



A comparative study of how British tits encode predator threat in their mobbing calls



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

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

Species vary substantially in the ways they encode information to communicate about predators. Meerkats, *Suricata suricatta*, for example, increase call rate along with a number of fine-scale

acoustic parameters to communicate an increase in the danger a predator poses (Manser, 2001), while yellow warblers, *Setophaga petechia*, use the likelihood of producing a particular call type (seet) to signal the presence of a nest predator (Gill & Sealy, 2004). Other species use strategies that range from employing a single way of encoding information to combining multiple ways of encoding information. Furthermore, some strategies may be driven entirely by the signaller's internal state while others reference external stimuli (Gill & Bierema, 2013; Magrath, Haff, Fallow, & Radford, 2014). American crows, *Corvus brachyrhynchos*, for example, use longer calls and higher call rate to signal increased danger (Yorzinski & Vehrencamp, 2009), while vervet monkeys, *Chlorocebus pygerythrus*, indicate not only predator type (leopard, eagle and snake) but also degree of danger through the propensity to use different call types (predator types) and an increase in the number of elements (degree of danger; Seyfarth, Cheney, & Marler, 1980). It is not clear why this variability across different taxa and species in encoding mechanisms exists. But, as many closely related species

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share similar vocalizations and may therefore share similar ways of encoding predator threat information, it might be that phylogenetic relationships provide part of the explanation (Hailman, 1989; Latimer, 1977; Randler, 2012).

The North American Paridae have been widely used to study the ways in which individuals encode predator threat particularly in their mobbing calls. These calls generally serve to harass the predator and/or to recruit conspecifics and heterospecifics for that harassment (Curio, 1978). In their mobbing calls, North American Paridae not only encode the presence or absence of a predator but they also differentiate between predators of different threat levels. These species indicate the presence of a higher threat predator by increases in: (1) call rate (black-capped chickadees, *Poecile atricapillus*, Carolina chickadees, *Poecile carolinensis*, mountain chickadees, *Poecile gambeli*, and tufted titmice, *Baeolophus bicolor*; Baker & Becker, 2002; Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Billings, Greene, La Lucia Jensen De, 2015; Hetrick & Sieving, 2011; Templeton, Greene, & Davis, 2005); (2) the number of elements in their calls (black-capped chickadees, Carolina chickadees, mountain chickadees and tufted titmice; Baker & Becker, 2002; Bartmess-LeVasseur et al., 2010; Billings et al., 2015; Courter & Ritchison, 2010; Hetrick & Sieving, 2011; Sieving, Hetrick, & Avery, 2010; Soard & Ritchison, 2009; Templeton et al., 2005); (3) the propensity to produce particular call types (tufted titmice and black-capped chickadees; Clemmons & Lambrechts, 1992; Sieving et al., 2010); and (4) the proportion of one call type used across mobbing events (black-capped chickadees; Baker & Becker, 2002). Of the North American species, black-capped chickadees have been shown to use all four of these ways of encoding information in response to predators of different levels of threat. While the remaining species have not been tested for all of the four ways, the available evidence suggests that they probably behave in the same fashion as black-capped chickadees and there is no indication that any of these species do not use any of the four ways of encoding information. The lack of evidence to the contrary combined with data from the outgroup, Japanese great tits, *Parus minor*, which share the four ways with black-capped chickadees, has led to the assumption that all Paridae species encode predator threat information in their mobbing calls using this particular suite of changes to their vocalizations (Hetrick & Sieving, 2011; Langham, Contreras, & Sieving, 2006; Suzuki, 2014; Wilson & Mennill, 2011).

As only a small number of the Paridae have actually been tested and most of the species tested are from the same genus (*Poecile*; Johansson et al., 2013), providing a general explanation for the ways in which animals encode predator threat is not straightforward. To test experimentally the degree to which phylogenetic conservatism might explain the distribution of encoding mechanisms within families, we induced mobbing events in flocks of tits found in the U.K. (six species across five genera) by simulating predator encounters using robotic taxidermy mounts of predators representing different threat levels. We then examined whether each of these species (1) differentiated between predators and nonpredators in their mobbing calls, (2) differentiated between high- and low-threat predators, and (3) used the same four ways of encoding predator threat as the previously tested Parid species. Here we use the term 'encode' simply to denote that the calls produced in response to different predators are statistically different and that they therefore have the potential to provide reliable information to receivers. Without playback experiments we cannot confirm that receivers decode and use this information.

We used these data to test whether phylogeny explains the number and ways of encoding information used by a given species, making the following predictions. (1) If the ways of encoding information are conserved within the Paridae, U.K. tit species should use all four ways of encoding information to differentiate predators

from nonthreats, and differentiate between predators of different threat levels. (2) If, however, any of these species vary in the way they encode information about predators, the pattern of relatedness should at least roughly match these differences such that those species that are more closely related (e.g. marsh and willow tits in the genus *Poecile*) would be more similar in the ways in which they encode information than those that are more distantly related (e.g. marsh tits in the genus *Poecile* and blue tits in the genus *Cyanistes*).

METHODS

Study Sites

We conducted experiments from January to March 2014 and 2015 in four general geographical regions in the U.K. (Fig. 1a), each of which had feeders at a number of different sites. Blue tits, *Cyanistes caeruleus*, great tits, *Parus major*, and coal tits, *Periparus ater*, are found across the U.K.; crested tits, *Lophophanes cristatus*, occur only in northern Scotland; marsh, *Poecile palustris*, and willow, *Poecile montanus*, tits occur only in the southern regions of the U.K. To test blue, great and coal tits we used feeders in and around St Andrews, Fife (56.331247°N, 2.838451°W; $N = 23$ feeder locations) from January to March 2014. To test crested tits along with blue, great and coal tits we used feeders in the northwestern Cairngorm mountains in Scotland (57.191208°N, 3.779156°W; $N = 15$ feeder locations) from January to March 2015. To test willow tits along with blue, great and coal tits, we used feeders in Doncaster (53.519235°N, 1.131355°W) and Newcastle upon Tyne (55.053305°N, 1.644546°W) from January to March 2015 ($N = 7$ feeder locations). To test marsh tits along with blue, great and coal tits we used feeders in Monk's Wood near Cambridge (52.401114°N, 0.238468°W; $N = 9$ feeder locations) from January to March 2015. Feeders were filled with black-oil sunflower seeds and peanuts and placed in either parks/forests or private gardens. To ensure that birds had enough time to locate and become accustomed to using the feeders, all of the bird feeders were put up a minimum of 2 weeks before we began the experiment.

Stimuli

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

We used custom-made robotic taxidermy mounts of each species (Carlson, Pargeter, & Templeton, 2016; Fig. 1b) to elicit mobbing responses by the tits. We used two different mounts of each species to reduce pseudoreplication. Our mounts included one male juvenile and one female adult sparrowhawk, two adult female buzzards

