests were conducted between 11am and 2pm during days with cloudless sky and
165 without strong wind or rainfall. After finding a great tit, a remotely controlled speaker
166 (Shopinnov 20W, frequency response 100 Hz - 15 kHz) was hung from a tree at 1.5 m from
167 the ground (Suzuki et al. 2016) and ~20 m away from the bird (Dutour et al. 2021). Before the
168 beginning of the test, the baseline behavior of the focal individual was observed during a pre-
169 trial period lasting one minute to ensure that the bird was not showing vigilance or
170 antipredator behaviors. To determine the responses of the focal tit to the different playback

171 treatments (mobbing calls or control), two behaviors were measured: the number of mobbing
172 vocalizations during 1 min of playback (Carlson et al. 2017) and the minimum distance to the
173 speaker using a tape measure after the playback (Kalb et al. 2019). We considered that a
174 closer approach to the loudspeaker and a greater number of mobbing calls reflect a higher
175 mobbing response from the focal bird. All signals were broadcast with the same intensity (~80
176 dB sound pressure level, measured at 1 m from the loudspeaker, which is within the range of
177 natural mobbing calls produced by great tits; Templeton et al. 2016, and within the range of
178 songs produced by chaffinches; Brumm and Ritschard 2011). In order to limit
179 pseudoreplication (Hurlbert 1984; Kroodsma et al. 2001), each control playback was used
180 only once. For the mobbing call playbacks, 20 exemplars were used once, while the other 20
181 were used twice. Immediately after each playback, the time of the playback was recorded, as
182 well as the air temperature (T0). To investigate time lag effects of heat, the mean temperatures
183 observed for the 5, 12, 24 and 48 hours before the test were calculated for each playback test
184 (T5 to T48) from hourly records collected from the nearest weather station (< 6 km from the
185 study area; <https://www.meteo-sain-bel.fr/>; 45.818000°N, 4.588517°E). We calculated T5
186 over the five hours before the test to ensure a mean temperature calculated on diurnal
187 temperatures only for all the tests (T6 would have included nocturnal temperatures in some
188 tests). Humidity levels during the tests were also recorded (these levels were obtained from
189 the local weather station in the same way that temperatures were obtained).

190

191 **Statistical analyses**

192

193 To test whether the mobbing calls generated the expected mobbing response on the behavioral
194 variables tested (B1: the observed number of mobbing vocalizations and B2: the minimum
195 distance to the speaker) we checked first whether responses to the mobbing calls were

196 different to responses to the control. We ran (generalized) mixed models with treatment
197 (mobbing calls or control) as a predictor term for (i) the number of mobbing vocalizations
198 (fitted with a Poisson distribution) and (ii) the minimum distance to the speaker (fitted with a
199 Normal distribution). In both models, the identity of the playbacks (exemplar ID) was
200 systematically added as random effect.

201 Once we had confirmed that the mobbing calls generated the expected mobbing
202 response and the control sounds triggered lower responses than conspecific mobbing calls, we
203 analyzed the impact of temperature on the behavioral responses to mobbing call playbacks
204 using two linear mixed models (M1 associated with B1 the number of mobbing vocalizations;
205 M2 associated with B2 the closest distance to the speaker). In the two models, the identities of
206 the playbacks (exemplar ID) were included as random effects. The time of day the playback
207 test was conducted, and the temperature were included as dependent variables. As
208 temperature scales (T0: Temperature during the test, T5-48: mean temperatures of the 5, 12,
209 24 and 48 hours before the test) were not independent and were highly correlated, a set of 5
210 mixed models were ran for each behavior (B1 and B2), each of them based on a different
211 scale of temperatures introduced in the model as dependent variables. As temperature
212 response curves are typically quadratic, with an intermediate optimum (Johnston and Bennett
213 1996; Uiterwaal and DeLong 2020), a quadratic effect of temperature was systematically
214 included in the models. For each behavior (B1 and B2), a model selection process (AICc
215 ranking; package *bbmle*, Bolker and Team 2017) was conducted on these five models, and an
216 additional null model and a model without temperature effect, to compare model fit and
217 identify the model that explained the most variation in data patterns (i.e. the model
218 incorporating the more relevant temporal scale of temperature). The significance of each
219 explanatory term (temperature, quadratic effect of temperature and time of day) was tested
220 using z tests. Since high humidity can make it more difficult for birds to dissipate heat due to

