

**A COMPARATIVE STUDY OF HOW BRITISH TITS ENCODE PREDATOR THREAT IN THEIR
MOBBING CALLS**

Nora V Carlson¹, Susan D Healy¹, Christopher N Templeton^{1,2}

¹ School of Biology, University of St Andrews, Scotland, UK

² Department of Biology, Pacific University, Forest Grove, OR, USA

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*Correspondence: Nora V Carlson

School of Biology

University of St Andrews

Harold Mitchell Building

St Andrews, Fife

KY16 9TH, Scotland, UK

+44(0)7541-967008

nc54@st-andrews.ac.uk

Co-correspondence: Christopher N Templeton,

Department of Biology,

Pacific University,

2043 College Way

Forest Grove, Oregon, 97116, USA

+1 503-352-3149

templeton@pacificu.edu

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3
4 Many species use anti-predator vocalizations to signal information about potential
5 predators, including the level of threat posed by a particular predator. It is not clear,
6 however, why only some prey species do this. Because they use multiple mechanisms to
7 encode threat specific information about predators, North American Paridae species have
8 been a particularly useful model for studying anti-predatory signals. Paridae as a group
9 are also useful for examining phylogenetic conservation of vocal signals because all of
10 these species (at least those studied previously) employ similar ways of encoding
11 information about predatory threat. To test whether the ways in which predator threat
12 information is encoded (here measured by a bird's vocal output) are conserved across a
13 family with similar vocalizations, we used taxidermy mounts to simulate low and high
14 threat predators to induce mobbing in six species across five genera of British Paridae.
15 We found that, like North American species, British tits all increased their call rate in
16 response to predators compared with non-threatening control mounts, but they all varied
17 in the number and types of additional ways they encoded this information. Some species
18 (blue & willow tits) used all four ways to differentiate between different threat predators,
19 while others used only two (crested tits), one (great & coal tits) or none at all (willow
20 tits). The variation in the way each species encoded predator threat information in their
21 calls was not explained by phylogenetic relatedness or by variation in life history. To
22 better understand patterns of information encoding across related species, we suggest that
23 playback experiments to determine how encoded information is used by conspecifics and

24 heterospecifics might provide insights about why some species encode information about
25 predator threat in multiple ways.

26

27 **KEY WORDS:** acoustic communication, anti-predator behaviour, information encoding,
28 mobbing, Paridae, predator-prey dynamics

1 A COMPARATIVE STUDY OF HOW BRITISH TITS ENCODE PREDATOR THREAT IN THEIR
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3

4 Many species, across a wide range of taxa, use vocalizations to warn about and
5 defend against predators (Gill & Bierema, 2013; Klump & Shalter, 1984;
6 Slobodchikoff, 2010; Townsend & Manser, 2013). These anti-predator vocalizations
7 can provide information about a predator's size, speed, distance, type/category, and
8 even behaviour (Evans, Macedonia, & Marler, 1993; Gill & Bierema, 2013; Griesser,
9 2008; Marler, 1955; Murphy, Lea, & Zuberbühler, 2013; Placer & Slobodchikoff,
10 2000; 2004).

11

12 Species vary substantially in the ways they encode information to communicate about
13 predators. Meerkats, *Suricata suricatta*, for example, increase call rate along with a
14 number of fine-scale acoustic parameters to communicate an increase in the danger a
15 predator poses (Manser, 2001), while yellow warblers *Setophaga petechia* use the
16 likelihood of producing a particular call type (seet) to signal the presence of a nest
17 predator (Gill & Sealy, 2004). Other species use strategies that range from employing
18 a single way of encoding information to combining multiple ways of encoding
19 information. Furthermore, some strategies may be driven entirely by the signaller's
20 internal state while others reference external stimuli (Gill & Bierema, 2013; Magrath,
21 Haff, Fallow, & Radford, 2014). American crows *Corvus brachyrhynchos*, for
22 example, use longer calls and higher call rate to signal increased danger (Yorzinski &
23 Vehrencamp, 2009), while vervet monkeys *Chlorocebus pygerythrus* indicate not
24 only predator type (leopard, eagle, and snake) but degree of danger through the
25 propensity to use different call types (predator types) and an increase in the number of

26 elements (degree of danger; Seyfarth, Cheney, & Marler, 1980). It is not clear why
27 this variability across different taxa and species in encoding mechanisms exists. But,
28 as many closely related species share similar vocalizations and may therefore share
29 similar ways of encoding predator threat information, it might be that phylogenetic
30 relationships provide part of the explanation (Hailman, 1989; Latimer, 1977; Randler,
31 2012)

32

33 The North American Paridae have been widely used to study the ways in which
34 individuals encode predator threat particularly in their mobbing calls. Mobbing calls
35 generally serve to harass the predator and/or to recruit conspecifics and
36 heterospecifics for that harassment (Curio, 1978). In their mobbing calls, North
37 American Paridae encode not only the presence or absence of a predator but they also
38 differentiate between predators of different threat levels. These species indicate the
39 presence of a higher threat predator by increases in: 1) call rate (black-capped
40 chickadees *Poecile atricapillus*, Carolina chickadees *Poecile carolinensis*, mountain
41 chickadees *Poecile gambeli*, and tufted titmice *Baeolophus bicolor*; Baker & Becker,
42 2002; Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Billings,
43 Greene, & La Lucia Jensen, 2015; Hetrick & Sieving, 2011; Templeton, Greene, &
44 Davis, 2005); 2) the number of elements in their calls (black-capped chickadees,
45 Carolina chickadees, mountain chickadees, and tufted titmice; (Baker & Becker,
46 2002; Bartmess-LeVasseur et al., 2010; Billings et al., 2015; Courter & Ritchison,
47 2010; Hetrick & Sieving, 2011; Sieving, Hetrick, & Avery, 2010; Soard & Ritchison,
48 2009; Templeton et al., 2005); 3) the propensity to produce particular call types
49 (tufted titmice and black-capped chickadees; Clemmons & Lambrechts, 1992; Sieving
50 et al., 2010); and 4) the proportion of one call type used across mobbing events

51 (black-capped chickadees; Baker & Becker, 2002). Of the North American species,
52 black-capped chickadees have been shown to use all four of these ways of encoding
53 information in response to predators of different levels of threat. While the remaining
54 species have not been tested for all of the four ways, the available evidence suggests
55 that they likely behave in the same fashion as black-capped chickadees and there is no
56 indication that any of these species do not use any of the four ways of encoding
57 information. The lack of evidence to the contrary combined with data from the out-
58 group ,Japanese great tits, *Parus minor*, which share the four ways with black-capped
59 chickadees, has led to the assumption that all Paridae species encode predator threat
60 information in their mobbing calls using this particular suite of changes to their
61 vocalizations (Hetrick & Sieving, 2011; Langham, Contreas & Sieving, 2006; Suzuki,
62 2014; Wilson & Mennill, 2011).

63

64 As only a small number of the Paridae have actually been tested and most of the
65 species tested are from the same genus (*Poecile*; Johansson et al., 2013), providing a
66 general explanation for the ways in which animals encode predator threat is not
67 straightforward. To test experimentally the degree to which phylogenetic
68 conservatism might explain the distribution of encoding mechanisms within families,
69 we induced mobbing events in flocks of tits found in the UK (six species across five
70 genera) by simulating predator encounters using robotic taxidermy mounts of
71 predators representing different threat levels. We then examined whether each of
72 these species 1) differentiated between predators and non-predators in their mobbing
73 calls, 2) differentiated between high and low threat predators, and 3) used the same
74 four ways of encoding predator threat as the previously-tested Parid species. Here we
75 use the term ‘encode’ simply to denote that the calls produced in response to different

76 predators are statistically different and that they therefore have the potential to
77 provide reliable information to receivers. Without playback experiments we cannot
78 confirm that receivers decode and use this information.

79

80 We used these data to test whether phylogeny explains the number and ways of
81 encoding information used by a given species, making the following predictions: 1) If
82 the ways of encoding information are conserved within the Paridae, UK tit species
83 should use all four ways of encoding information to differentiate predators from non-
84 threats, and differentiate between predators of different threat levels. 2) If, however,
85 any of these species vary in the way they encode information about predators, the
86 pattern of relatedness should at least roughly match these differences such that those
87 species that are more closely related (e.g. marsh and willow tits in the genus *Poecile*)
88 to be more similar in the ways in which they encode information than those that are
89 more distantly related (e.g. marsh tits in the genus *Poecile* and blue tits in the genus
90 *Cyanistes*).