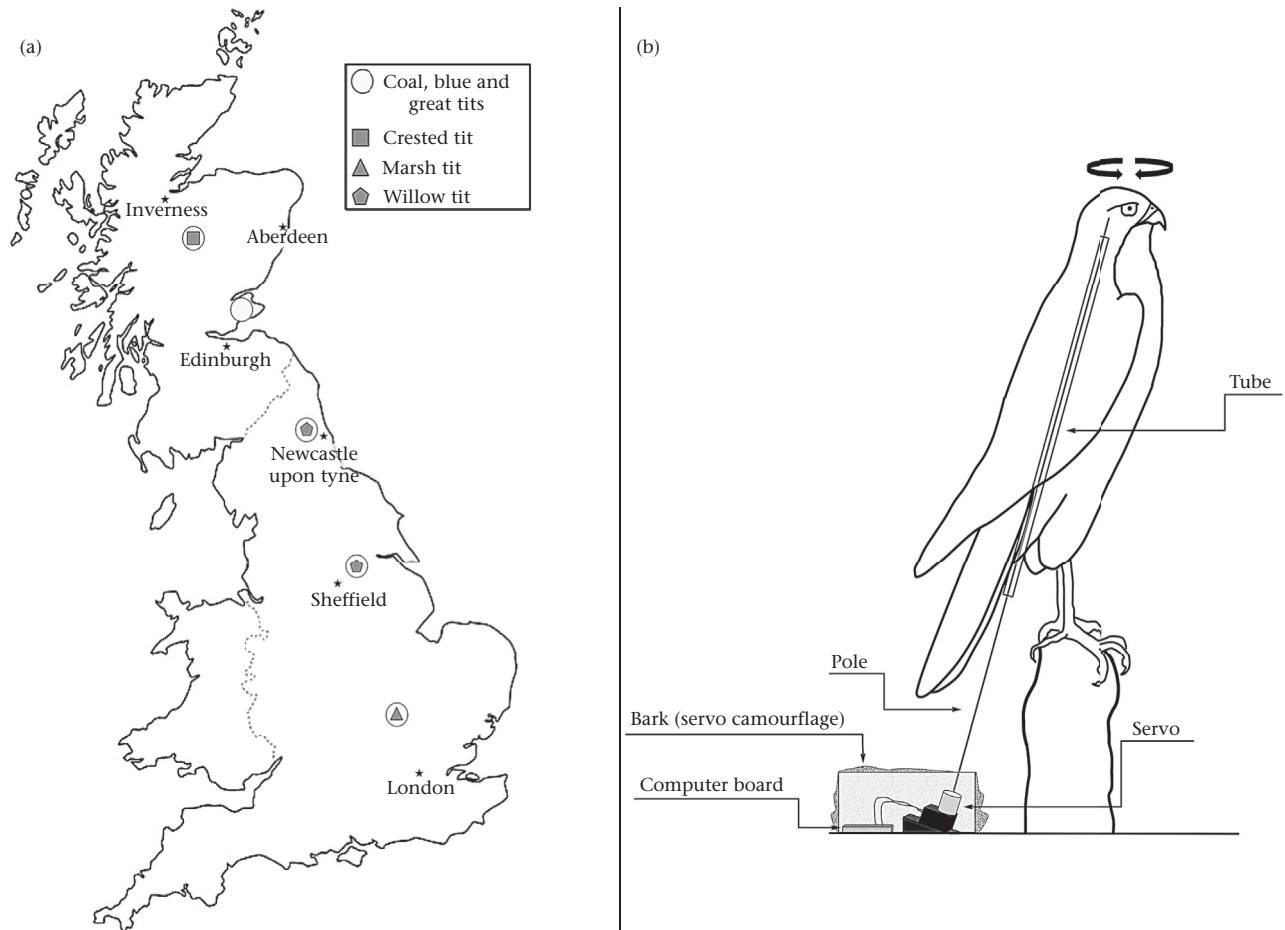


Figure 1. (a) Feeder locations in the four regions across the U.K. Blue, great and coal tits were found in all regions as shown by the light grey circles. The additional presence of crested (square), marsh (triangle) or willow tits (pentagons) is indicated by the corresponding dark grey symbol inside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

and two adult male grey partridges. All mounts were perched on a tree branch or log, and their heads rotated to mimic natural perched head movements. An Arduino computer board (Arduino Duemilanove from Arduino LLC, <https://www.arduino.cc>) controlled a servo motor, which was programmed with 15 different commands that controlled the head movement of the mounts to create a series of movements that mimicked natural behaviour. These 15 commands were the same for all three types of stimulus and the head moved for the entire time the mount was exposed. The total movement of the head ranged ca. 100° and as the chest of the mounts faced the feeder, the head faced in the direction of the bird feeder and the nearby surrounding cover all of the time (Fig. 1b; Book & Freeberg, 2015).

Predator Presentations

At each study site, we presented birds with all three treatments (sparrowhawk, buzzard, partridge) in a randomized order; the mount exemplar for each presentation was selected randomly. We conducted experiments from 1 h after dawn to 1 h before dusk to allow the birds time to recover from the presentations and allow sufficient time to forage in preparation for overnight, as these presentations were all carried out during the winter (January–March). We separated all buzzard and sparrowhawk presentations and most control and predator presentations by a minimum of 8 h at each feeder location. Owing to time constraints at some study sites, on occasion if we presented the control

(partridge) first and the birds continued to feed normally, we waited for 15 min and then presented a predator trial (six sparrowhawk and five buzzard trials). We excluded from the analyses those trials in which birds obviously responded to something other than the stimulus (e.g. when we observed a sparrowhawk flying overhead or initial behaviour suggesting birds had encountered a predator just before we arrived; $N = 7$). At nine locations the focal species were not present for one or more trials and thus we collected data for fewer than three treatments.

We began presentations once we had confirmed the presence of the focal species (acoustically or visually) near the feeder. We placed the taxidermy mount on a 1.5 m pole approximately 2 m from the bird feeder. Because head orientation is important in predator threat assessment (Book & Freeberg, 2015), we ensured that the mount faced the bird feeder in all trials. We then retreated to at least 4 m away and hid behind cover. A trial began when an individual of the focal species either: (1) came within 5 m of the mount; (2) came within 7 m of the mount with its body and head oriented towards the mount for 20 s more than once in 2 min; or (3) began mobbing the mount, by producing mobbing calls, rapidly changing perches, and wing flicking while oriented towards the mount, or flying at the mount in an aggressive fashion. Starting at this time point, we recorded when birds began to mob, and all vocalizations that were produced for 5 min before removing the mount. Distances were not physically marked in the field but, prior to beginning the manipulations, the researchers were trained to determine by eye when birds were within 3, 5 and 7 m of the

mount. We recorded all trials with a Sennheiser ME 66 supercardioid microphone (Sennheiser Electronics, Hanover, Germany) and a Marantz PMD660 solid-state sound recorder (Marantz America, LLC., Mahwah, N.J., U.S.A.) with a bit-depth of 24 bits and a sampling rate of 48 kHz.

At each simulated predator encounter we recorded the total number of individuals of each species present and kept track of which species met any of the above mobbing criteria, and therefore was considered to participate in the mobbing event. Owing to environmental conditions and the variation in flock size (mean \pm SE: 7.47 ± 0.40 individuals/flock) and composition (number of species: 2.86 ± 0.09 species/flock), sample sizes varied across species: blue: $N = 47$ locations (control $N = 41$, buzzard $N = 42$, sparrowhawk $N = 43$); great: $N = 43$ locations (control $N = 35$, buzzard $N = 41$, sparrowhawk $N = 42$); coal: $N = 41$ locations (control $N = 34$, buzzard $N = 35$, sparrowhawk $N = 36$); crested: $N = 14$ locations (control $N = 14$, buzzard $N = 14$, sparrowhawk $N = 13$); marsh: $N = 9$ locations (control $N = 9$, buzzard $N = 9$, sparrowhawk $N = 9$); willow: $N = 7$ locations (control $N = 7$, buzzard $N = 6$, sparrowhawk $N = 7$). The average number of conspecifics present during a trial also varied (mean \pm SE): blue: 3.00 ± 0.21 ; great: 2.37 ± 0.14 ; coal: 3.51 ± 0.38 ; crested: 1.73 ± 0.11 ; marsh: 1.59 ± 0.10 ; willow: 1.52 ± 0.11 .

Ethical Note

All of this work was approved by the University of St Andrews School of Biology Ethics Committee (01112013) and Scottish National Heritage, and followed ASAB/ABS guidelines for treatment of animals in research. As we conducted predator presentations during the winter months, we restricted our simulated predator encounters to the period from 1 h after sunrise to 1 h before sundown so that birds could prepare for, and recover from, the hours of darkness. As predator encounters are stressful for the animals involved, we limited predator presentations to 5 min once individuals began to respond. We then removed the stimulus and left the area as quickly as possible to allow the individuals to recover and return to feeding.

Acoustic Analysis

For all acoustic analyses, we used Raven Pro v 1.5 software (Bioacoustics Research Program, 2014) with a fast Fourier transform (FFT) size of 1050 samples, a Hann window function and a spectrogram frequency grid resolution of 23.04 Hz. We analysed all calls produced within 3 min of the onset of mobbing by manually selecting all calls and visually categorizing them by call type and call features (Table 1, Fig. 2). All call types were clearly

Table 1
Definition of call and element types for each tit species with references to spectrogram examples (Fig. 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: Fig. 2a iv 5	Intro	Narrowband	2a iv 4
	Frequency-modulated	Churr calls containing D elements that vary in peak frequency across the call: Fig. 2a ii	Mid	D elements structurally different from those before and after	2a iii 3
			Exit	D elements structurally different from those before	2a i 2
	Chirp	Calls containing chirp elements	Chirp	Broadband short call with two distinct dots on right side	2a v
Great tit	Tonal	Calls containing only tonal elements	Tonal	Narrowband	2a vi
	Jar/rattle	Calls containing jar/rattle elements	Jar/rattle	Broadband with no distinct frequency bands and triangle shape at bottom	2b i 2
	D	Calls containing D elements	Intro D	Narrowband Broadband with distinct peak shaped frequency bands	2b i 1 2b iii
	Chirp	Calls containing chirp elements	Intro Chirp	Narrowband Broadband short call with two distinct dots on right side	2b ii
Coal tit	Tonal	Calls containing only tonal elements	Intro Tonal	Narrowband Narrowband	2b iv
	Single or multi	Single calls contain strings of only one element type, multi calls contain strings of multiple element types	Bowl	Bowl shape	2c i
			Chirp	Peak with thin broadband line	2c ii
			Dot	Line with dot on right side	2c iii
			Hook	Hook shape at top and line under	2c iv
			Mound	Mound shape	2c v
			Mt	Bumpy mound shape	2c vi
			Peak	Narrowband increase in frequency	2c vii
			S-dot	S shape with dot/dash under	2c viii
			S	S shape with no dot/dash under	2c ix
			Squeak	Broadband with frequency bands	2c x
Crested tit	Trill	Calls containing trill elements	Slide Trill	Narrowband decreasing in frequency Broadband line	2c xi
	Frequency-modulated	Calls containing trill notes that shift in frequency over the course of the call: Fig. 2d ii	Intro	Narrowband	2d i & ii
Marsh tit	Tonal		Tonal	Narrowband	2d iii
	Complete	Calls containing both dā/D and tonal elements	Dā/D	Broadband with distinct frequency bands	2e i–iii 1
	Tonal	Nonbroadband frequency-modulated notes	Whole Broken	Peak shape meets at top Peak shape does not meet at top	2e i 2 2e iii 4