221 evaporative cooling and may have affected behavior, and date can have an effect on mobbing
222 behavior (Coomes et al. 2019b), the impacts of humidity and date have been controlled
223 through additional models derivated from the final models selected, to avoid over-
224 parametrization of the models (all details available in Online Resources 2 and 3). All statistics
225 were carried out using R v.3.5 software (R Development Core Team 2019). All models were
226 analyzed using the package *glmmTMB* (Brook et al. 2017), and the quality of the model
227 estimates was monitored using Pearson residuals. For all statistical tests, the level of
228 significance was set at $P < 0.05$.

229

230 **Results**

231

232 **Responses to mobbing calls versus songs (control)**

233

234 There was a significant difference in minimum approach to the speaker in relation to playback
235 treatment (mobbing calls – mean distance = 12.58 or control – mean distance = 19.24,
236 generalized linear mixed model: $\chi^2 = 23.394$, $P < 0.001$), with individuals approaching closer
237 to the speaker during the playback of mobbing calls (Fig. 2a). Similarly, focal individuals
238 produced significantly more mobbing vocalizations in response to the mobbing call playback
239 (mean number of vocalizations = 5.30) than the control playback (mean number of
240 vocalizations = 0.21) (generalized linear mixed model using Poisson family: $\chi^2 = 57.271$, $P <$
241 0.001 ; Fig. 2b).

242

243 **Temperature effect on responses to mobbing calls**

244

245 The different temporal scales of temperature tested (from the temperature during the tests to
246 the mean temperature in the 48 hours before the test) showed distinct patterns with the
247 behavioral variables. The number of mobbing vocalizations given in response to playback was
248 best explained by temperature during the test (T0, Table 1), whereas the minimum distance to
249 the speaker reached by focus individuals was best explained by the temperature experienced
250 in the five hours prior to the test (T5) (Table 1). Accordingly, the final models implemented,
251 as a temperature effect, (i) the immediate temperature during the test when considering the
252 number of vocalizations (B1) as a dependent variable, and (ii) the mean temperatures
253 observed for the 5 hours before the test when considering minimum distance to the speaker
254 reached by focal individuals (B2) as a dependent variable.

255 The temperature during playback affected the number of mobbing calls emitted by
256 focal individuals (Table 2; Fig. 3). This effect of the temperature was quadratic ($Y = -38.376$
257 $+ 3.472X - 0.067X^2$), with individuals calling more often during mobbing call playback when
258 the temperature averaged 25.9°C ($\text{Max}\{x\} \in \mathbb{R}(-38.376 + 3.472X - 0.067X^2)$). At both high
259 and low temperatures, immediate current temperature (T0) negatively correlated with the
260 number of mobbing calls given by the focal individual. The time of day at which the
261 playbacks were conducted did not affect calling behavior (Table 2).

262 The temperature during the five hours prior the playback was related to the minimum
263 distance of approach to the speaker during mobbing call playback (Table 2; Fig. 4). This
264 effect of the temperature was quadratic ($Y = 41.033 - 3.233X + 0.083X^2$), with individuals
265 approaching closer to the speaker during mobbing call playback when the mean temperature
266 in the five hours before the playback averaged 19.5°C ($\text{Max}\{x\} \in \mathbb{R}(41.033 - 3.233X + 0.083$
267 $X^2)$). At high temperatures, the mean temperature in the five hours before the playback thus
268 negatively correlated with the approach of individuals. The time of day at which the
269 playbacks were conducted did not affect approach behavior (Table 2).