91

92 **METHODS**

93

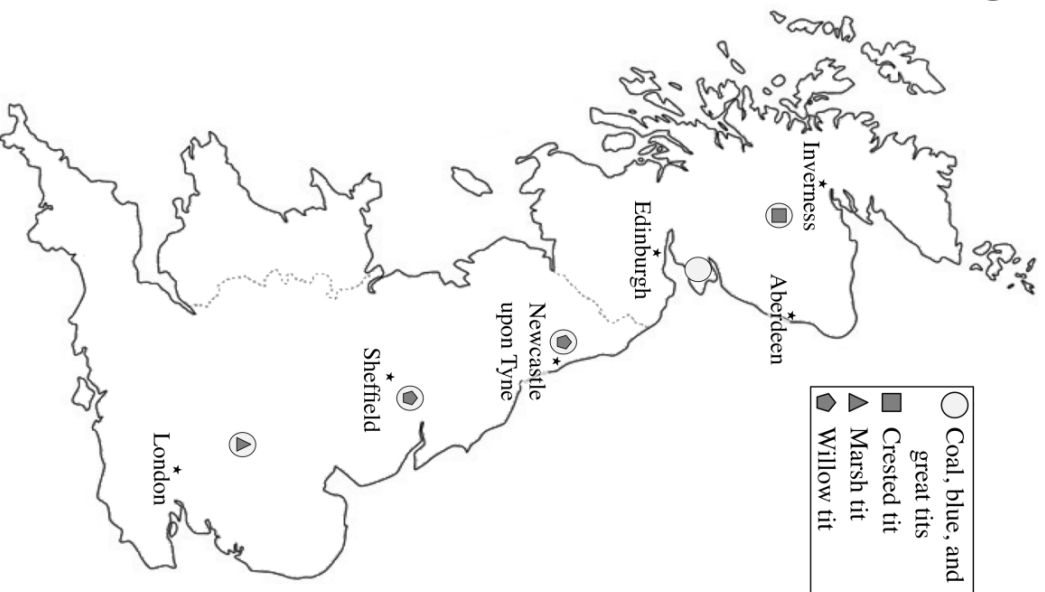
94 *Study sites*

95

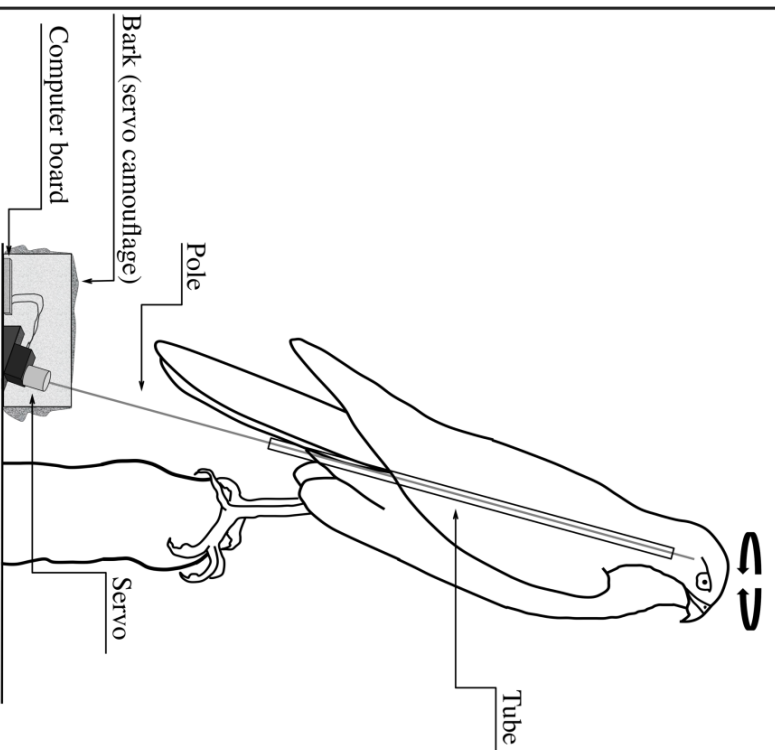
96 We conducted experiments from January to March 2014 and 2015 in four general
97 geographical regions in the UK (Figure 1a), each of which had feeders at a number of
98 different sites. Blue tits, *Cyanistes caeruleus*, great tits, *Parus major*, and coal tits,
99 *Parus ater*, are found across the UK; crested tits, *Lophophanes cristatus*, occur
100 only in northern Scotland; marsh, *Poecile palustris*, and willow, *Poecile montanus*,

101 tits occur only in the southern regions of the UK. To test blue, great, and coal tits we
102 used feeders in and around St Andrews, Fife (latitude, longitude; 56.331247, -
103 2.838451; n = 23 feeder locations) from January-March 2014. To test crested tits
104 along with blue, great and coal tits we used feeders in the north-western Cairngorm
105 mountains in Scotland (57.191208, -3.779156; n = 15 feeder locations) from January-
106 March 2015. To test willow tits along with blue, great, and coal tits, we used feeders
107 in Doncaster (53.519235, -1.131355) and Newcastle upon Tyne (55.053305, -
108 1.644546) from January-March 2015 (n = 7 feeder locations). To test marsh tits along
109 with blue, great, and coal tits we used feeders in Monk's Wood near Cambridge
110 (52.401114, -0.238468; n = 9 feeder locations) from January-March 2015. Feeders
111 were filled with black-oil sunflower seeds and peanuts and placed in either
112 parks/forests or private gardens. To ensure that birds had enough time to locate and
113 become accustomed to using the feeders, all of the bird feeders were put up a
114 minimum of two weeks before we began the experiment.
115

a)



b)



- 117 Figure 1. a) Feeder locations in the four regions across the UK. Blue, great, and coal tits were found in all regions as shown by the light grey
118 circles. The additional presence of crested (square), marsh (triangle), or willow tits (pentagons) is indicated by the corresponding dark grey
119 symbol inside the circle. b) Schematic of the robo-raptors used for these experiments. A hidden servo and computer board were used to control
120 the head of each taxidermy mount to produce realistic head movements for a perched raptor.

121

122 *Stimuli*

123

124 To test whether and how the tit species encode information about predator threat in
125 their mobbing calls we simulated encounters with three common British species,
126 which vary dramatically in the level of threat they pose to adult tits: 1) sparrowhawks,
127 *Accipiter nisus*, are high-threat predators for tits and prey almost exclusively on small
128 to medium sized birds including tit species (Curio, Klump, & Regelmann, 1983;
129 Millon, Nielsen, Bretagnolle, & Møller, 2009; Petty, Patterson, Anderson, Little, &
130 Davison, 1995); 2) common buzzards, *Buteo buteo*, are low-threat predators for tits
131 as, although the majority of their diet (~ 73%) made up of mammals and larger birds
132 such as pigeons, buzzards do occasionally eat small passerines (~ 16% of their diet;
133 Graham, Redpath, & Thirgood, 1995), including tit species (Swann & Etheridge,
134 2009); 3) grey partridges, *Pedrix pedrix*, were used as a control to ensure that the tit
135 species responded to the specific features of the predators and not simply to the
136 presence of a moving taxidermy bird. This species is found across the UK, is similar
137 in size to a sparrowhawk, but as it does not eat birds it poses no threat to tit species
138 (Šálek, Marhoul, Pintř, Kopecký, & Slabý, 2004).

139

140 We used custom-made robotic taxidermy mounts of each species (Carlson et al.
141 submitted; Figure 1b) to elicit mobbing responses by the tits. We used two different
142 mounts of each species to reduce pseudoreplication. Our mounts included: one male
143 juvenile and one female adult sparrowhawk, two adult female buzzards, and two adult
144 male grey partridges. All mounts were perched on a tree branch or log, and their
145 heads rotated to mimic natural perched head movements. An Arduino computer board
146 (Arduino Duemilanove from Arduino LLC, <https://www.arduino.cc>) controlled a

147 servo motor, which was programmed with 15 different commands that controlled the
148 head movement of the mounts to create a series of movements that mimicked natural
149 behaviour. These 15 commands were the same for all three types of stimulus and the
150 head moved for the entire time the mount was exposed. The total movement of the
151 head ranged $\sim 100^\circ$ and as the chest of the mounts faced the feeder, the head faced in
152 the direction of the bird feeder and the nearby surrounding cover all of the time
153 (Figure 1b; Book & Freeberg, 2015).

154

155 *Predator presentations*

156

157 At each study site we presented birds with all three treatments (sparrowhawk,
158 buzzard, partridge) in a randomized order; the mount exemplar for each presentation
159 was selected randomly. We conducted experiments from one hour after dawn to one
160 hour before dusk to allow the birds time to recover from the presentations and allow
161 sufficient time to forage in preparation for overnight, as these presentations were all
162 carried out during the winter (Jan-March). We separated all buzzard and sparrowhawk
163 presentations and most control and predator presentations by a minimum of 8 hours at
164 each feeder location. Due to time constraints at some study sites, on occasion if we
165 presented the control (partridge) first and the birds continued to feed normally, we
166 waited for 15 minutes and then presented a predator trial (sparrowhawk $n = 6$,
167 buzzard $n = 5$ trials). We excluded from the analyses those trials in which birds
168 obviously responded to something other than the stimulus (e.g. when we observed a
169 sparrowhawk flying overhead or initial behaviour suggesting birds had encountered a
170 predator just before we arrived; $n = 7$). At some locations the focal species were not

171 present for one or more trials and thus we collected data for fewer than three
172 treatments (n = 9 sites).

173

174 We began presentations once we had confirmed the presence of the focal species
175 (acoustically or visually) near the feeder. We placed the taxidermy mount on a 1.5 m
176 pole approximately 2 m from the bird feeder. Because head orientation is important in
177 predator threat assessment (Book & Freeberg, 2015), we ensured that the mount faced
178 the bird feeder in all trials. We then retreated to a minimum distance of 4 m away and
179 hid behind cover. A trial began when an individual of the focal species either: 1) came
180 within 5 m of the mount; 2) came within 7 m of the mount with its body and head
181 oriented towards the mount for 20 seconds more than once in 2 minutes; or 3) began
182 mobbing the mount, by producing mobbing calls, rapidly changing perches, and wing
183 flicking while oriented towards the mount, or flying at the mount in an aggressive
184 fashion. Starting at this time point, we recorded when birds began to mob, and all
185 vocalizations that were produced for 5 minutes before removing the mount. Distances
186 were not physically marked in the field but, prior to beginning the manipulations, the
187 researchers were trained to determine by eye when birds were within 3, 5, and 7
188 meters of the mount. We recorded all trials with a Sennheiser ME 66 super-cardioid
189 microphone (Sennheiser Electronics, Hanover, Germany) and a Marantz PMD660
190 solid-state sound recorder (Marantz America, LLC., Mahwah, N.J., USA) with a bit-
191 depth of 24 bits and a sampling rate of 48 kHz.

192

193 At each simulated predator encounter we recorded the total number of individuals of
194 each species present and kept track of which species met any of the above mobbing
195 criteria, and therefore was considered to participate in the mobbing event. Due to

196 environmental conditions and the variation in flock size (mean \pm standard error: $7.47 \pm$
197 0.40 individuals/flock) and composition (number of species: 2.86 ± 0.09
198 species/flock), sample sizes varied across species: blue: $n = 47$ locations (control $n =$
199 41 , buzzard $n = 42$, sparrowhawk $n = 43$), great: $n = 43$ locations (control $n = 35$,
200 buzzard $n = 41$, sparrowhawk $n = 42$), coal: $n = 41$ locations (control $n = 34$, buzzard
201 $n = 35$, sparrowhawk $n = 36$), crested: $n = 14$ locations (control $n = 14$, buzzard $n =$
202 14 , sparrowhawk $n = 13$), marsh: $n = 9$ locations (control $n = 9$, buzzard $n = 9$,
203 sparrowhawk $n = 9$), and willow: $n = 7$ locations (control $n = 7$, buzzard $n = 6$,
204 sparrowhawk $n = 7$), as did the average number of conspecifics present during a trial
205 (mean \pm standard error): blue: 3.00 ± 0.21 , great: 2.37 ± 0.14 , coal: 3.51 ± 0.38 ,
206 crested: 1.73 ± 0.11 , marsh: 1.59 ± 0.10 , and willow: 1.52 ± 0.11 .