Table 1 (continued)

Species	Call type	Call description	Element type	Element description	Spectrogram figure
Willow tit	Dä / D	Calls containing only dä/D elements.	Full	Has both peak and slide element	2e i 2 & iii 4
			Peak	Only has peak element	2e ii 3
	Ptew Si-tää-tää	Calls containing only ptew elements Calls containing both D and si intro elements: Fig. 2f ii	Dä / D	Broadband with distinct frequency bands	
			Ptew	Tonal calls	2e iv
	Tää-tää	Calls containing only D elements: Fig. 2f i	Tää / D	Broadband with distinct frequency bands	2f i & ii 2
Si intro			Narrowband	2f ii 1	
Zizi	Calls containing only zi elements: Fig. 2f iii	Tää / D	Broadband with distinct frequency bands	2f i	
			Zi	Narrowband	2f iii

distinguished from one another as they were classed into different types based on clearly visible structural differences. Additionally, each species has a unique repertoire of calls making species identification relatively straightforward even when multiple species were calling during a trial (Table 1, Fig. 2). To confirm the reliability of the categorization of calls by N.C., we asked six people to categorize the calls. Nearly all of the classifications (89%) had high repeatability across individuals (interclass correlation (ICC) values > 0.80; Nakagawa & Schielzeth, 2010). The four calls that received scores below 0.80 all included subtle variation, and so were rescored by an individual familiar with Paridae vocalizations. Repeated scores conducted by this trained individual ranged from 0.77 to 1.0, with only one call type (short calls) receiving an ICC score below 0.80. In instances in which multiple calls overlapped it could have been more difficult to determine the number or type of elements, but this occurred infrequently and closer examination of each instance allowed the number of elements to be determined.

Statistical Analysis

Effect of predator threat on calling behaviour

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

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

We used these statistical models to test whether the bird changed a specific call/note type in response to different predator threat levels for each of the four ways of encoding information. Our response variable was the way information was encoded for each call/note type described above, and our fixed effects were the predator threat

level and three variables that accounted for the experimental design: the mount presentation order, the mount exemplar and the number of conspecifics present. To control for between-feeder variation we included date and geographical region as random effects. We also included a nested term 'calls per trial' that accounted for the number of calls (each trial at each location had varying numbers of calls produced by each species) at each feeder location during each trial. This term helped to minimize pseudoreplication of calls. We transformed the data using a log or Box Cox transform for any response variable with non-normal residuals. For the binomial models where all calls of one of the levels of stimulus:order or stimulus:mount exemplar consisted of all 1 or 0, the models could not converge, so we ran these models as linear mixed models. We ran type III Wald chi-square tests to check for significant effects of threat level for each call type for each way of information encoding for all species (Table 1). For models where threat level had a significant effect, we tested whether the effect was different for different predator threats by running a planned comparison between buzzard and sparrowhawk by reordering stimulus levels and rerunning the model (Table 1). Generalized linear mixed models were fitted by maximum likelihood using the Laplace approximation, while linear mixed models were fitted using REML and *t* tests used Satterthwaite approximations to generate degrees of freedom. This allowed us to test what call/note types each species used to differentiate between predator threats, and what information encoding mechanisms each species used. While the chance of committing a type I error is higher when multiple tests are being performed, we did not apply a correction such as a Bonferroni correction as we, like others, felt that the chance of committing type II errors was sufficiently high that biologically meaningful patterns would have been obscured (Feise, 2002; Perneger, 1998; Rothman, 1990). Instead, to help assess the robustness of our results, we calculated both marginal and conditional R^2 values specific for linear and generalized linear mixed models (Nakagawa & Schielzeth, 2012) for the overall models and 95% confidence intervals for model estimates (Table A1) We conducted all statistical analyses in R v3.1.2 (R Core Team, 2014), using the lme4 (Bates, Maechler, Bolker, & Walker, 2014) package. In our results the ways of encoding information about predator threat are reported as follows: (1) call rates as calls/individual/min, (2) element number values as the number of elements/call, (3) all proportions as the number of calls that were of a call type/total number of calls or the number of calls containing that element type/total number of calls that can contain that element type (e.g. as within great tit rattle/jar call types some calls have introductory elements, we calculated the proportion of calls that contain introductory elements by dividing the number of rattle/jar calls with introductory elements by the total number of rattle/jar calls; Fig. 2, Table 1), and (4) propensities as the number of mobbing events where the call or element type occurred/total number of mobbing events.

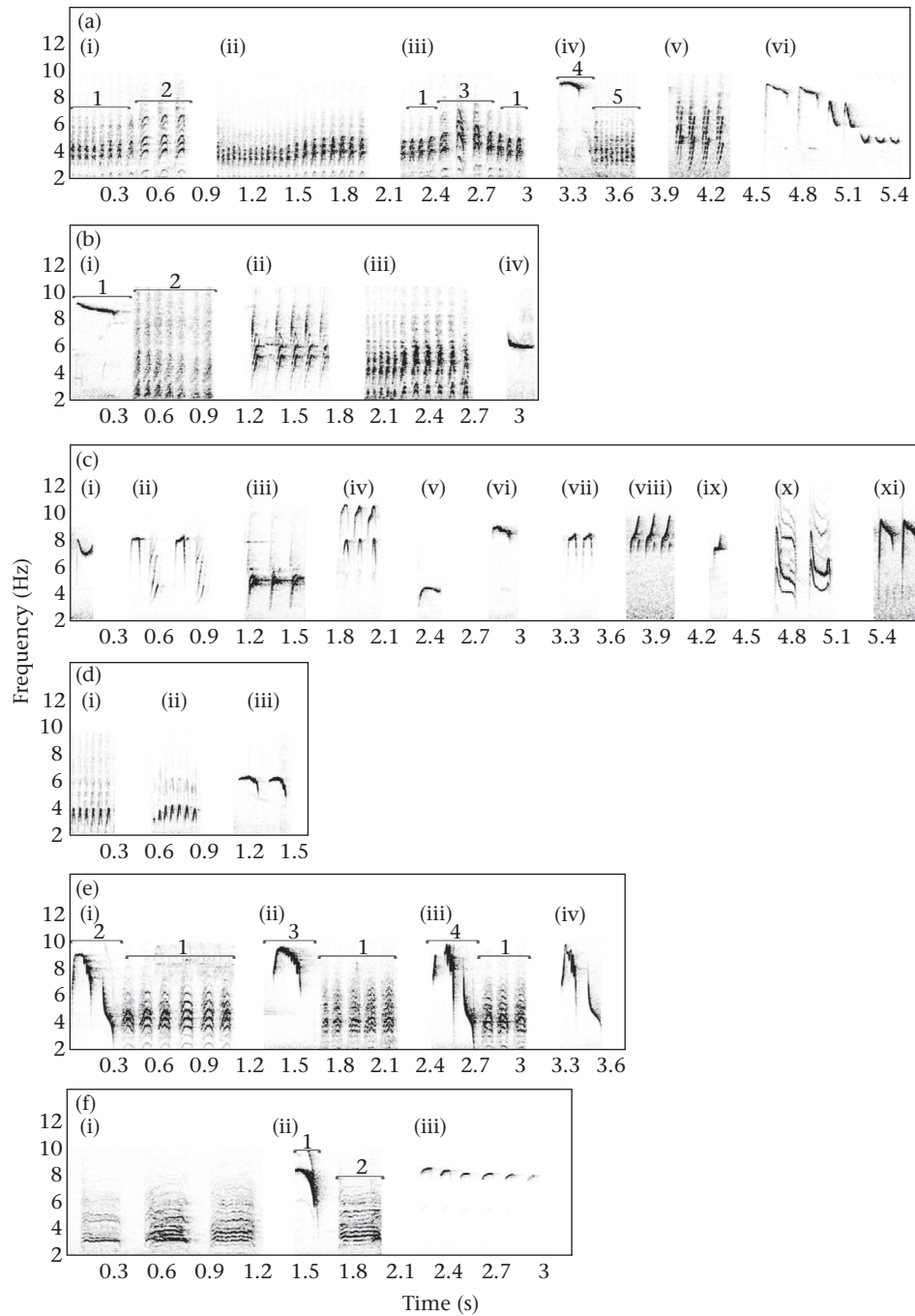


Figure 2. Spectrograms of U.K. tit mobbing calls. (a) Blue tits: (i–iv) churr call with (1) normal D elements and (2) exit elements, (ii) frequency-modulated call, (3) mid elements, (4) introductory (intro) element (similar to A or B elements in chick-a-dee calls), (5) short D elements, (v) chirp call (elements similar to C elements in chickadee calls), (vi) tonal call (similar to blue tit song). (b) Great tits: (i) jar/rattle call with (1) intro element (similar to chickadee A or B elements) and (2) jar/rattle elements, (ii) chirp call, (iii) D call, (iv) tonal call. (c) Coal tits: (i) bowl element, (ii) chirp elements (with peak elements), (iii) dot elements, (iv) hook elements, (v) mound elements, (vi) mt elements, (vii) peak elements, (viii) s-dot element, (ix) s elements, (x) squeak elements, (xi) slide elements. (d) Crested tits: (i) normal trill call, (ii) frequency-modulated trill call, (iii) tonal call. (e) Marsh tits: (i–iii) dā/D or complete calls with (1) dā/D elements, (2) full whole tonal element, (3) peak whole tonal element, (4) broken whole tonal element, (iv) ptew call. (f) Willow tits: (i) tää-tää call, (ii) si-tää-tää call, with (1) si intro element and (2) tää/D element, (iii) zizi call. All spectrograms are scaled to one another. For some call names we used new phonetic terminology, while for others call names came from other sources: all species: (Hailman, 1989); marsh and willow tits: (Haftorn, 1993); (Japanese) great tit: (Suzuki, 2014).