270

271 **Discussion**

272

273 The approach and emission of mobbing calls by focal great tits were affected by temperatures
274 experienced during or prior to playback. Our results suggested a significant lag effect of
275 temperature on the approach of great tits during mobbing. This result indicates that longer
276 term heat is a greater influence on movement response than immediate heat, perhaps because
277 it may cause a cumulative effect of heat stress (Conradie et al. 2019; Fernandez et al. 2021).

278 The quadratic effect of temperature suggested that the behavioral response of great tits
279 to mobbing calls is the strongest at temperatures of approximately 19.5°C for the approach
280 behavior (typical average temperature in June for the region) and 26°C for calling behavior,
281 suggesting an impact of temperature on the mobbing behavior of great tits. This result
282 contrasts with the study of Strauss et al. (2020), where the minimum approach distance of
283 great tits for territory defense behaviors was not affected by temperature. This could be due to
284 the fact that temperature did not exceed 27°C in their study. Indeed, in our research, the
285 mobbing behavior was particularly inhibited during the playback of mobbing calls at high
286 temperatures (Fig. 3 and Fig. 4), although we cannot determine whether the lower number of
287 calls and approach distance during high temperatures were due to behavioral flexibility in
288 mobbing behavior (for example, a behavioral trade-off between off-setting heat and other
289 behaviors, *sensu* du Plessis et al. 2012), or a temperature-related physiological mechanism
290 limiting their movements. It is possible that excessive heat leads to a generalized drop in
291 motivation to respond and that great tits were less motivated to respond to mobbing calls
292 during high temperatures. There could also be an increase of sound attenuation during signal
293 propagation at high temperature. Indeed, a previous study showed that air temperature affects
294 the active space of acoustic signal (Larom et al. 1997). Nevertheless, while modification of

295 active space on long-range communication is mainly due to temperature inversions and low
296 surface wind, Harris (1966) showed that signal attenuation for frequency range between 2 and
297 5 kHz (corresponding to great tit mobbing calls) is poorly affected by temperature between 15
298 and 30 degrees (0.2 to 1 dB of excess attenuation per 100 m with a 50% humidity rate).
299 Hence, we could dismiss that our observed decrease of mobbing response could be due to the
300 fact that tested birds did not hear our soundtrack emitted at ~20 m from them.

301 High temperatures can have strong physiological effects on wildlife (Stillman 2019),
302 leading to mortality in extreme cases (Welbergen et al. 2008; McKechnie et al. 2012). In this
303 study we investigated the impact of high temperatures in the short-term, with a very short
304 latency time. Average temperatures experienced immediately during the test or during the
305 previous few hours did affect behavior, suggesting short-term impacts of temperature on
306 behavior. Short term impacts could lead to longer term effects on survival and development,
307 as have been observed in other species (Bourne et al. 2020 a and b).

308 High temperature events will become increasingly frequent under future climate
309 scenarios. Predicting how these high temperatures and heatwaves will impact animal behavior
310 is therefore crucial (Cunningham et al 2021; Soravia et al 2021). Our study suggests high
311 temperatures are likely to induce behavioral shifts in response to antipredator signals in great
312 tits. The predicted increase in summer heatwave number and intensity may alter mobbing
313 behavior perpetuation in this species in the future, and hence may impact survival rates in
314 birds because this behavior is known to repel predators in great tits (personal obs. MD) and
315 other species (Flasskamp 1994; Pavey and Smyth 1998). However, it remains unknown what
316 impact temperature will have on the behavior of great tit predators.