207

208 *Ethical note*

209

210 All of this work was approved by the University of St Andrews School of Biology
211 Ethics Committee (01112013) and Scottish National Heritage, and followed
212 ASAB/ABS guidelines for treatment of animals in research. As we conducted
213 predator presentations during the winter months, we restricted our simulated predator
214 encounters to the period from one hour after sunrise to one hour before sundown so
215 that birds could prepare for, and recover from, the hours of darkness. As predator
216 encounters are stressful for the animals involved, we limited predator presentations to
217 5 minutes once individuals began to respond. We then removed the stimulus and left
218 the area as quickly as possible to allow the individuals to recover and return to
219 feeding.

220

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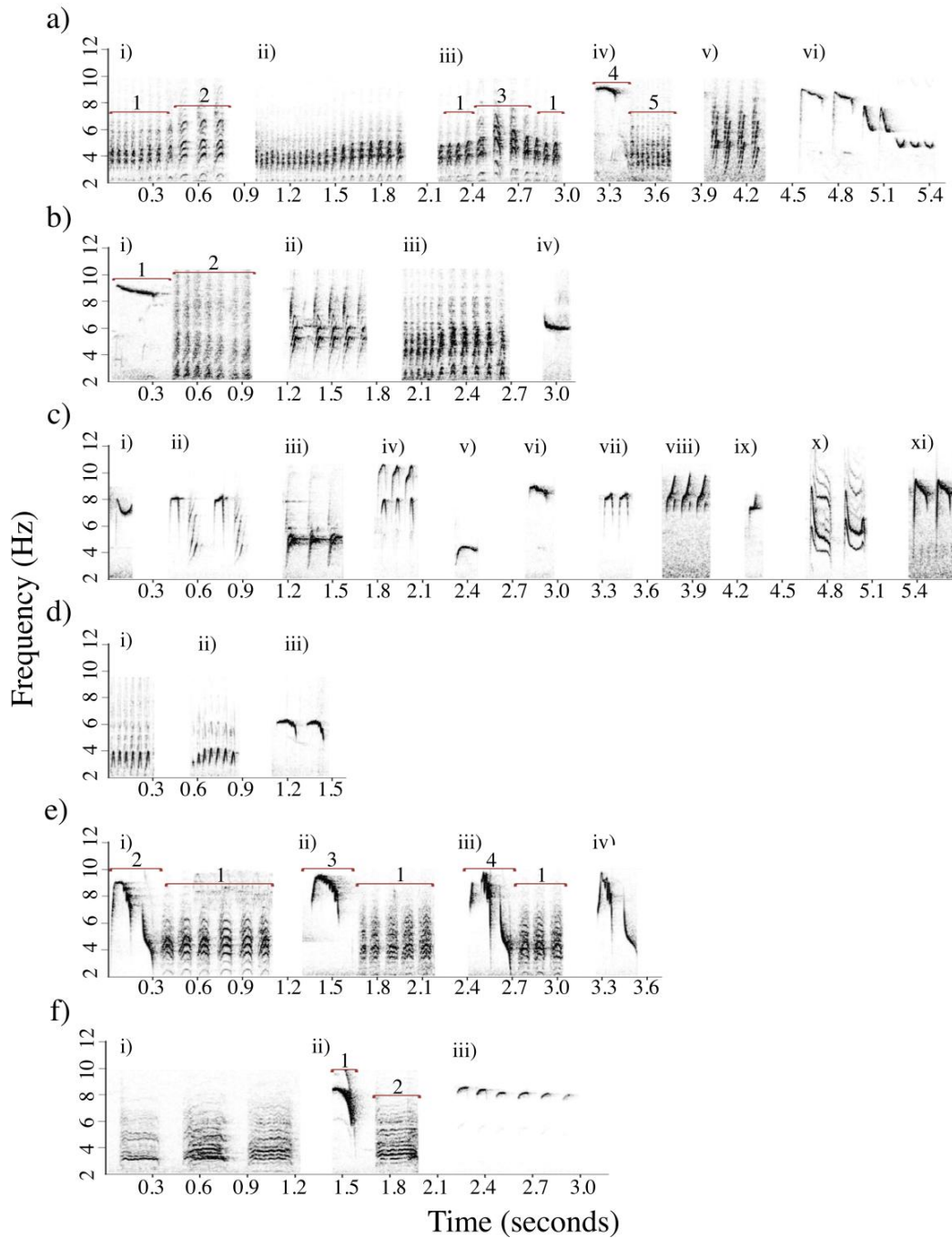
222 *Acoustic analysis*

223

224 For all acoustic analyses, we used Raven Pro v 1.5 software (Bioacoustics Research
225 Program, 2014) with a fast Fourier transform (FFT) size of 1050 samples, a Hann
226 window function, and a spectrogram frequency grid resolution of 23.04 Hz. We
227 analyzed all calls produced within three minutes of the onset of mobbing by manually
228 selecting all calls and visually categorizing them by call type and call features (Table
229 1, Figure 2). All call types were clearly distinguished from one another as they were
230 classed into different types based on clearly visible structural differences.
231 Additionally, each species has a unique repertoire of calls making species
232 identification relatively straightforward even when multiple species were calling
233 during a trial (Table 1, Figure 2). To confirm the reliability of the categorization of
234 calls by NC, we asked six people to categorize the calls. Nearly all of the
235 classifications (89%) had high repeatability across individuals (inter-class correlation
236 (ICC) values > 0.80 ; Nakagawa & Schielzeth, 2010). The four calls that received
237 scores below 0.80 all included subtle variation, and so were re-scored by an individual
238 familiar with Paridae vocalizations. Repeated scores conducted by this trained
239 individual ranged from 0.77 – 1.0, with only one call type (short calls) receiving an
240 ICC score below 0.80. In instances in which multiple calls overlapped it could have
241 been more difficult to determine the number or type of elements, but this occurred
242 infrequently and closer examination of each instance allowed the number of elements
243 to be determined.

244

245



246

247 Figure 2. Spectrograms of UK tit mobbing calls. a) Blue tits: i-iv) churr call with 1)
 248 normal D elements and 2) exit elements, ii) frequency-modulated call, 3) mid
 249 elements, 4) introductory (intro) element (similar to A or B elements in chick-a-dee
 250 calls), 5) short D elements, v) chirp call (elements similar to C elements in chickadee

251 calls), vi) tonal call (similar to blue tit song). b) Great tits: i) jar/rattle call with 1)
252 intro element (similar to chickadee A or B elements) and 2) jar/rattle elements , ii)
253 chirp call, ix) D call, x) tonal call. c) Coal tits: i) bowl element, ii) chirp elements
254 (with peak elements), iii) dot elements, iv) hook elements, v) mound elements, vi) mt
255 elements, vii) peak elements, viii) s-dot element, ix), s elements, x) squeak elements,
256 xi) slide elements. d) Crested tits: i) normal trill call, ii) frequency-modulated trill
257 call, iii) tonal call. e) Marsh tits: i-iii) dā/D or complete calls with 1) dā/D elements,
258 2) full whole tonal element, 3) peak whole tonal element, 4) broken whole tonal
259 element, iv) ptew call. f) Willow tits: i) tää-tää call, ii) si-tää-tää call, with 1) si intro
260 element and 2) tää/D element, iii) zizi call. All spectrograms are scaled to one
261 another. For some call names we used new phonetic terminology, while for others call
262 names came from other sources: all species: (J. P. Hailman, 1989), marsh & willow
263 tits: (Haftorn, 1993), (Japanese) great tit: (Suzuki, 2014).

Table 1. Definition of call and element types for each tit species with references to spectrogram examples (Figure 2).

Species	Call type	Call description	Element type	Element description	Spectrogram figure			
Blue tit	Churr	Calls containing D elements	D	broadband with distinct peak shaped frequency bands	2a i - iv			
	~ Short	Churr calls containing short D elements that appear as a stack of dots -- Figure 2.2a iv 5	intro	narrowband	2a iv 4			
	~Frequency-modulated	Churr calls containing D elements that vary in peak frequency across the call -- Figure 2.2a ii	mid	D elements structurally different from those before and after	2a iii 3			
Great tit	Chirp	Calls containing chirp elements	exit	D elements structurally different from those before	2a i 2			
	Tonal	Calls containing only tonal elements	chirp	broadband short call with two distinct dots on right side	2a v			
	Jar / rattle	Calls containing jar / rattle elements	intro	narrowband	2a vi			
	D	Calls containing D elements	tonal	narrowband	2b i 2			
	Chirp	Calls containing chirp elements	intro	broadband with no distinct frequency bands and triangle shape at bottom	2b i 1			
Coal tit	Tonal	Calls containing only tonal elements	intro	broadband with distinct peak shaped frequency bands	2b iii			
	Single or multi	Single calls contain strings of only one element type, multi calls contain strings of multiple element types	jar / rattle	narrowband	2b ii			
			intro	narrowband	2b iv			
			D	broadband	2c i			
			chirp	peak with thin broadband line	2c ii			
Crested tit	Trill ~Frequency-modulated	Calls containing trill elements Calls containing trill notes that shift in frequency over the course of the call -- Figure 2.2d ii	chirp	line with dot on right side	2c iii			
			dot	hook shape at top and line under	2c iv			
			hook	hook shape	2c v			
			mound	mound shape	2c vi			
			mt	bumpy mound shape	2c vii			
			peak	narrowband increase in frequency	2c viii			
			s-dot	s shape with dot/dash under	2c ix			
			S	s shape with no dot/dash under	2c x			
			squeak	broadband with frequency bands	2c xi			
			slide	narrowband decreasing in frequency	2d i & ii			
			trill	broadband line				
			intro	narrowband				
			Marsh tit	Tonal Complete Tonal	Calls containing both di / D and tonal elements Non-broadband frequency-modulated notes	tonal	narrowband	2d iii
						di/D	broadband with distinct frequency bands	2e i - iii 1
						whole	peak shape meets at top	2e i 2
broken	peak shape doesn't meet at top	2e iii 4						