Effect of phylogeny on calling behaviour

To determine whether phylogeny explained the pattern of ways encoding information across the species tested, we looked for phylogenetic signal using Pagel's lambda (Freckleton, Harvey, & Pagel, 2002, Pagel, 1999). We calculated Pagel's lambda for a tree with correct branch lengths, and one that had been collapsed into a large polytomy (no phylogenetic signal) and then compared the maximum likelihood of both lambdas using a maximum likelihood test. However, as many

of the measures of phylogenetic signal are not as reliable with trees under 20 species (Freckleton et al., 2002; Münkemüller et al., 2012; Pagel, 1999) we are cautious about the results of these tests.

Effect of ecology on behaviour

To determine whether ecology explained the pattern of ways of encoding information across the species, we collected ecological information from the published literature (Alatalo, 1981; Cramp,

1993; Deadman, 1973; Ekman, 1989; Fisher, 1982; Gibb, 1960; Morse, 1978; Perrins, 1979) on foraging niche, dominance and gregariousness for each species and included them as explanatory variables in our statistical models. We chose these variables because each has been suggested as having an effect on anti-predator behaviour (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010).

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

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

Gregariousness, measured as the average size of a conspecific winter flock, could also affect the chance of seeing a predator, and therefore the propensity to produce calls, and the complexity of signalling might increase with increased group size (Freeberg & Harvey, 2008; Goodale et al., 2010; Magrath et al., 2014; Manser et al., 2014). Orange-billed babblers, *Turdoides rufescens* (Goodale & Kotagama, 2005b) and red-cap moustached tamarins (Peres, 1993) are the most abundant species in their mixed-species flocks and tend to spend more time scanning and respond to more potential threats, respectively, than do their flock mates. Downy woodpeckers, *Picoides pubescens* (Sullivan, 1985) and yellow mongooses, *Cynictis penicillata* (le Roux, Cherry, & Manser, 2008) tend to produce alarm calls only when heterospecifics are present, while the anti-predator vocal repertoire size of mongoose species, Herpestidae, increases with group size and social complexity (Manser et al., 2014).

To determine whether there was a correlation between each species' ecology and the ways in which they encoded predator threat information we ran four generalized linear models with binomial error structure including the ways of encoding information as our response variable. We ran an analysis of deviance on the model to test for significant effects of the three ecological variables, foraging niche, dominance and gregariousness, on the ways that each species encoded information about predator threat.

RESULTS

Blue Tits

Blue tits used all four ways of encoding information to differentiate between predators and nonthreats and to differentiate between different levels of threat (Table 2, Fig. 3). Blue tits increased their call rate to predators: they called the least to controls, more to buzzards and the most to sparrowhawks (mean \pm SE, conditional R^2_{GLMM} ; control: 1.06 ± 0.24 ; buzzard: 2.12 ± 0.37 ; sparrowhawk:

6.21 ± 0.73 ; $R^2_{\text{GLMM}} = 0.613$). Blue tits increased the total number of elements and D notes as threat increased, and decreased the number of mid notes to buzzards compared to the other stimuli (elements: control: 8.69 ± 0.21 ; buzzard: 10.38 ± 0.25 ; sparrowhawk: 13.01 ± 0.17 ; $R^2_{\text{GLMM}} = 0.305$; D: control: 9.26 ± 0.28 ; buzzard: 11.53 ± 0.33 ; sparrowhawk: 14.05 ± 0.19 ; $R^2_{\text{GLMM}} = 0.699$; mid: control: 2.57 ± 0.30 ; buzzard: 1.76 ± 0.17 ; sparrowhawk: 3.22 ± 0.19 ; $R^2_{\text{GLMM}} = 0.478$; Table 2). Blue tits produced a smaller proportion of the churr mobbing calls that include exit notes to either controls or sparrowhawks than to buzzards, and a smaller proportion of calls with chirp notes to sparrowhawks than to controls or buzzards (exit: control: 0.21 ± 0.02 ; buzzard: 0.16 ± 0.01 ; sparrowhawk: 0.21 ± 0.01 ; $R^2_{\text{GLMM}} = 0.469$; chirp: control: 0.31 ± 0.02 ; buzzard: 0.32 ± 0.02 ; sparrowhawk: 0.10 ± 0.01 ; $R^2_{\text{GLMM}} = 0.668$; Table 2). Blue tits also increased the proportion of tonal notes as threat increased (control: 0.12 ± 0.01 ; buzzard: 0.15 ± 0.02 ; sparrowhawk: 0.20 ± 0.01 ; $R^2_{\text{GLMM}} = 0.533$). Blue tits increased their propensity to produce mid, exit, tonal, frequency-modulated and short notes to high-threat predators compared to low-threat predators or controls (mid: control: 0.07 ± 0.04 ; buzzard: 0.15 ± 0.05 ; sparrowhawk: 0.44 ± 0.08 ; $R^2_{\text{GLMM}} = 0.488$; exit: control: 0.40 ± 0.08 ; buzzard: 0.40 ± 0.07 ; sparrowhawk: 0.84 ± 0.06 ; $R^2_{\text{GLMM}} = 0.251$; tonal: control: 0.24 ± 0.07 ; buzzard: 0.40 ± 0.07 ; sparrowhawk: 0.65 ± 0.07 ; $R^2_{\text{GLMM}} = 0.247$; frequency-modulated: control: 0.31 ± 0.07 ; buzzard: 0.32 ± 0.07 ; sparrowhawk: 0.67 ± 0.07 ; $R^2_{\text{GLMM}} = 0.607$; short: 0.44 ± 0.08 ; exit: 0.84 ± 0.06 ; sparrowhawk: 0.95 ± 0.03 ; $R^2_{\text{GLMM}} = 0.370$; Table 2).

Great Tits

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

Coal Tits

Coal tits encoded information in three ways to differentiate between controls and predator threats: call rate, element number and propensity (Table 2). Coal tits only used element number, however, to differentiate between predators of varying threat levels in their mobbing calls (Table 2, Fig. 3). Coal tits increased their call rate as threat increased (control: 0.45 ± 0.11 ; buzzard: 2.53 ± 0.56 ; sparrowhawk: 5.25 ± 1.00 ; $R^2_{\text{GLMM}} = 0.347$). They produced more hook and mt elements to buzzards than either controls or sparrowhawks (hook: control: 1.69 ± 0.16 ; buzzard: 3.91 ± 0.23 ; sparrowhawk: 3.62 ± 0.30 ; $R^2_{\text{GLMM}} = 0.490$; mt: control: 1.43 ± 0.14 ; buzzard: 2.97 ± 0.38 ; sparrowhawk: 1.47 ± 0.12 ; $R^2_{\text{GLMM}} = 0.313$; Table 2). Coal tits produced fewer squeak and more mound elements to controls than to predator threats, and more s-dot elements as threat increased (squeak: control: 2.71 ± 1.39 ; buzzard: 2.73 ± 0.16 ; sparrowhawk: 2.79 ± 0.10 ; $R^2_{\text{GLMM}} = 0.198$; mound: control: 2.50 ± 0.50 ; buzzard: 1.93 ± 0.28 ; sparrowhawk: 1.77 ± 0.14 ; $R^2_{\text{GLMM}} = 0.608$; s-dot: control: 2.09 ± 0.34 ; buzzard:

Table 2
Type III Wald chi-square test results for predator type (control, buzzard or sparrowhawk) as a significant predictor of variation in vocal response, and planned comparison t (LMM) and z (GLMM) test results for predator threat differentiation