317 Mobbing calls are anti-predator signals that contain critical information for avoiding
318 predation (Templeton et al. 2005; Magrath et al. 2015). The failure to detect and interpret the
319 risk-based information encoded in these calls at high temperatures could thus lead to reduced

320 survival rates, inducing for instance a decrease in the flight initiation distance with increasing
321 temperatures (Díaz et al. 2021). However, our results indicate that there is no evidence for
322 complete failure to detect and interpret information encoded in mobbing calls. Indeed, such
323 failure would have induced a complete lack of behavioral response from the targeted great
324 tits, which is not what is observed in the present study. Our results suggest that tested birds
325 changed their investment in approaching behavior, suggesting that high temperatures limit the
326 movement of individuals (i.e. their approach when hearing alarm calls), as well as the calling
327 behavior itself. There is thus a temperature-related effect on the ability of great tits to emit
328 mobbing calls and on investment in approaching callers producing mobbing calls. This result
329 supports the increasing body of research indicating a lower investment in behaviors at higher
330 temperature. For example, temperate passerine birds sing earlier with rising temperatures in
331 spring (Bruni et al. 2014), and in pied babblers (*Turdoides bicolor*) parents provision young
332 less at high temperatures (Wiley and Ridley 2016). Our results are, to our knowledge, the first
333 to provide experimental support that high temperatures affect the behavioral response to
334 mobbing calls in a wild bird population. In the current context of rapid climate change, we
335 argue that there is an urgent need to quantify the costs of heat exposure in natural populations,
336 and to improve our understanding of the contexts in which animals change their behavior in
337 response to climate conditions.

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342

343 **Declarations**

344

345

346 **Funding** No funding.

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

348

349 **Ethics approval** This study included no animal keeping; birds were observed in their natural
350 habitat. All tested great tits returned to normal activity relatively quickly following playbacks,
351 so we were confident that they were not unduly stressful. All applicable international,
352 national, and/or institutional guidelines for the care and use of animals were followed.

353

354

355 **Consent to participate & Consent for publication:** Not applicable

356

357 **Availability of data and material:** The datasets generated are available on the Zenodo
358 repository; <https://doi.org/10.5281/zenodo.5656901>.

359

360

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531 **Table 1.** Δ AICc ranking based on the two set of models investigating behavioral response to
532 playback of mobbing calls: M1 = number of observed vocalizations by the focal bird during
533 playback and M2 = minimum distance to the speaker by the focal bird during playback, and
534 comparing the null model and a model without temperature effect with models incorporating
535 the effect of temperatures at several temporal scales (T0: temperature observed during the
536 playback to T48: mean of the 48 hours before the playback) (N = 60). A null value indicates
537 the model ranked as the best model; models in which the difference in AICc relative to
538 AICcmin is < 2 can be considered to have substantial support (Burnham et al. 2011).

Model Name	Delta AICc for number of mobbing vocalizations	Delta AICc for min. distance to the speaker
Null model	53.2	9.8
No temperature	2.4	4.2
T0	0	6.2
T5	3.4	0
T12	2.2	4.1
T24	2.6	5.2
T48	2.3	6.1

539
540 **Table 2.** Test results and parameter estimates of the two models M1 and M2. M1 = terms
541 influencing the number of mobbing vocalizations (R-squared = 0.105), M2 = terms
542 influencing the minimum distance to the speaker (R-squared = 0.250). Temperature (T0 =
543 temperature during the test, T5 = mean temperature during the 5 hours before the test), and
544 hour when the test was performed have been used as independent variables. Signif codes: * =
545 < 0.05 .

M1: number of mobbing vocalizations

Variable	Estimate	Std. Error	z value	P. value
Intercept	-38.376	19.046	-2.015	0.044*
T0	3.472	1.441	2.409	0.016*
T0 Quad. effect	-0.067	0.027	-2.492	0.013*
Time of day	-0.033	0.626	-0.053	0.957

M2: minimum distance to the speaker

Variable	Estimate	Std. Error	z value	P. value
Intercept	41.033	16.883	2.430	0.015 *
T5	-3.233	1.545	-2.093	0.036 *
T5 Quad. effect	0.083	0.035	2.406	0.016 *
Time of day	0.957	1.062	0.901	0.367

546

547 The results were overall similar when the date (Online Resource 2) or humidity (Online
548 Resource 3) were included in the models, although the statistical power required to detect
549 significant differences was limited due to the number of factors incorporated. The humidity
550 seemed to induce an additional stress as it negatively affected both the number of
551 vocalizations and the individual approach to the speaker, but this negative effect is stronger
552 under low temperatures (see Online Resource 3 for details).