Information encoding in Paridae

Willow tit	Dä / D Plew Si-tää-tää	Calls containing only tä / D elements. Calls containing only plew elements Calls containing both D and si intro elements -- Figure 2.2f ii	full peak Dä / D plew tää / D	has both peak and slide element only has peak element broadband with distinct frequency bands tonal calls broadband with distinct frequency bands	2e i 2 & iii 4 2e ii 3 2e iv 2f i & ii 2 2f ii 1 2f iii
	Tää-tää Zi zi	Calls containing only D elements -- Figure 2.2f i Calls containing only zi elements -- Figure 2.2f iii	si intro tää / D zi	narrowband broadband with distinct frequency bands narrowband	2f i 2f ii 2f iii

265 *Statistical analysis*

266 *Effect of predator threat on calling behaviour*

267 To test how UK tit species encode information about predator threat in their mobbing
268 calls, we focused on the four ways in which the other Parids encode information: 1)
269 call rate (calls/individual/minute), 2) total number of elements in a call (henceforth
270 ‘element number’; or in the case of call types that are composed of different element
271 types, the number of each element type), 3) proportion of all calls produced during a
272 mobbing event that contained particular note types during a mobbing event
273 (henceforth ‘proportion’), and 4) the number of mobbing events in which birds
274 produced a particular call type divided by the total number of mobbing events
275 (henceforth ‘propensity’; Baker & Becker, 2002; Bartmess-LeVasseur et al., 2010;
276 Ficken, Hailman, & Hailman, 1994; Hetrick & Sieving, 2011; Soard & Ritchison,
277 2009; Templeton et al., 2005).

278

279 To determine whether the birds used any of these ways of encoding information, we
280 generated linear mixed models or generalized linear mixed models with a Gaussian or
281 binomial error structure respectively depending on the distribution and type
282 (continuous or binomial) of the data. We constructed these models for each species
283 separately as they appeared to differ in their combinations of different call and note
284 types (Figure 2), and as each species had a range of call/note types, we tested if each
285 species employed the encoding mechanisms for each call/note type to differentiate
286 between different threat predators.

287

288 We used these statistical models to test if the bird changed a specific call/note type in
289 response to different predator threat levels for each of the four ways of encoding

290 information. Our response variable was the way information was encoded for each
291 call/note type described above, and our fixed effects were the predator threat level and
292 three variables that accounted for the experimental design: the mount presentation
293 order, the mount exemplar, and the number of conspecifics present. To control for
294 between-feeder variation we included date and geographic region as random effects.
295 We also included a nested term ‘calls per trial’ that accounted for the number of calls
296 (each trial at each location had varying numbers of calls produced by each species) at
297 each feeder location during each trial. This term helped to minimize pseudoreplication
298 of calls. We transformed the data using a log or boxcox transform for any response
299 variable with non-normal residuals. For the binomial models where all calls of one of
300 the levels of stimulus:order or stimulus:mount exemplar consisted of all 1 or 0, the
301 models could not converge, so we ran these models as linear mixed models. We ran
302 type III Wald Chi-square tests to check for significant effects of threat level for each
303 call type for each way of information encoding for all species (Table 1). For models
304 where threat level had a significant effect, we tested if the effect was different for
305 different predator threats by running a planned comparison between buzzard and
306 sparrowhawk by re-ordering stimulus levels and re-running the model (Table 1).
307 Generalized linear mixed models were fit by maximum likelihood using the Laplace
308 approximation, while linear mixed models were fit using REML and t-tests used
309 Satterthwaite approximations to generate degrees of freedom. This allowed us to test
310 what call/note types each species used to differentiate between predator threats, and
311 what information encoding mechanisms each species used. While the chance of
312 committing a type I error is higher when multiple tests are being performed, we did
313 not apply a correction such as a Bonferroni correction as we, like others, felt that the
314 chance of committing type II errors sufficiently high that biologically meaningful

315 patterns would have been obscured (Feise, 2002; Perneger, 1998; Rothman, 1990).
316 Instead, to help assess the robustness of our results, we calculated both marginal and
317 conditional R^2 values specific for linear and generalized linear mixed models
318 (Nakagawa & Schielzeth, 2012) for the overall models (Table 2) and 95% confidence
319 intervals for model estimates (Table 3) We conducted all statistical analyses in R
320 v3.1.2 (R Core Team, 2014), using the lme4 (Bates, Maechler, Bolker, & Walker,
321 2014) package. In our results the ways of encoding information about predator threat
322 are as follows: 1) call rates are reported as calls/individual/minute, 2) element number
323 values as the number of elements/call, 3) all proportions as the number of calls that
324 were of a call type/total number of calls or the number of calls containing that element
325 type/total number of calls that can contain that element type (e.g. as within great tit
326 jar/rattle call types some calls have introductory elements, we calculated the
327 proportion of calls that contain introductory elements by dividing the number of calls
328 rattle/jar calls with introductory elements by the total number of rattle/jar calls; Figure
329 2, Table 1), and 4) propensities as the number of mobbing events where the call or
330 element type occurred/ total number of mobbing events.

331

332 *Effect of phylogeny on calling behaviour*

333 To determine if phylogeny explained the pattern of ways encoding information across
334 the species tested, we looked for phylogenetic signal using Pagel's lambda
335 (Freckleton, Harvey, & Pagel, 2002; Pagel, 1999). We calculated Pagel's lambda for
336 a tree with correct branch lengths, and one that had been collapsed into a large
337 polytomy (no phylogenetic signal) and then compared the maximum likelihood of
338 both lambdas using a maximum likelihood test. However, as many of the measures of
339 phylogenetic signal are not as reliable with trees under 20 species (Freckleton,

340 Harvey, & Pagel, 2002; Münkemüller et al., 2012; Pagel, 1999) we are cautious about
341 the results of these tests.

342

343 *Effect of ecology on behaviour*

344 To determine if ecology explained the pattern of ways of encoding information across
345 the species, we collected ecological information from the published literature

346 (Alatalo, 1981; Cramp, 1993; Deadman, 2014; Ekman, 1989; Fisher, 1982; Gimm,
347 1960; Morse, 1978; Perrins, 1979) on foraging niche, dominance, and gregariousness
348 for each species and included them as explanatory variables in our statistical models.

349 We chose these variables because each has been suggested as having an effect on
350 anti-predatory behaviour (Goodale et al., 2010).

351

352 Foraging niche, as measured by the height and distance from a tree trunk, influences
353 the exposure and vulnerability of a species when foraging and can therefore affect the
354 vulnerability of a species to predation. For example a species that forages high up in
355 trees or on insects in the air spend more time scanning the sky and may be more likely
356 to see, and respond to, an aerial predator while a species that forages near to, or on,
357 the ground may not (Goodale et al., 2010; Goodale & Kotagama, 2005a; Lima, 1993;
358 Magrath et al., 2014). Greater racket-tailed drongos, *Dicrurus paradiseus* (Goodale &
359 Kotagama, 2005a) and red-cap moustached tamarins, *Saguinus mystax pileatus*
360 (Peres, 1993) for example, both forage high up off the ground (sallying and upper
361 canopy respectively) and are the species in their mixed-species groups that are most
362 likely to detect aerial predators.

363

364 Interspecific dominance, as measured by shifts in foraging niche in the presence and
365 absence of heterospecifics (Alatalo, 1981; Perrins, 1979), can affect the likelihood of
366 a species to eavesdrop on, rather than produce information about predator threats.
367 Because a dominant individual is in a better position to eavesdrop on information
368 provided by subordinates (Gill & Bierema, 2013; Goodale et al., 2010), rather than to
369 produce information about predators, it has less need of a variety of ways to encode
370 information (Furrer & Manser, 2009; Marler, 1967).

371

372 Gregariousness, measured as the average size of a conspecific winter flock, could also
373 affect the chance of seeing a predator, and therefore the propensity to produce calls,
374 and the complexity of signalling might increase with increased group size (Freeberg
375 & Harvey, 2008; Goodale et al., 2010; Magrath et al., 2014; Manser et al., 2014).

376 Orange-billed babblers, *Turdoide rufescens* (Goodale & Kotagama, 2005b) and red-
377 cap moustached tamarinds (Peres, 1993) are the most abundant species in their mixed
378 species flocks and tend to spend more time scanning and respond to more potential
379 threats, respectively, than do their flock mates. Downy woodpeckers, *Picoides*
380 *pubescens* (Sullivan, 1985) and yellow mongoose, *Cynictis penicillata* (le Roux,
381 Cherry, & Manser, 2008) tend to produce alarm calls only when heterospecifics are
382 present, while the anti-predator vocal repertoire size of mongoose species,
383 *Herpestidae*, increases with group size and social complexity (Manser et al., 2014).

384

385 To determine if there was a correlation between each species' ecology and the ways
386 in which they encoded predator threat information we ran four generalized linear
387 models with binomial error structure including the ways of encoding information as
388 our response variable. We ran an analysis of deviance on the model to test for

389 significant effects of the three ecological variables – foraging niche, dominance, and
390 gregariousness – on the ways that each species encoded information about predator
391 threat.