Species	Encoding method	Element type	R^2_{GLMM}		χ^2	P	Control-Buzzard		Control-Sparrowhawk		Buzzard-Sparrowhawk	
			Marginal	Conditional			t/z	P	t/z	P	t/z	P
Blue tit	Call rate	All	0.409	0.613	43.10	<0.001	0.164	0.870	6.345	<0.001	5.452	<0.001
		Number of										
		Total elements	0.105	0.305	20.54	<0.001	-1.546	0.126	1.914	0.059	3.248	0.002
		Mid elements	0.120	0.478	6.76	0.034	-1.279	0.242	0.563	0.584	2.579	0.276
		D elements	0.178	0.699	28.84	<0.001	0.888	0.375	5.346	<0.001	3.564	<0.001
	Proportion of	Exit calls	0.113	0.469	6.27	0.044	-1.060	0.289	1.677	0.094	2.435	0.015
		Chirp calls	0.221	0.668	17.04	<0.001	2.511	0.012	-1.878	0.060	-4.104	<0.001
	Propensity to use	Tonal calls	0.153	0.533	14.17	0.001	1.105	0.269	3.649	<0.001	2.587	0.010
		Mid elements	0.288	0.488	33.01	<0.001	-0.389	0.698	5.280	<0.001	5.044	<0.001
		Exit elements	0.218	0.251	14.78	0.001	3.604	<0.001	-0.694	0.489	3.264	0.001
Tonal calls		0.243	0.247	14.35	0.001	0.490	0.625	3.695	<0.001	2.925	0.004	
Frequency-modulated calls		0.223	0.607	9.63	0.008	-1.538	0.124	2.200	0.028	2.981	0.003	
Short calls		0.312	0.370	17.27	<0.001	0.368	0.713	4.014	<0.001	3.312	0.001	
Great tit	Call rate	All	0.382	0.465	44.00	<0.001	1.822	0.071	6.569	<0.001	4.489	<0.001
	Proportion of	Chirp calls	0.065	0.578	7.55	0.023	-1.162	0.249	-2.723	0.008	-1.740	0.086
	Propensity to use	Jar/rattle calls	0.192	0.271	10.96	0.004	2.625	0.010	2.870	0.005	0.346	0.730
Coal tit	Call rate	All	0.239	0.347	15.46	<0.001	2.093	0.039	3.856	<0.001	1.216	0.227
		Number of										
		Hook elements	0.226	0.490	11.19	0.004	3.098	0.004	0.625	0.537	-2.700	0.012
		Mound elements	0.072	0.608	7.05	0.029	0.307	0.761	-1.557	0.128	-2.258	0.033
		Mt elements	0.310	0.313	21.84	<0.001	3.993	<0.001	0.049	0.961	-4.667	<0.001
		S-dot elements	0.139	0.319	11.97	0.003	1.771	0.083	1.343	0.187	-0.773	0.446
		Squeak elements	0.057	0.198	7.27	0.026	-2.656	0.008	-2.663	0.008	0.193	0.848
Propensity to use	Mound elements	0.250	0.300	9.75	0.008	2.137	0.035	2.889	0.005	0.393	0.695	
	Squeak elements	0.269	0.473	18.58	<0.001	3.703	<0.001	3.331	0.001	-0.651	0.517	
	All	0.321	0.479	6.21	0.045	-0.047	0.963	2.432	0.022	1.602	0.121	
Crested tit	Proportion of	Frequency-modulated calls	0.144	0.346	6.32	0.042	2.496	0.013	0.456	0.648	-2.207	0.027
	Propensity to use	Tonal calls	0.289	0.289	6.45	0.040	-1.173	0.251	1.940	0.063	2.318	0.028
Marsh tit	Call rate	All	0.469	0.740	10.39	0.006	-1.732	0.108	2.816	0.013	3.140	0.006
		Number of	dä/D elements	0.259	0.324	12.69	0.002	0.061	0.952	-3.491	0.001	-3.084
	Proportion of	Full tonal elements	0.255	0.370	6.88	0.031	-1.996	0.046	0.834	0.404	2.482	0.013
	Propensity to use	All tonal elements	0.398	0.398	8.28	0.016	-0.636	0.534	2.703	0.016	2.519	0.023
		Peak tonal elements	0.501	0.608	12.36	0.002	3.091	0.008	2.316	0.036	0.144	0.888
Willow tit	Call rate	Ptew calls	0.398	0.398	8.29	0.016	-0.636	0.534	2.703	0.016	2.519	0.023
		All	0.445	1.000	46.36	<0.001	3.721	0.007	1.994	0.086	0.602	0.561
	Number of	Total elements	0.129	0.201	7.89	0.019	-0.222	0.826	2.803	0.025	1.634	0.167
		Si intro elements	0.207	0.207	16.46	<0.001	0.360	0.719	-4.053	<0.001	-1.685	0.093
	Propensity to use	Zizi calls	0.234	1.000	5.96	0.051	2.420	0.036	-1.234	0.246	-0.446	0.665

Only comparisons with P values ≤ 0.05 are shown here (with the exception of zizi calls); a table including results from chi square tests with P values > 0.05 is given in the Appendix (Table A2). P values ≤ 0.05 are indicated in bold.

3.36 ± 0.10 ; sparrowhawk: 4.15 ± 0.17 ; $R^2_{GLMM} = 0.319$; Table 2). Coal tits decreased their propensity to produce mound or squeak elements in response to controls compared to predatory stimuli (mound: control: 0.06 ± 0.04 ; buzzard: 0.29 ± 0.08 ; sparrowhawk: 0.51 ± 0.08 ; $R^2_{GLMM} = 0.300$; squeak: control: 0.14 ± 0.06 ; buzzard: 0.47 ± 0.09 ; sparrowhawk: 0.63 ± 0.08 ; $R^2_{GLMM} = 0.473$; Table 2).

Crested Tits

Crested tits differentiated one or both predators from the control in three ways: call rate, proportion and propensity. However, they only used proportion and propensity to differentiate between predators of different threat levels (Table 2, Fig. 3). They increased their call rate as threat increased, produced a higher proportion of frequency-modulated calls, and had a lower propensity to produce tonal notes in response to buzzards compared to controls and sparrowhawks (rate: control: 11.71 ± 4.33 ; buzzard: 14.92 ± 3.38 ; sparrowhawk: 16.32 ± 2.30 ; $R^2_{GLMM} = 0.479$; frequency-modulated proportion: control: 0.61 ± 0.02 ; buzzard: 0.75 ± 0.01 ; sparrowhawk: 0.73 ± 0.01 ; $R^2_{GLMM} = 0.364$; tonal propensity: control: 0.21 ± 0.11 ; buzzard: 0.08 ± 0.08 ; sparrowhawk: 0.38 ± 0.14 ; $R^2_{GLMM} = 0.289$; Table 2, Fig. 3).

Marsh Tits

Marsh tits used all four ways of encoding information to differentiate both between predators and nonthreats and between

predators of different threat levels (Table 2, Fig. 3). They increased their call rate to predators compared to controls, decreased the number of dä/D elements in response to buzzards compared to controls or sparrowhawks, and decreased the proportion of full tonal notes to buzzards compared to controls and sparrowhawks (rate: control: 1.24 ± 0.35 ; buzzard: 1.26 ± 0.30 ; sparrowhawk: 4.56 ± 0.85 ; $R^2_{GLMM} = 0.740$; dä/D elements: control: 0.21 ± 0.11 ; buzzard: 0.08 ± 0.08 ; sparrowhawk: 0.38 ± 0.14 ; $R^2_{GLMM} = 0.324$; proportion of full tonal notes: control: 0.71 ± 0.07 ; buzzard: 0.49 ± 0.08 ; sparrowhawk: 0.53 ± 0.03 ; $R^2_{GLMM} = 0.370$; Table 2). They also increased their propensity to produce peak tonal elements, all tonal and ptew calls to higher threat predators (peak tonal: control: 0.33 ± 0.17 ; buzzard: 0.56 ± 0.18 ; sparrowhawk: 0.89 ± 0.11 ; $R^2_{GLMM} = 0.608$; tonal: control: 0.78 ± 0.15 ; buzzard: 0.89 ± 0.11 ; sparrowhawk: 1.00 ± 0.00 ; $R^2_{GLMM} = 0.398$; ptew: control: 0.78 ± 0.05 ; buzzard: 0.89 ± 0.11 ; sparrowhawk: 1.00 ± 0.00 ; $R^2_{GLMM} = 0.398$; Table 2).