553

554

FIGURE CAPTIONS

555 **Fig. 1.** Spectrogram of typical (a) mobbing call uttered by great tits, and (b) song uttered by
556 chaffinches. The mobbing call of great tit is made of the combination of introductory note
557 followed by broadband frequency notes (D notes). The song of chaffinch consists of two or
558 three trill-like phrases, followed by an end phrase of more complex and dissimilar notes

559

560 **Fig. 2** Great tit response to mobbing calls and control treatments (N = 92 individuals) in terms
561 of (a) minimum distance (in meters) to the loudspeaker and (b) Number of mobbing
562 vocalizations produced during 1 min of playback. The boxes range from Q1 (the first quartile)
563 to Q3 (the third quartile) of the distribution and the range represents the IQR (interquartile
564 range). The median is indicated by a line across the box. The “whiskers” on box plots extend
565 from Q1 and Q3 to the most extreme data points. Outliers are represented as white dots. The
566 mean and standard error for each treatment are shown in red. Different letters (a and b)
567 indicate significant differences

568

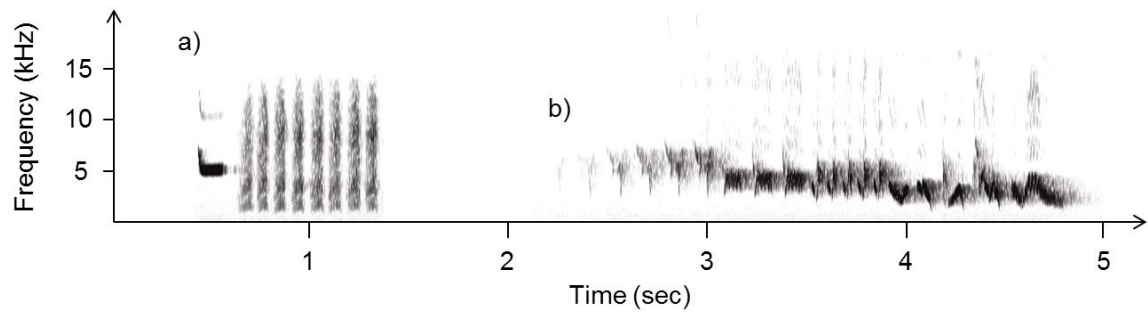
569 **Fig. 3** Relationship between the immediate temperature during the playback test and the
570 number of mobbing vocalizations produced by the focal great tit during the playback (N =
571 60). The confidence band (shaded – 95% CI) and the regression line (bold) have been
572 calculated based on the values predicted by the model

573

574 **Fig. 4** Relationship between the mean temperature during the five hours before the playback
575 test and the minimum distance between the focal great tit and the speaker reached during the
576 playback test (N = 60). The confidence band (shaded – 95% CI) and the regression line (bold)
577 have been calculated based on the values predicted by the model