392

393 **RESULTS**

394

395 *Blue tits*

396

397 Blue tits used all four ways of encoding information to differentiate between
398 predators and non-threats and to differentiate between different levels of threat (Table
399 2; Figure 3). Blue tits increased their call rate to predators: they called the least to
400 controls, more to buzzards, and the most to sparrowhawks (mean \pm standard error,
401 conditional R^2_{GLMM} ; control: 1.06 ± 0.24 ; buzzard: 2.12 ± 0.37 ; sparrowhawk: $6.21 \pm$
402 0.73 ; $R^2_{\text{GLMM}} = 0.613$). Blue tits increased the total number of elements and D notes
403 as threat increased, and decreased the number of mid notes to buzzards compared to
404 the other stimuli (elements: control 8.69 ± 0.21 , buzzard 10.38 ± 0.25 , sparrowhawk
405 13.01 ± 0.17 , $R^2_{\text{GLMM}} = 0.305$; D: control 9.26 ± 0.28 , buzzard 11.53 ± 0.33 ,
406 sparrowhawk 14.05 ± 0.19 , $R^2_{\text{GLMM}} = 0.699$; mid: control 2.57 ± 0.30 , buzzard $1.76 \pm$
407 0.17 , sparrowhawk 3.22 ± 0.19 , $R^2_{\text{GLMM}} = 0.478$; Table 2). Blue tits produced a
408 smaller proportion of the churr mobbing calls that include exit notes compared to
409 either controls or sparrowhawks than to buzzards, and a smaller proportion of calls
410 with chirp notes to sparrowhawks than to controls or buzzards (exit: control $0.21 \pm$
411 0.02 , buzzard 0.16 ± 0.01 , sparrowhawk 0.21 ± 0.01 , $R^2_{\text{GLMM}} = 0.469$; chirp: control
412 0.31 ± 0.02 ; buzzard 0.32 ± 0.02 , sparrowhawk 0.10 ± 0.01 , $R^2_{\text{GLMM}} = 0.668$; Table
413 2). Blue tits also increase the proportion of tonal notes as threat increases (control

414 0.12 ± 0.01, buzzard 0.15 ± 0.02, sparrowhawk 0.20 ± 0.01, $R^2_{\text{GLMM}} = 0.533$). Blue
 415 tits increased their propensity to produce mid, exit, tonal, frequency modulated, and
 416 short notes to high-threat predators compared to low-threat predators or controls (mid:
 417 control 0.07 ± 0.04, buzzard 0.15 ± 0.05, sparrowhawk 0.44 ± 0.08, $R^2_{\text{GLMM}} = 0.488$;
 418 exit: control 0.40 ± 0.08, buzzard 0.40 ± 0.07, sparrowhawk 0.84 ± 0.06, $R^2_{\text{GLMM}} =$
 419 0.251; tonal: control 0.24 ± 0.07, buzzard 0.40 ± 0.07, sparrowhawk 0.65 ± 0.07,
 420 $R^2_{\text{GLMM}} = 0.247$; frequency modulated: control 0.31 ± 0.07, buzzard 0.32 ± 0.07,
 421 sparrowhawk 0.67 ± 0.07, $R^2_{\text{GLMM}} = 0.607$; short: 0.44 ± 0.08, exit 0.84 ± 0.06,
 422 sparrowhawk 0.95 ± 0.03, $R^2_{\text{GLMM}} = 0.370$; Table 2).

423

424 *Great tits*

425

426 To differentiate one or both predators from the control great tits used three ways of
 427 encoding information: call rate, proportion, and propensity. However, they only used
 428 call rate to differentiate between high and low threat predators (Table 2; Figure 3).
 429 Great tits had a higher call rate in response to high threats compared to controls and
 430 buzzards (control: 1.00 ± 0.21, buzzard: 3.27 ± 0.61, sparrowhawk: 8.54 ± 1.17,
 431 $R^2_{\text{GLMM}} = 0.465$; Table 2). They decreased the proportion of calls that contained chirp
 432 elements and increased the propensity to produce jar/rattle calls during a mobbing
 433 event to predators compared to controls (chirp proportion: control 0.14 ± 0.21,
 434 buzzard 0.02 ± 0.01, sparrowhawk 0.009 ± 0.002, $R^2_{\text{GLMM}} = 0.578$; jar/rattle
 435 propensity: control 0.68 ± 0.08, buzzard 0.81 ± 0.06, sparrowhawk 0.95 ± 0.03,
 436 $R^2_{\text{GLMM}} = 0.271$; Table 2).

437

438 *Coal tits*

439

440 Coal tits encoded information in three ways to differentiate between controls and
441 predator threats: call rate, element number, and propensity (Table 2). Coal tits only
442 used element number, however, to differentiate between predators of varying threat
443 levels in their mobbing calls (Table 2; Figure 3). Coal tits increased their call rate as
444 threat increased (control: 0.45 ± 0.11 , buzzard: 2.53 ± 0.56 , sparrowhawk: $5.25 \pm$
445 1.00 , $R^2_{\text{GLMM}} = 0.347$). Coal tits produced more hook and mt elements to buzzards
446 than either controls or sparrowhawks (hook: control 1.69 ± 0.16 , buzzard 3.91 ± 0.23 ,
447 sparrowhawk 3.62 ± 0.30 , $R^2_{\text{GLMM}} = 0.490$, mt: control 1.43 ± 0.14 , buzzard $2.97 \pm$
448 0.38 , sparrowhawk 1.47 ± 0.12 , $R^2_{\text{GLMM}} = 0.313$; Table 2). Coal tits produced fewer
449 squeak and more mound elements to controls than to predator threats, and more s-dot
450 elements as threat increased (squeak: control 2.71 ± 1.39 , buzzard 2.73 ± 0.16 ,
451 sparrowhawk 2.79 ± 0.10 , $R^2_{\text{GLMM}} = 0.198$; mound: control 2.50 ± 0.50 , buzzard 1.93
452 ± 0.28 , sparrowhawk 1.77 ± 0.14 , $R^2_{\text{GLMM}} = 0.608$; s-dot: control 2.09 ± 0.34 , buzzard
453 3.36 ± 0.10 , sparrowhawk 4.15 ± 0.17 , $R^2_{\text{GLMM}} = 0.319$; Table 2). Coal tits decreased
454 their propensity to produce mound or squeak elements in response to controls
455 compared to predatory stimuli (mound: control 0.06 ± 0.04 , buzzard 0.29 ± 0.08 ,
456 sparrowhawk 0.51 ± 0.08 , $R^2_{\text{GLMM}} = 0.300$; squeak: control $0.14 \pm 0.01=6$, buzzard
457 0.47 ± 0.09 , sparrowhawk 0.63 ± 0.08 , $R^2_{\text{GLMM}} = 0.473$; Table 2).

458

459 *Crested tits*

460

461 Crested tits differentiated one or both predators from the control in three ways: call
462 rate, proportion, and propensity. However, they only used proportion and propensity
463 to differentiate between different threat predators (Table 2; Figure 3). They increased

464 their call rate as threat increased, produced a higher proportion of frequency
465 modulated calls, and a lower propensity to produce tonal notes in response to
466 buzzards compared to controls and sparrowhawks (rate: control 11.71 ± 4.33 , buzzard
467 14.92 ± 3.38 , sparrowhawk 16.32 ± 2.30 , $R^2_{\text{GLMM}} = 0.479$; frequency modulated
468 proportion: control 0.61 ± 0.02 , buzzard 0.75 ± 0.01 , sparrowhawk 0.73 ± 0.01 ,
469 $R^2_{\text{GLMM}} = 0.364$; tonal propensity: control 0.21 ± 0.11 , buzzard 0.08 ± 0.08 ,
470 sparrowhawk 0.38 ± 0.14 , $R^2_{\text{GLMM}} = 0.289$; Table 2; Figure 3).

471

472 *Marsh tits*

473

474 Marsh tits used all four ways of encoding information to differentiate both between
475 predators and non-threats and between predators of different threat levels (Table 2;
476 Figure 3). Marsh tits increased their call rate to predators compared to controls,
477 decreased the number of $\text{d}\ddot{\text{a}}/\text{D}$ elements in response to buzzards compared to controls
478 or sparrowhawks, and decreased the proportion of full tonal notes to buzzards
479 compared to controls and sparrowhawks (rate: control: 1.24 ± 0.35 ; buzzard: $1.26 \pm$
480 0.30 ; sparrowhawk: 4.56 ± 0.85 , $R^2_{\text{GLMM}} = 0.740$; $\text{d}\ddot{\text{a}}/\text{D}$ elements: control: $0.21 \pm$
481 0.11 ; buzzard: 0.08 ± 0.08 ; sparrowhawk: 0.38 ± 0.14 , $R^2_{\text{GLMM}} = 0.324$; proportion of
482 full tonal notes: control: 0.71 ± 0.07 ; buzzard: 0.49 ± 0.08 ; sparrowhawk: 0.53 ± 0.03 ,
483 $R^2_{\text{GLMM}} = 0.370$; Table 2). They also increased their propensity to produce peak tonal
484 elements, all tonal, and ptew calls to higher threat predators (peak tonal: control 0.33
485 ± 0.17 , buzzard 0.56 ± 0.18 , sparrowhawk 0.89 ± 0.11 , $R^2_{\text{GLMM}} = 0.608$; tonal: control
486 0.78 ± 0.15 , buzzard 0.89 ± 0.11 , sparrowhawk 1.00 ± 0.00 , $R^2_{\text{GLMM}} = 0.398$; ptew:
487 control 0.78 ± 0.05 , buzzard 0.89 ± 0.11 , sparrowhawk 1.00 ± 0.00 , $R^2_{\text{GLMM}} = 0.398$;
488 Table 2).