Willow Tits

Willow tits varied several call features between the control and predator treatments but did not differentiate between predators of different threat levels (Table 2, Fig. 3). They increased their call rate in response to predators (buzzard: 1.72 ± 0.42 ; sparrowhawk: 2.04 ± 0.25 ; $R^2_{GLMM} > 0.999$) compared to controls (control: 0.71 ± 0.28 ; Table 2). They also increased the number of total elements and decreased the number of si intro elements as predator

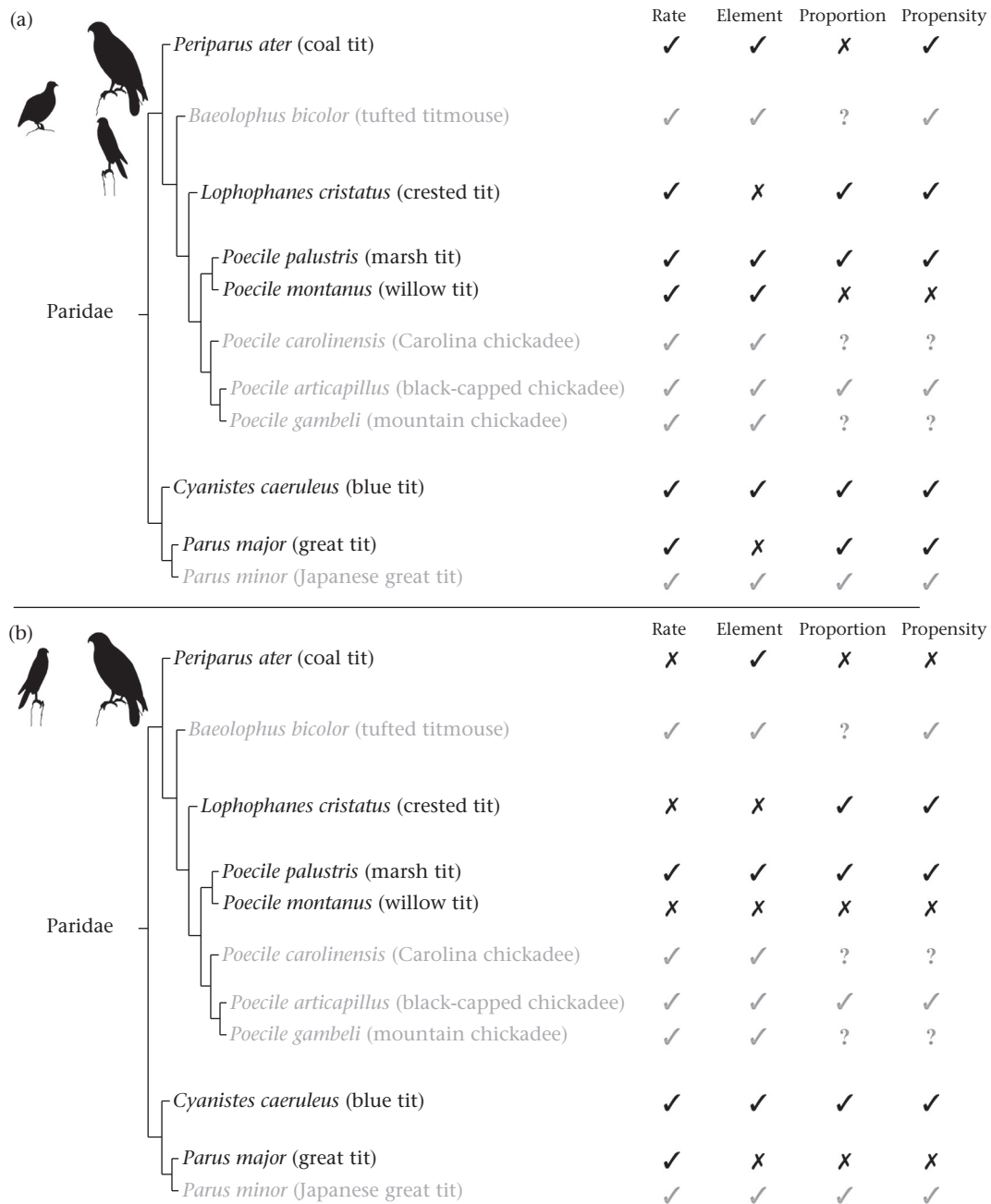


Figure 3. The four ways in which each of the previously studied Paridae encode information differentiating (a) predators (sparrowhawk and buzzard) from nonpredators (partridge) and (b) high- (sparrowhawk) from low- (buzzard) threat predators. Rate: call rate; element: number of elements in a call; proportion: the proportion of call types used within a mobbing event; propensity: the propensity to produce call types across mobbing events. Light grey text indicates those species tested in previous studies; question marks indicate encoding mechanisms not previously tested; Xs show mechanisms that are not used. Phylogeny information was based on Johansson et al. (2013). Sources of published data: black-capped chickadee: Baker and Becker (2002); Billings et al. (2015); Clemmons and Lambrechts (1992); Templeton et al. (2005); tufted titmouse: Bartmess-LeVasseur et al. (2010); Courter and Ritchison (2010); Hetrick and Sieving (2011); Sieving et al. (2010); Carolina chickadee: Bartmess-LeVasseur et al. (2010); Hetrick and Sieving (2011); Soard and Ritchison (2009); mountain chickadee: Billings et al. (2015); Japanese great tit: Suzuki (2012, 2014); Suzuki and Ueda (2013).

threat increased (elements: control: 2.40 ± 0.22 ; buzzard: 2.86 ± 0.14 ; sparrowhawk: 3.59 ± 0.12 ; $R^2_{GLMM} = 0.201$; si intro: control: 2.00 ± 0.49 ; buzzard: 2.51 ± 0.19 ; sparrowhawk: 2.83 ± 0.14 ; $R^2_{GLMM} = 0.207$; Table 2).

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

Phylogeny and Ecology

Phylogenetic signal did not explain which species used which ways of encoding information about predator threat in their mobbing calls (rate: $\chi^2_1 = -0.03$, $P = 1$; number of elements: $\chi^2_1 = -1.37$, $P = 1$; proportion: $\chi^2_1 = -6.36$, $P = 1$; propensity: $\chi^2_1 = -1.30$, $P = 1$). Ecology also did not explain the variation in which species used each method of encoding information about predator threat in their mobbing calls (rate: foraging niche:

$F_2 = 1.05$, $P = 0.431$; dominance: $F_2 = 6.59$, $P = 0.054$; gregariousness: $F_2 = 2.77$, $P = 0.176$; number of elements: foraging niche: $F_2 = 2.66$, $P = 0.184$; dominance: $F_2 = 1.91$, $P = 0.262$; gregariousness: $F_2 = 1.05$, $P = 0.431$; proportion: foraging niche: $F_2 = 0.26$, $P = 0.810$; dominance: $F_2 = 1.39$, $P = 0.515$; gregariousness: $F_2 < 0.001$, $P > 0.999$; propensity: foraging niche: $F_2 = 0.52$, $P = 0.657$; dominance: $F_2 = 2.77$, $P = 0.265$; gregariousness: $F_2 < 0.001$, $P > 0.999$; Table 3).

DISCUSSION

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

Variation across species in signalling strategy could potentially be explained by relatedness: those species more closely related should be more similar in terms of the ways in which they encode information about predators. The presence or absence of alarm calling as a behaviour in rodents appears to be well explained by phylogeny, although this says nothing about the specific ways of encoding information in these calls (Shelly & Blumstein, 2005). We found no correlation between the Parid phylogeny and the pattern of ways of encoding information. Additionally, we could find no patterns in the ways the traits mapped onto the phylogeny that would explain the ways of encoding information used by the species we tested. Marsh tits, for example, encoded information in the same ways as blue tits, one of their more distant relatives, while they shared only half of the ways of communicating the presence of a predator and none of the same ways of communicating the threat of a predator, with congeneric willow tits. Relatedness similarly failed to explain the variation in the number and mechanisms across the rest of the phylogeny. These patterns are similar to those found in yellow-bellied marmots, *Marmota flaviventris*, which also vary the ways in which they encode information about predators based on a factor other than phylogenetic relatedness (Blumstein, 2007).

If relatedness does not explain the number or ways of encoding information used by U.K. tits, aspects of their natural history might. Some species may be predisposed through their ecology to be better equipped to notice and respond to predators, and these species therefore may use a greater variety of ways of communicating that information (Goodale et al., 2010). However, our tests indicated no correlations between any of the three ecological variables we examined and the ways in which the different species

encoded predator threat information. If foraging niche explained ways of encoding information then we would have expected that outer/upper canopy-foraging blue and coal tits should be more similar in the ways in which they encode information, relative to species that forage in locations with limited visibility (lower trunk foraging: marsh, willow and great tits) as these species are less exposed to predatory raptors (Gibb, 1960; Morse, 1978; Nakamura, 1970; Perrins, 1979). Blue and marsh tits were, however, more similar in the ways in which they responded to predators (both presence and threat) than were blue and coal tits. Foraging niche, at least, does not seem to be an especially useful explanation for the variation in the ways of encoding information. Similarly, we would have expected species that travel in larger winter flocks, such as blue, great and coal tits, to use more ways of encoding information relative to less gregarious species (crested, marsh and willow tits; Deadman, 1973; Ekman, 1979; 1989; Fisher, 1982; Morse, 1978). As the more gregarious tit species were, however, no more likely to use more ways of encoding information than the less gregarious species, gregariousness during winter also is not a good explanation for the variation we see. Finally, if interspecific dominance influenced ways of encoding information we would have expected the more dominant great and blue tits to use more similar ways of encoding information. However, blue and great tits were no more similar in the ways they encoded information than the more subordinate coal or willow tits (Alatalo, 1981; Cramp, 1993; Perrins, 1979). Given that neither phylogeny nor any of the more plausible natural history traits provide an explanation for the variation in the number or ways that the U.K. species use to encode predator information in their mobbing calls, the question becomes why do these species communicate predator threat with such variety?