578

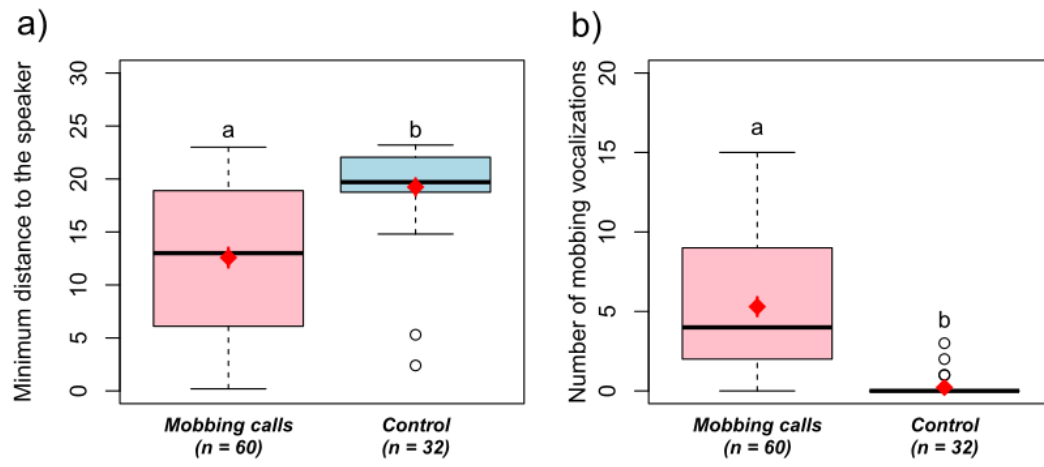
579 **Fig. 1.**



580

581

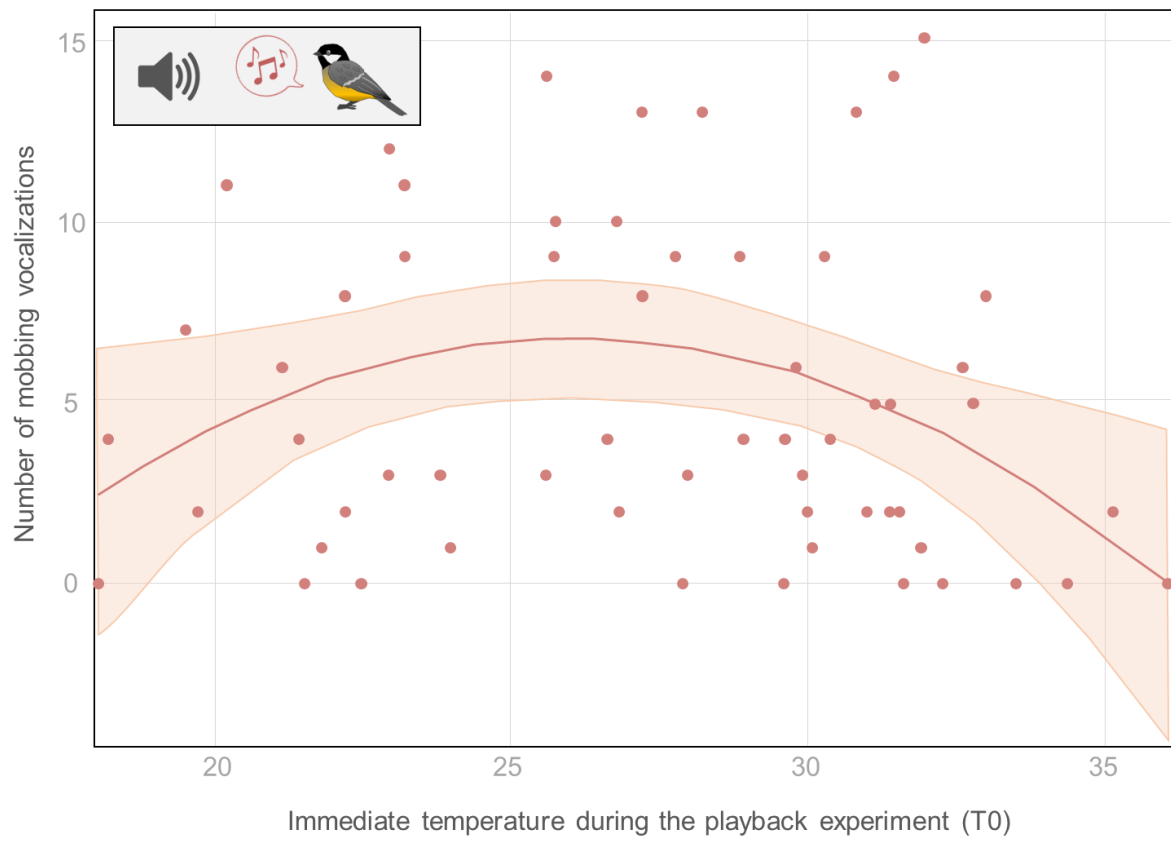
582 **Fig. 2.**



583

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585 **Fig. 3.**



586

587