489

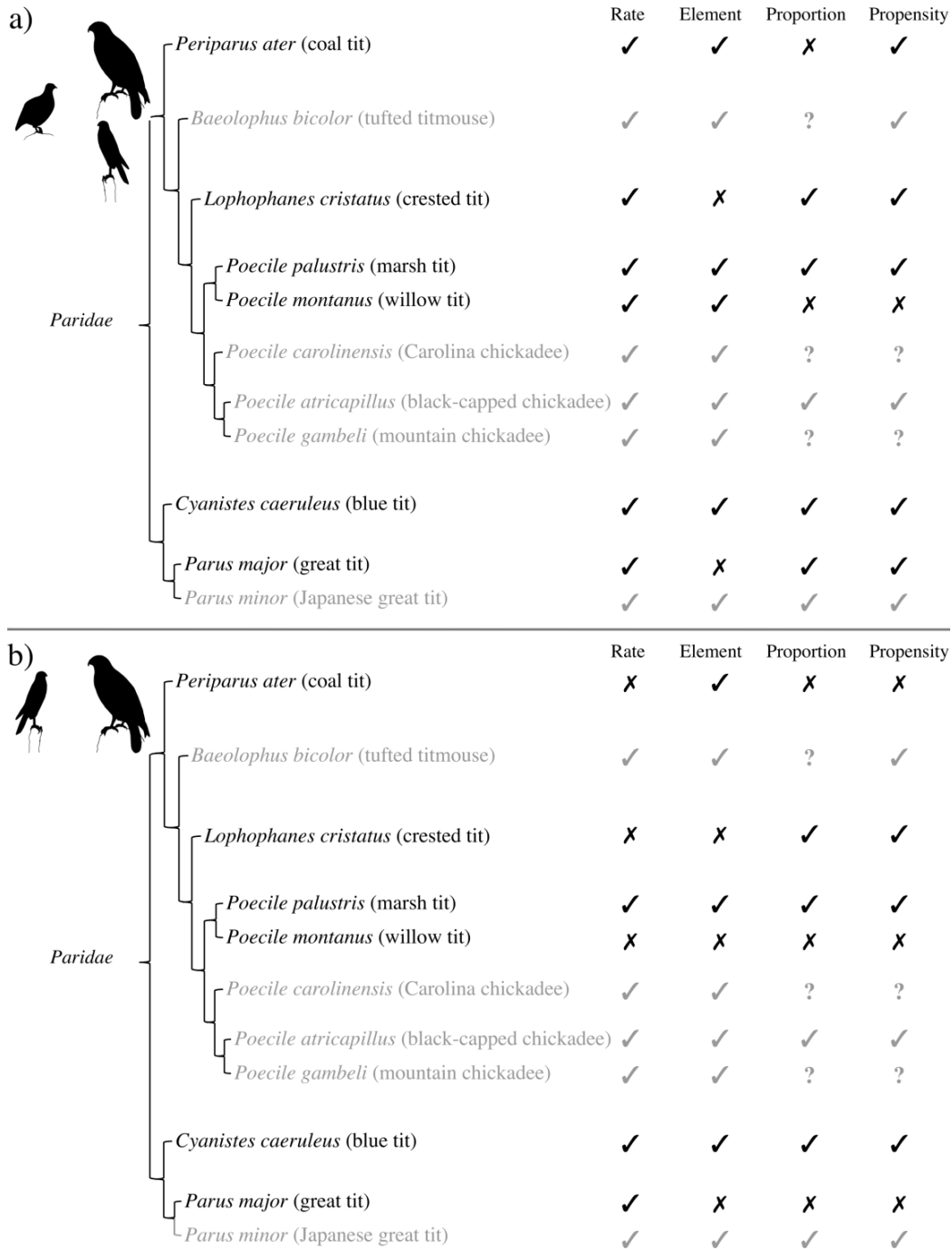
490 *Willow tits*

491

492 Willow tits varied several call features between the control and predator treatments
493 but did not differentiate between predators of different threat levels (Table 2; Figure
494 3). Willow tits increased their call rate in response to predators (mean \pm standard
495 error; buzzard: 1.72 ± 0.42 ; sparrowhawk; 2.04 ± 0.25 , $R^2_{\text{GLMM}} > 0.999$) compared to
496 controls (control: 0.71 ± 0.28 ; Table 2). Willow tits also increased the number of total
497 elements and decreased the number of si intro elements as predator threat increased
498 (elements: control 2.40 ± 0.22 , buzzard 2.86 ± 0.14 , sparrowhawk, 3.59 ± 0.12 ,
499 $R^2_{\text{GLMM}} = 0.201$; si intro: control 2.00 ± 0.49 , buzzard 2.51 ± 0.19 , sparrowhawk 2.83
500 ± 0.14 , $R^2_{\text{GLMM}} = 0.207$; Table 2).

501

502 For all species, we observed some order and mount exemplar effects in the statistical
503 models, but as none of these effects were consistent across call types, ways of
504 encoding information, stimulus species, or responding tit species, they are not
505 included in our results.



506

507 Figure 3. The four ways in which each of the previously studied Paridae encode
 508 information differentiating a) predators (sparrowhawk and buzzard) from non-
 509 predators (partridge) and b) high (sparrowhawk) from low (buzzard) threat predators.
 510 Rate: call rate, Element: number of elements in a call, Proportion: the proportion of
 511 call types used within a mobbing event, Propensity: the propensity to produce call

512 types across mobbing events. Light grey text indicates those species tested in previous
513 studies, question marks indicate encoding mechanisms not previously tested, and Xs
514 show mechanisms that are not used. Phylogeny information was based on (Johansson
515 et al., 2013). Published data derived from: black-capped chickadee: (Baker & Becker,
516 2002; Billings et al., 2015; Clemmons & Lambrechts, 1992; Templeton et al., 2005),
517 tufted titmouse: (Bartmess-LeVasseur et al., 2010; Courter & Ritchison, 2010;
518 Hetrick & Sieving, 2011; Sieving et al., 2010), Carolina chickadee: (Bartmess-
519 LeVasseur et al., 2010; Hetrick & Sieving, 2011; Soard & Ritchison, 2009), Mexican
520 chickadee: (Billings et al., 2015), Japanese great tit: (Suzuki, 2012; 2014; Suzuki &
521 Ueda, 2013).
522

	Propensity to use	All tonal elements	Peak tonal elements	Plew calls	All	Total elements	Si intro elements	Zizi calls
Willow Tit	Propensity to use	0.398	0.398	8.28	0.016	-0.636	0.534	2.703
		0.501	0.608	12.36	0.002	3.091	0.008	2.316
		0.398	0.398	8.29	0.016	-0.636	0.534	2.703
Call rate	Number of	0.445	1.000	46.36	<0.001	3.721	0.007	1.994
		0.129	0.201	7.89	0.019	-0.222	0.826	2.803
		0.207	0.207	16.46	<0.001	0.360	0.719	-4.053
Propensity to use	Zizi calls	0.234	1.000	5.96	<i>0.051</i>	2.420	0.036	-1.234

526

527 Table 3. Model estimates and 95% confidence intervals for linear and generalized
 528 linear mixed models determining if predatory type (control, buzzard, or sparrowhawk)
 529 had a significant effect on the variation in vocal response of UK tit species (Table 2).

Species	Encoding Method	Element Type	Stimulus	95% Confidence interval		
				model estimate	lower	upper
Blue Tit	Call rate	All	Control	4.076	-2.090	4.468
			Buzzard	1.189	-2.470	10.623
			Sparrowhawk	8.971	0.834	17.109
	Number of	Total elements	Control	9.620	6.802	12.438
			Buzzard	7.310	1.563	13.057
			Sparrowhawk	12.463	6.734	18.191
	Number of	Mid elements	Control	3.716	1.439	5.993
			Buzzard	2.235	-2.311	6.782
			Sparrowhawk	4.241	0.138	8.344
	Number of	D elements	Control	1.745	1.597	1.894
			Buzzard	1.810	1.518	2.102
			Sparrowhawk	2.121	1.835	2.407
	Proportion of	Exit calls	Control	-1.822	-3.016	-0.628
			Buzzard	-2.705	-5.532	0.122
			Sparrowhawk	-0.606	-3.221	2.009
	Proportion of	Chirp calls	Control	-2.933	-4.600	-1.266
			Buzzard	-0.376	-4.039	3.286
			Sparrowhawk	-4.924	-8.668	-1.179
	Proportion of	Tonal calls	Control	-4.670	-6.436	-2.903
			Buzzard	-3.759	-7.140	-0.379
			Sparrowhawk	-1.672	-5.048	1.704
	Propensity to use	Mid elements	Control	0.034	-0.177	0.244
			Buzzard	-0.017	-0.486	0.451
			Sparrowhawk	0.779	0.292	1.267
Propensity to use	Exit elements	Control	0.133	0.046	0.569	
		Buzzard	0.134	-0.286	0.903	
		Sparrowhawk	0.792	0.346	1.585	
Propensity to use	Tonal calls	Control	-0.009	-0.250	0.232	
		Buzzard	0.074	-0.500	0.648	
		Sparrowhawk	0.666	0.067	1.264	
Propensity to use	Frequency-modulated calls	Control	0.691	0.125	0.972	
		Buzzard	0.793	0.132	1.617	
		Sparrowhawk	1.613	0.692	1.963	
Propensity to use	Short calls	Control	0.288	0.069	0.506	
		Buzzard	0.344	-0.175	0.864	
		Sparrowhawk	0.948	0.407	1.490	
Great Tit	Call rate	All	Control	2.479	-0.433	5.391
			Buzzard	6.122	-0.709	12.953
			Sparrowhawk	16.091	9.117	23.064
	Proportion of	Chirp calls	Control	0.131	0.028	0.235
			Buzzard	0.200	-0.156	0.282
			Sparrowhawk	0.301	-0.264	0.187
Propensity to use	Jar/rattle calls	Control	0.438	0.206	0.670	
		Buzzard	0.849	0.311	1.388	
		Sparrowhawk	0.911	0.356	1.466	
Coal Tit	Call rate	All	Control	0.431	-2.258	3.120
			Buzzard	4.633	-1.991	11.257
			Sparrowhawk	7.247	1.094	13.400
	Number of	Hook elements	Control	1.737	1.055	2.862