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

The second explanation is that each way of encoding information is used to communicate different information about the threat, enabling a signaller to increase the amount of information it can deliver (Marler et al., 1992; Suzuki, Wheatcroft, & Griesser, 2016). Here the information, while pertaining to the same threat, is not redundant. For example, Japanese great tit mobbing calls contain different element types that elicit two different types of behaviour:

Table 3
Ecology of tested Paridae species

Species	Encoding method				Preferred foraging height			Dominance			Gregariousness (flock size)		
	Call	Element number	Proportion	Propensity	Upper	Mid	Low/ground	Dominant	Mid	Subordinate	Small	Medium	Large
Black-capped chickadee	0	0	0	0	0			0				0	
Japanese great tit	0	0	0	0			0	0				0	
Marsh tit	0	0	0	0			0		0		0		
Blue tit	0	0	0	0	0			0					0
Tufted titmouse	0	0	?	?		0		0			0		
Carolina chickadee	0	0	?	?		0			0		0		
Mountain chickadee	0	0	?	?	0					0		0	
Great tit	0	X	X	X			0	0				0	
Coal tit	X	0	X	X	0					0			0
Crested tit	X	X	0	0		0			0		0		
Willow tit	X	X	X	X			0			0	0		

Species are grouped by the number and type of ways they encode information about predator threat (left-hand columns).

A, B and C notes elicit scanning behaviour, while D notes elicit approach behaviour (Suzuki, 2016). To address why related species use different ways of encoding predator threat, we need to establish what specific information it is that they encode (Templeton et al., 2005). Redundancy does seem to explain changes in the acoustic features of the calls that California ground squirrels, *Spermophilus beecheyi*, use to signal state of arousal (Owings & Virginia, 1978). Conversely, signallers might use different ways of encoding information for different types of information, for example using propensity for category of predator and call rate for distance (Griesser, 2008; Suzuki et al., 2016). This appears to be relatively common among primates. Blue monkeys, *Cercopithecus mitis stuhlmanni*, for example, signal predator type using propensity of certain call types, but change the rate of each call type as predator distance decreases to signal increased threat (Murphy et al., 2013).

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

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APPENDIX

Table A1

Model estimates and 95% confidence intervals for linear and generalized linear mixed models determining whether predatory type (control, buzzard or sparrowhawk) had a significant effect on the variation in vocal response of U.K. tit species (Table A1)

Species	Encoding method	Element type	Stimulus	Model estimate	95% Confidence interval	
					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

Table A1 (continued)

Species	Encoding method	Element type	Stimulus	Model estimate	95% Confidence interval		
					Lower	Upper	
Great tit	Number of	D elements	Sparrowhawk	4.241	0.138	8.344	
			Control	1.745	1.597	1.894	
			Buzzard	1.810	1.518	2.102	
	Proportion of	Exit calls	Sparrowhawk	2.121	1.835	2.407	
			Control	-1.822	-3.016	-0.628	
			Buzzard	-2.705	-5.532	0.122	
	Proportion of	Chirp calls	Sparrowhawk	-0.606	-3.221	2.009	
			Control	-2.933	-4.600	-1.266	
			Buzzard	-0.376	-4.039	3.286	
	Proportion of	Tonal calls	Sparrowhawk	-4.924	-8.668	-1.179	
			Control	-4.670	-6.436	-2.903	
			Buzzard	-3.759	-7.140	-0.379	
	Propensity to use	Mid elements	Sparrowhawk	-1.672	-5.048	1.704	
			Control	0.034	-0.177	0.244	
			Buzzard	-0.017	-0.486	0.451	
	Propensity to use	Exit elements	Sparrowhawk	0.779	0.292	1.267	
			Control	0.133	0.046	0.569	
			Buzzard	0.134	-0.286	0.903	
	Propensity to use	Tonal calls	Sparrowhawk	0.792	0.346	1.585	
			Control	-0.009	-0.250	0.232	
			Buzzard	0.074	-0.500	0.648	
	Propensity to use	Frequency-modulated calls	Sparrowhawk	0.666	0.067	1.264	
			Control	0.691	0.125	0.972	
			Buzzard	0.793	0.132	1.617	
	Propensity to use	Short calls	Sparrowhawk	1.613	0.692	1.963	
			Control	0.288	0.069	0.506	
			Buzzard	0.344	-0.175	0.864	
	Great tit	Call rate	All	Sparrowhawk	0.948	0.407	1.490
				Control	2.479	-0.433	5.391
				Buzzard	6.122	-0.709	12.953
	Proportion of	Chirp calls	Sparrowhawk	16.091	9.117	23.064	
			Control	0.131	0.028	0.235	
			Buzzard	0.200	-0.156	0.282	
	Propensity to use	Jar/rattle calls	Sparrowhawk	0.301	-0.264	0.187	
			Control	0.438	0.206	0.670	
			Buzzard	0.849	0.311	1.388	
Coal tit	Call rate	All	Sparrowhawk	0.911	0.356	1.466	
			Control	0.431	-2.258	3.120	
			Buzzard	4.633	-1.991	11.257	
Number of	Hook elements	Sparrowhawk	7.247	1.094	13.400		
		Control	1.737	1.055	2.862		
		Buzzard	4.608	2.528	8.455		
Number of	Mound elements	Sparrowhawk	2.959	1.706	5.153		
		Control	2.707	0.960	7.627		
		Buzzard	3.905	1.338	11.435		
Number of	Mt elements	Sparrowhawk	3.192	1.156	8.832		
		Control	1.607	1.035	2.495		
		Buzzard	7.049	3.404	14.997		
Number of	S-dot elements	Sparrowhawk	2.619	1.666	4.116		
		Control	2.315	1.293	4.148		
		Buzzard	4.258	2.224	4.395		
Number of	Squeak elements	Sparrowhawk	3.853	2.113	4.495		
		Control	10.472	3.042	36.042		
		Buzzard	10.647	3.091	36.676		
Propensity to use	Mound elements	Sparrowhawk	10.655	3.095	36.681		
		Control	-0.057	-0.287	0.173		
		Buzzard	0.368	-0.251	0.988		
Propensity to use	Squeak elements	Sparrowhawk	0.452	-0.123	1.027		
		Control	0.036	-0.209	0.281		
		Buzzard	0.801	0.151	1.451		
Crested tit	Call rate	All	Sparrowhawk	0.654	0.046	1.262	
			Control	10.084	-5.110	25.277	
			Buzzard	9.511	-29.763	48.786	
Proportion of	Frequency-modulated calls	Sparrowhawk	31.261	-0.998	63.519		
		Control	-0.430	-2.066	1.205		
		Buzzard	2.832	-1.365	7.029		
Propensity to use	Tonal calls	Sparrowhawk	-0.057	-3.297	3.183		
		Control	0.186	-0.309	0.680		
		Buzzard	-0.309	-1.632	1.013		
Marsh tit	Call rate	All	Sparrowhawk	0.751	-0.315	1.817	
			Control	4.076	-0.043	8.196	
			Buzzard	1.189	-6.198	8.576	
			Sparrowhawk	8.971	1.444	16.498	

(continued on next page)

Table A1 (continued)

Species	Encoding method	Element type	Stimulus	Model estimate	95% Confidence interval			
					Lower	Upper		
Willow tit	Number of	Dã/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		
	Call rate	All	Control	1.335	-0.194	2.864		
			Buzzard	3.045	0.615	5.475		
			Sparrowhawk	2.817	-0.169	5.804		
			Control	4.012	1.738	9.261		
			Buzzard	4.953	2.289	10.869		
			Sparrowhawk	6.649	3.077	14.456		
			Number of	Total 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	

Table A2

Type III Wald chi-square test results for predator type (control, buzzard or sparrowhawk) as a significant predictor of variation in vocal response