			Buzzard	4.608	2.528	8.455
			Sparrowhawk	2.959	1.706	5.153
Number of	Mound elements		Control	2.707	0.960	7.627
			Buzzard	3.905	1.338	11.435
			Sparrowhawk	3.192	1.156	8.832
Number of	Mt elements		Control	1.607	1.035	2.495
			Buzzard	7.049	3.404	14.997
			Sparrowhawk	2.619	1.666	4.116
Number of	S-dot elements		Control	2.315	1.293	4.148
			Buzzard	4.258	2.224	4.395
			Sparrowhawk	3.853	2.113	4.495
Number of	Squeak elements		Control	10.472	3.042	36.042
			Buzzard	10.647	3.091	36.676
			Sparrowhawk	10.655	3.095	36.681
Propensity to use	Mound elements		Control	-0.057	-0.287	0.173
			Buzzard	0.368	-0.251	0.988
			Sparrowhawk	0.452	-0.123	1.027
Propensity to use	Squeak elements		Control	0.036	-0.209	0.281
			Buzzard	0.801	0.151	1.451
			Sparrowhawk	0.654	0.046	1.262
Crested Tit	Call rate	All	Control	10.084	-5.110	25.277
			Buzzard	9.511	-29.763	48.786
			Sparrowhawk	31.261	-0.998	63.519
Proportion of	Frequency-modulated calls		Control	-0.430	-2.066	1.205
			Buzzard	2.832	-1.365	7.029
			Sparrowhawk	-0.057	-3.297	3.183
Propensity to use	Tonal calls		Control	0.186	-0.309	0.680
			Buzzard	-0.309	-1.632	1.013
			Sparrowhawk	0.751	-0.315	1.817
Marsh Tit	Call rate	All	Control	4.076	-0.043	8.196
			Buzzard	1.189	-6.198	8.576
			Sparrowhawk	8.971	1.444	16.498
Number of	Dä/D elements		Control	-7.905	-17.199	1.389
			Buzzard	-7.717	-23.088	7.653
			Sparrowhawk	-21.884	-39.026	-4.741
Proportion of	Full intro elements		Control	0.997	0.849	1.000
			Buzzard	1.029	0.850	1.484
			Sparrowhawk	1.821	0.960	1.994
Propensity to use	All tonal elements		Control	0.821	0.145	1.498
			Buzzard	0.643	-0.584	1.870
			Sparrowhawk	1.571	0.351	2.792
Propensity to use	Peak tonal elements		Control	-0.827	-1.761	0.107
			Buzzard	0.416	-1.306	2.137
			Sparrowhawk	0.505	-1.556	2.567
Propensity to use	Ptew calls		Control	0.821	0.145	1.498
			Buzzard	0.643	-0.584	1.870
			Sparrowhawk	1.571	0.351	2.792
Willow Tit	Call rate	All	Control	1.335	-0.194	2.864
			Buzzard	3.045	0.615	5.475
			Sparrowhawk	2.817	-0.169	5.804
Number of	Total elements		Control	4.012	1.738	9.261
			Buzzard	4.953	2.289	10.869
			Sparrowhawk	6.649	3.077	14.456
Number of	Si intro elements		Control	0.745	0.555	0.936
			Buzzard	0.772	0.437	1.108
			Sparrowhawk	0.563	0.285	0.842
Propensity to use	Zizi calls		Control	-0.065	-1.300	1.169
			Buzzard	1.008	-1.096	3.111
			Sparrowhawk	-0.959	-3.613	1.695

530

531

532 PHYLOGENY AND ECOLOGY

533 Phylogenetic signal did not explain which species used which ways of encoding
534 information about predator threat in their mobbing calls (rate: $\chi^2_1 = -0.03$, $P = 1$;
535 number of elements: $\chi^2_1 = -1.37$, $P = 1$; proportion: $\chi^2_1 = -6.36$, $P = 1$; propensity: χ^2_1
536 $= -1.30$, $P = 1$). Ecology also did not explain variation in which species used each
537 method of encoding information about predator threat in their mobbing calls (rate:
538 foraging niche $F(2) = 1.05$, $P = 0.431$, dominance $F(2) = 6.59$, $P = 0.054$,
539 gregariousness $F(2) = 2.77$, $P = 0.176$; number of elements: foraging niche $F(2) =$
540 2.66 , $P = 0.184$, dominance $F(2) = 1.91$, $P = 0.262$, gregariousness $F(2) = 1.05$, $P =$
541 0.431 ; proportion: foraging niche $F(2) = 0.26$, $P = 0.810$, dominance $F(2) = 1.39$, $P =$
542 0.515 , gregariousness $F(2) < 0.001$, $P > 0.999$; propensity: foraging niche $F(2) = 0.52$,
543 $P = 0.657$, dominance $F(2) = 2.77$, $P = 0.265$, gregariousness $F(2) < 0.001$, $P >$
544 0.999).

545 Table 4. Ecology of tested Paridae species. Species grouped by number and type of ways they encode information about predator threat (left
 546 columns).

Species	Call	Encoding Method Element number	Preferred foraging height			Dominance			Gregariousness		
			Proportion	Propensity	upper mid low/ground	mid subordinate	small	medium	large		
Black-capped chickadee	0	0	0	0	0	0	0	0	0	0	
Japanese great tit	0	0	0	0	0	0	0	0	0	0	
Marsh tit	0	0	0	0	0	0	0	0	0	0	
Blue tit	0	0	0	0	0	0	0	0	0	0	
Tufted titmouse	0	0	?	0	0	0	0	0	0	0	
Carolina chickadee	0	0	?	?	0	0	0	0	0	0	
Mountain chickadee	0	0	?	?	0	0	0	0	0	0	
Great tit	0	X	X	X	0	0	0	0	0	0	
Coal tit	X	0	X	X	0	0	0	0	0	0	
Crested tit	X	X	0	0	0	0	0	0	0	0	
Willow tit	X	X	X	X	0	0	0	0	0	0	

547 **DISCUSSION**

548

549 We found that the UK tit species varied in both the types and degree to which they
550 encode information about predators. UK tits all responded to predators with mobbing
551 calls and all communicated the presence of a predator by increasing call rate relative
552 to their responses in control trials. Each species varied in the ways they
553 communicated predator presence and differentiated between low and high threat
554 predators. These results are not consistent with the presumption that all Paridae use
555 the same mechanisms to encode similar information about predators.

556

557 Variation across species in signalling strategy could potentially be explained by
558 relatedness: those species more closely related should be more similar in terms of the
559 ways of encoding information they use to encode information about predators. The
560 presence or absence of alarm calling as a behaviour in rodents appears to be well
561 explained by phylogeny, though this says nothing concerning the specific ways of
562 encoding information in these calls (Shelly & Blumstein, 2005). We found no
563 correlation between the Parid phylogeny and the pattern of ways of encoding
564 information. Additionally, we could find no patterns in the ways the traits mapped
565 onto the phylogeny that would explain the ways of encoding information used by the
566 species we tested. Marsh tits, for example, encode information in the same ways as do
567 blue tits, one of their more distant relatives, while they share only half of the ways of
568 communicating the presence of a predator and none of the same ways of
569 communicating the threat of a predator, with congeneric willow tits. Relatedness
570 similarly fails to explain the variation in the number and mechanisms across the rest
571 of the phylogeny. These patterns are similar to those found in marmots, which also

572 vary the ways in which they encode information about predators based on a factor
573 other than phylogenetic relatedness (Blumstein, 2007).
574
575 If relatedness does not explain the number or ways of encoding information used by
576 UK tits, aspects of their natural history might. Some species may be pre-disposed
577 through their ecology to be better equipped to notice and respond to predators, and
578 these species therefore may use a greater variety of ways of communicating that
579 information (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010). However, our
580 tests indicated no correlations between any of the three ecological variables we
581 examined and the ways in which the different species encoded predator threat
582 information. If foraging niche explained ways of encoding information then we would
583 have expected that outer/upper canopy-foraging blue and coal tits should be more
584 similar in the ways in which they encode information, relative to species that forage in
585 locations with limited visibility (lower trunk foraging: marsh, willow, and great tits)
586 as these species are less exposed to predatory raptors (Gibb, 1960; Morse, 1978;
587 Nakamura, 1970; Perrins, 1979). Blue and marsh tits are, however, more similar in
588 the ways in which they respond to predators (both presence and threat) than are blue
589 and coal tits. Foraging niche, at least, does not seem to be an especially useful
590 explanation for the variation in the ways of encoding information. Similarly, we
591 would have expected species that travel in larger winter flocks, such as blue, great,
592 and coal tits, to use more ways of encoding information relative to those less
593 gregarious species (crested, marsh, and willow tits; Deadman, 2014; Ekman, 1979;
594 1989; Fisher, 1982; Morse, 1978). As the more gregarious tit species are, however, no
595 more likely to use more ways of encoding information than the less gregarious
596 species, gregariousness during winter also is not a good explanation for the variation

597 we see . Finally, if interspecific dominance influenced ways of encoding information
598 we would have expected the more dominant great and blue tits to use more similar
599 ways of encoding information. However blue and great tits were no more similar in
600 the ways they encode information than are the more subordinate coal or willow tits
601 (Alatalo, 1981; Cramp, 1993; Perrins, 2012). Given that neither phylogeny or any of
602 the more plausible natural history traits provide an explanation for the variation in the
603 number or ways that the UK species use to encode predator information in their
604 mobbing calls, the question becomes why do these species communicate predator
605 threat with such variety?

606

607 There are two common explanations for the use of multiple ways of encoding
608 information about a single event or threat. The first is that the multiplicity is an
609 artefact of the signaller's internal state: as the animal's internal state affects a suite of
610 aspects of its vocal response via arousal, an increase in that animal's arousal (fear)
611 will result in an increase in the call rate, number of elements, or even different call
612 types (Blumstein, 2007; Blumstein & Armitage, 1997; J. P. Hailman & Ficken, 1996;
613 Marler, Evans, & Hauser, 1992; Seyfarth & Cheney, 2003). This explanation
614 presupposes that the information provided to receivers is redundant but that the
615 variety in the ways the information is provided leads to a stronger or more urgent
616 signal (Blumstein & Armitage, 1997; Marler et al., 1992).

617

618 The second explanation is that each way of encoding information is used to
619 communicate different information about the threat, enabling a signaller to increase
620 the amount of information it can deliver (Marler et al., 1992; Suzuki, Wheatcroft, &
621 Griesser, 2016). Here the information, while pertaining to the same threat, is not

622 redundant. For example, Japanese great tit mobbing calls contain different element
623 types that elicit two different types of behaviour: A, B and C notes elicit scanning
624 behaviour, while D notes elicit approach behaviour (Suzuki, 2016). In order to
625 address why related species use different ways to encode predator threat, we need to
626 establish what specific information it is that they encode (Templeton et al., 2005).
627 Redundancy does seem to explain changes in the acoustic features of the calls that
628 California ground squirrels, *Spermophilus beecheyi*, use to signal state of arousal
629 (Owings & Virginia, 1978). Conversely, signallers might use different ways of
630 encoding information to encode different types of information, predatory category
631 using propensity and distance using call rate (Griesser, 2008; Suzuki et al., 2016).
632 This appears to be relatively common among primates. Blue monkeys, *Cercopithecus*
633 *mitis stuhlmanni*, for example, signal predator type using propensity of certain call
634 types, but change the rate of each call type as predator distance decreases to signal
635 increased threat (Murphy et al., 2013).

636

637 As UK tit species each use different ways to encode information in their calls, and as
638 there is no explanation for this variation in either their phylogenetic relatedness or
639 their ecology, they may provide a fruitful system for investigating how species might
640 use different ways of encoding information to encode redundant or additive
641 information. Although the information encoded in these types of vocalizations is well
642 researched, the causes of the intra- and interspecific differences remain unclear.
643 Investigating the prevalence of the multiple ways of encoding information across
644 species and by addressing the types of information that these different approaches
645 achieve may allow us to derive further evolutionary insights into variation in
646 information encoding strategies.

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- 970 Supplementary table 1. Type III Wald Chi-square test results for predator type (control, buzzard, or sparrowhawk) as a significant predictor of
- 971 variation in vocal response. Planned comparison t and z test results. § indicates either non-normally distributed residuals (linear mixed models) or
- 972 over-dispersion of maximum value of 1.20 (generalized linear mixed models).

Species	Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	χ^2	p value
Blue Tit	Call rate Number of	All			Inner	identity	log	43.10	<0.001
		Total elements			Inner	Gaussian	identity	20.54	<0.001
		Intro elements		log	Inner	Gaussian	identity	2.38	0.305
		Mid elements			Inner	Gaussian	identity	6.76	0.034
		Exit elements		log	Inner	Gaussian	identity	0.18	0.912
		D elements		boxcox: 0.29	Inner	Gaussian	identity	28.84	<0.001
		Chirp elements			Inner	Gaussian	identity	0.92	0.630
		Tonal elements			Inner	Gaussian	identity	1.26	0.553
		Intro calls			glmer	binomial	logit	1.68	0.432
		Mid calls		§	Inner	Gaussian	identity	3.25	0.197
		Exit calls			glmer	binomial	logit	6.27	0.044
		D calls			glmer	binomial	logit	4.18	0.124
Proportion of		Chirp calls			glmer	binomial	logit	17.04	<0.001
		Tonal calls			glmer	binomial	logit	14.17	0.001
		Frequency-modulated calls			glmer	binomial	logit	3.16	0.206
		Short calls			glmer	binomial	logit	3.83	0.148
		Intro elements			glmer	binomial	logit	1.59	0.451
		Mid elements			Inner	Gaussian	identity	33.01	<0.001
		Exit elements			Inner	Gaussian	identity	14.78	0.001
		D elements		§	Inner	Gaussian	identity	3.06	0.217
		Chirp elements		§	glmer	binomial	logit	4.78	0.092
		Tonal elements			Inner	Gaussian	identity	14.35	0.001
		Frequency-modulated calls			glmer	binomial	logit	9.63	0.008
		Great Tit	Call rate Number of	Short elements			Inner	Gaussian	identity
All					Inner	identity	log	44.00	<0.001
Total elements				log	Inner	Gaussian	identity	0.65	0.721
Intro elements					Inner	Gaussian	identity	0.38	0.827
Jar/rattle elements				log	Inner	Gaussian	identity	0.05	0.975
D elements				§	Inner	Gaussian	identity	3.44	0.179

Information encoding in Paridae

Proportion of	Chirp elements	Inner	Gaussian	identity	0.40	0.819	
	Total elements	Inner	Gaussian	identity	5.11	0.078	
	Intro calls	glmer	binomial	logit	1.85	0.397	
	Jar/rattle calls	glmer	binomial	logit	0.56	0.756	
	D calls	glmer	binomial	logit	0.13	0.939	
Propensity to use	Chirp calls	Inner	Gaussian	identity	7.55	0.023	
	Total calls	Inner	Gaussian	identity	0.48	0.789	
	Intro elements	glmer	binomial	logit	3.71	0.157	
	Jar/rattle elements	Inner	Gaussian	identity	10.96	0.004	
	D elements	Inner	Gaussian	identity	1.87	0.393	
Coal tit Call rate Number of	Chirp elements	Inner	Gaussian	identity	0.50	0.779	
	Total elements	Inner	Gaussian	identity	4.25	0.119	
	All	Inner	identity	log	15.46	<0.001	
	Total elements	Inner	Gaussian	identity	3.68	0.159	
Proportion of	Bowl elements	Inner	Gaussian	identity	0.53	0.766	
	Chirp elements	Inner	Gaussian	identity	0.39	0.825	
	Dot elements	Inner	Gaussian	identity	0.63	0.729	
	Hook elements	Inner	Gaussian	identity	11.19	0.004	
	Mound elements	Inner	Gaussian	identity	7.05	0.029	
	Mt elements	Inner	Gaussian	identity	21.84	<0.001	
	Peak elements	Inner	Gaussian	identity	1.78	0.412	
	S elements	Inner	Gaussian	identity	3.18	0.204	
Proportion of	S-dot elements	Inner	Gaussian	identity	11.97	0.003	
	Slide elements	Inner	Gaussian	identity	3.16	0.206	
	Squeak elements	Inner	Gaussian	identity	7.27	0.026	
	Bowl elements	Inner	Gaussian	identity	0.34	0.844	
	Chirp elements	Inner	Gaussian	identity	2.25	0.324	
	Dot elements	glmer	binomial	cloglog	0.98	0.614	
	Hook elements	Inner	Gaussian	identity	3.18	0.204	
	Mound elements	Inner	Gaussian	identity	1.44	0.486	
Proportion of	Mt elements	Inner	Gaussian	identity	1.64	0.441	
	Peak elements	glmer	binomial	logit	1.21	0.545	
	S elements	Inner	Gaussian	identity	0.56	0.758	
	S-dot elements	glmer	binomial	cloglog	2.95	0.229	
	Slide elements	glmer	binomial	cloglog	2.70	0.260	
	Squeak elements	Inner	Gaussian	identity	3.54	0.170	
	Multi calls	glmer	binomial	logit	5.42	0.067	

Information encoding in Paridae

Propensity to use	Bowl elements	Inner	Gaussian	identity	1.64	0.440	
	Chirp elements	Inner	Gaussian	identity	2.41	0.300	
	Dot elements	Inner	Gaussian	identity	3.06	0.216	
	Hook elements	Inner	Gaussian	identity	2.22	0.329	
	Mound elements	Inner	Gaussian	identity	9.75	0.008	
	Mt elements	Inner	Gaussian	identity	1.61	0.447	
	Peak elements	glmer	binomial	logit	1.44	0.488	
	S elements	Inner	Gaussian	identity	5.59	0.061	
	S-dot elements	Inner	Gaussian	identity	3.88	0.144	
	Slide elements	glmer	binomial	logit	2.83	0.243	
	Squeak elements	Inner	Gaussian	identity	18.58	<0.001	
	Multi calls	Inner	Gaussian	identity	1.07	0.586	
	Crested Tit	Call rate Number of	All	Inner	Gaussian	identity	6.21
Total elements			Inner	Gaussian	identity	2.93	0.231
Trill elements			Inner	Gaussian	identity	0.55	0.760
Tonal elements			Inner	Gaussian	identity	2.83	0.243
Trill calls			Inner	Gaussian	identity	0.49	0.784
Tonal calls			Inner	Gaussian	identity	0.50	0.778
Frequency-modulated calls			glmer	binomial	logit	6.32	0.042
Trill calls			Inner	Gaussian	identity	4.72	0.094
Frequency-modulated calls			Inner	Gaussian	identity	6.45	0.040
Tonal calls			Inner	Gaussian	identity	4.72	0.094
All			Inner	Gaussian	identity	10.39	0.006
Total elements			Inner	Gaussian	identity	1.38	0.503
Intro elements			Inner	Gaussian	identity	4.03	4.031
Marsh Tit	Call rate Number of	Intro elements	Inner	Gaussian	identity	12.69	0.002
		dã/D elements	Inner	Gaussian	identity	0.10	0.950
		Intro elements	Inner	Gaussian	identity	0.06	0.972
		dã/D elements	Inner	Gaussian	identity	0.06	0.972
		All tonal elements	Inner	Gaussian	identity	0.06	0.972
		Full tonal elements	glmer	binomial	logit	6.88	0.031
		Peak tonal elements	Inner	Gaussian	identity	3.38	0.184
		Broken tonal elements	glmer	binomial	logit	4.06	0.131
		Whole tonal elements	glmer	binomial	logit	5.44	0.066
		Prew calls	Inner	Gaussian	identity	0.06	0.972
		dã/D calls	Inner	Gaussian	identity	0.96	0.618
		Complete calls	Inner	Gaussian	identity	0.08	0.960
		Propensity to use	Intro elements	dã/D elements	Inner	Gaussian	identity
All tonal elements	Inner			Gaussian	identity	8.28	0.016
Full tonal elements	Inner			Gaussian	identity	2.98	0.226
Peak tonal elements	Inner			Gaussian	identity	12.37	0.002
	Inner			Gaussian	identity		

Willow	Call rate	Broken tonal elements	§	Inner	Gaussian	identity	2.15	0.341
		Whole tonal elements		Inner	Gaussian	identity	2.73	0.256
Tit	Number of	Prew calls		Inner	Gaussian	identity	8.29	0.016
		dā/D calls		Inner	Gaussian	identity	0.41	0.815
		All		Inner	Gaussian	identity	46.36	<0.001
		Total elements		Inner	Gaussian	identity	7.89	0.019
			log	Inner				
			boxcox:-	Inner	Gaussian	identity	16.46	<0.001
		Si intro elements	0.22	Inner	Gaussian	identity	1.03	0.599
		Zi elements	boxcox:-	Inner	Gaussian	identity	5.73	0.057
		Tää elements	0.48	Inner	Gaussian	identity	0.13	0.938
		Si intro elements	log	glnmer	binomial	logit	0.17	0.919
	Proportion of	Zi elements		glnmer	binomial	logit	0.46	0.795
		Tää elements		glnmer	binomial	logit	0.13	0.938
		Tää-tää calls		glnmer	binomial	logit	1.88	0.391
		Si-tää-tää calls		Inner	Gaussian	identity	0.76	0.684
		Zizi calls	§	Inner	Gaussian	identity	2.71	0.258
		Si intro elements		Inner	Gaussian	identity	2.71	0.258
	Propensity to use	Zi elements		Inner	Gaussian	identity	5.75	0.057
		Tää elements		Inner	Gaussian	identity	3.65	0.162
		Si-tää-tää calls		Inner	Gaussian	identity	5.96	0.057
		Zizi calls		Inner	Gaussian	identity		

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