Species	Encoding method	Call/element type	Normality	Transform	Model type	Family	Link	χ^2	P						
Blue tit	Call rate	All			Lmer	Identity	Log	43.10	<0.001						
					Lmer	Gaussian	Identity	20.54	<0.001						
	Number of	Total elements			Log	Lmer	Gaussian	Identity	2.38	0.305					
						Lmer	Gaussian	Identity	6.76	0.034					
						Lmer	Gaussian	Identity	0.18	0.912					
						Lmer	Gaussian	Identity	28.84	<0.001					
						Lmer	Gaussian	Identity	0.92	0.630					
						Lmer	Gaussian	Identity	1.26	0.553					
						Proportion of	Intro calls		§		Glmer	Binomial	Logit	1.68	0.432
											Lmer	Gaussian	Identity	3.25	0.197
											Glmer	Binomial	Logit	6.27	0.044
											Glmer	Binomial	Logit	4.18	0.124
											Glmer	Binomial	Logit	17.04	<0.001
											Glmer	Binomial	Logit	14.17	0.001
	Propensity to use	Intro elements		§	Boxcox: 0.29	Glmer	Binomial	Logit	3.16	0.206					
						Glmer	Binomial	Logit	3.83	0.148					
						Glmer	Binomial	Logit	1.59	0.451					
						Lmer	Gaussian	Identity	33.01	<0.001					
						Lmer	Gaussian	Identity	14.78	0.001					
						Lmer	Gaussian	Identity	3.06	0.217					
						Lmer	Gaussian	Identity	4.78	0.092					
						Lmer	Gaussian	Identity	14.35	0.001					
						Glmer	Binomial	Logit	9.63	0.008					
						Lmer	Gaussian	Identity	17.27	<0.001					
Great tit						Call rate	All			Lmer	Identity	Log	44.00	<0.001	
										Lmer	Gaussian	Identity	0.65	0.721	
	Number of	Total elements			Log	Lmer	Gaussian	Identity	0.38	0.827					
						Lmer	Gaussian	Identity	0.05	0.975					
						Lmer	Gaussian	Identity	3.44	0.179					
						Lmer	Gaussian	Identity	0.40	0.819					
						Lmer	Gaussian	Identity	5.11	0.078					
						Lmer	Gaussian	Identity	1.85	0.397					
	Proportion of	Intro calls		§		Glmer	Binomial	Logit	0.56	0.756					
						Glmer	Binomial	Logit	0.13	0.939					
						Lmer	Gaussian	Identity	7.55	0.023					
						Lmer	Gaussian	Identity	0.48	0.789					
						Lmer	Gaussian	Identity	3.71	0.157					
						Lmer	Gaussian	Identity	10.96	0.004					
	Propensity to use	Intro elements		§		Glmer	Binomial	Logit	3.71	0.157					
						Lmer	Gaussian	Identity	10.96	0.004					

Table A2 (continued)

Species	Encoding method	Call/element type	Normality	Transform	Model type	Family	Link	χ^2	P	
Coal tit	Call rate	D elements			Lmer	Gaussian	Identity	1.87	0.393	
		Chirp elements	§		Lmer	Gaussian	Identity	0.50	0.779	
	Number of	Tonal elements	§		Lmer	Gaussian	Identity	4.25	0.119	
		All			Lmer	Identity	Log	15.46	<0.001	
	Proportion of	Total elements			Log	Lmer	Gaussian	Identity	3.68	0.159
		Bowl elements			Boxcox: -8.41	Lmer	Gaussian	Identity	0.53	0.766
		Chirp elements				Lmer	Gaussian	Identity	0.39	0.825
		Dot elements			Boxcox: -1.70	Lmer	Gaussian	Identity	0.63	0.729
		Hook elements			Log	Lmer	Gaussian	Identity	11.19	0.004
		Mound elements			Log	Lmer	Gaussian	Identity	7.05	0.029
		Mt elements			Log	Lmer	Gaussian	Identity	21.84	<0.001
		Peak elements			Boxcox: -0.48	Lmer	Gaussian	Identity	1.78	0.412
		S elements			Log	Lmer	Gaussian	Identity	3.18	0.204
		S-dot elements			Log	Lmer	Gaussian	Identity	11.97	0.003
		Slide elements			Log	Lmer	Gaussian	Identity	3.16	0.206
		Squeak elements			Boxcox: -0.30	Lmer	Gaussian	Identity	7.27	0.026
		Bowl elements				Lmer	Gaussian	Identity	0.34	0.844
		Chirp elements				Lmer	Gaussian	Identity	2.25	0.324
		Dot elements				Glmer	Binomial	Cloglog	0.98	0.614
		Hook elements				Lmer	Gaussian	Identity	3.18	0.204
	Mound elements				Lmer	Gaussian	Identity	1.44	0.486	
	Mt elements		§		Lmer	Gaussian	Identity	1.64	0.441	
	Peak elements				Glmer	Binomial	Logit	1.21	0.545	
	S elements		§		Lmer	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				Lmer	Gaussian	Identity	3.54	0.170	
	Propensity to use	Multi calls		§		Glmer	Binomial	Logit	5.42	0.067
		Bowl elements				Lmer	Gaussian	Identity	1.64	0.440
		Chirp elements				Lmer	Gaussian	Identity	2.41	0.300
		Dot elements				Lmer	Gaussian	Identity	3.06	0.216
		Hook elements				Lmer	Gaussian	Identity	2.22	0.329
		Mound elements				Lmer	Gaussian	Identity	9.75	0.008
		Mt elements				Lmer	Gaussian	Identity	1.61	0.447
		Peak elements				Glmer	Binomial	Logit	1.44	0.488
		S elements				Lmer	Gaussian	Identity	5.59	0.061
		S-dot elements				Lmer	Gaussian	Identity	3.88	0.144
		Slide elements		§		Glmer	Binomial	Logit	2.83	0.243
		Squeak elements				Lmer	Gaussian	Identity	18.58	<0.001
		Multi calls				Lmer	Gaussian	Identity	1.07	0.586
Crested tit		Call rate	All			Lmer	Gaussian	Identity	6.21	0.045
		Number of	Total elements		Log	Lmer	Gaussian	Identity	2.93	0.231
			Trill elements		Log	Lmer	Gaussian	Identity	0.55	0.760
	Proportion of	Tonal elements		Log	Lmer	Gaussian	Identity	2.83	0.243	
		Trill calls		§		Lmer	Gaussian	Identity	0.49	0.784
	Propensity to produce	Tonal calls		§		Lmer	Gaussian	Identity	0.50	0.778
Frequency-modulated calls			§		Glmer	Binomial	Logit	6.32	0.042	
Trill calls					Lmer	Gaussian	Identity	4.72	0.094	
Frequency-modulated calls					Lmer	Gaussian	Identity	6.45	0.040	
Marsh tit	Call rate	Tonal calls			Lmer	Gaussian	Identity	4.72	0.094	
		All			Lmer	Gaussian	Identity	10.39	0.006	
	Number of	Total elements			Log	Lmer	Gaussian	Identity	1.38	0.503
		Intro elements			Log	Lmer	Gaussian	Identity	4.03	4.031
	Proportion of	Dä/D elements				Lmer	Gaussian	Identity	12.69	0.002
		Intro elements		§		Lmer	Gaussian	Identity	0.10	0.950
		Dä/D elements		§		Lmer	Gaussian	Identity	0.06	0.972
		All tonal elements		§		Lmer	Gaussian	Identity	0.06	0.972
		Full tonal elements		§		Glmer	Binomial	Logit	6.88	0.031
		Peak tonal elements				Lmer	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
		Ptew calls		§		Lmer	Gaussian	Identity	0.06	0.972
		Dä/D calls		§		Lmer	Gaussian	Identity	0.96	0.618
	Propensity to use	Complete calls		§		Lmer	Gaussian	Identity	0.08	0.960
		Intro elements				Lmer	Gaussian	Identity	0.54	0.764
Dä/D elements					Lmer	Gaussian	Identity	0.54	0.764	
All tonal elements					Lmer	Gaussian	Identity	8.28	0.016	
Full tonal elements					Lmer	Gaussian	Identity	2.98	0.226	
Peak tonal elements					Lmer	Gaussian	Identity	12.37	0.002	
Broken tonal elements			§		Lmer	Gaussian	Identity	2.15	0.341	
Whole tonal elements					Lmer	Gaussian	Identity	2.73	0.256	
Ptew calls					Lmer	Gaussian	Identity	8.29	0.016	
Dä/D calls					Lmer	Gaussian	Identity	0.41	0.815	

(continued on next page)

Table A2 (continued)

Species	Encoding method	Call/element type	Normality	Transform	Model type	Family	Link	χ^2	<i>P</i>		
Willow tit	Call rate	All			Lmer	Gaussian	Identity	46.36	<0.001		
		Number of	Total elements		Log	Lmer	Gaussian	Identity	7.89	0.019	
	Proportion of	Number of	Si intro elements		Boxcox: -0.22	Lmer	Gaussian	Identity	16.46	<0.001	
			Zi elements		Boxcox: -0.48	Lmer	Gaussian	Identity	1.03	0.599	
		Proportion of	Tää elements			Lmer	Gaussian	Identity	5.73	0.057	
			Si intro elements			Glmer	Binomial	Logit	0.13	0.938	
		Proportion of	Zi elements			Glmer	Binomial	Logit	0.17	0.919	
			Tää elements			Glmer	Binomial	Logit	0.46	0.795	
		Propensity to use	Proportion of	Tää-tää calls			Glmer	Binomial	Logit	0.13	0.938
				Si-tää-tää calls	§		Lmer	Gaussian	Identity	1.88	0.391
			Propensity to use	Zizi calls			Lmer	Gaussian	Identity	0.76	0.684
				Si intro elements			Lmer	Gaussian	Identity	2.71	0.258
				Zi elements			Lmer	Gaussian	Identity	2.71	0.258
				Tää elements			Lmer	Gaussian	Identity	5.75	0.057
		Propensity to use	Si-tää-tää calls			Lmer	Gaussian	Identity	3.65	0.162	
			Zizi calls			Lmer	Gaussian	Identity	5.96	0.051	

P values ≤ 0.05 are indicated in bold.

§ Indicates either non-normally distributed residuals (linear mixed models) or overdispersion of maximum value of 1.20 (generalized linear mixed models).