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

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Many species use anti-predator 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 anti-predatory 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 predatory 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 non-threatening control mounts, but they all varied in the number and types of additional ways they encoded this information. Some species (blue & willow tits) used all four ways to differentiate between different threat predators, while others used only two (crested tits), one (great & 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.

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

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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 anti-predator 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 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 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. Mobbing 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 encode not only 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, 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 likely 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 out-group ‚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, Contreas & 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 UK (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 non-predators 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 Pariadae, UK tit species should use all four ways of encoding information to differentiate predators from non-threats, 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*) to 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 UK (Figure 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 UK; 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 UK. To test blue, great, and coal tits we used feeders in and around St Andrews, Fife (latitude, longitude; 56.331247, -2.838451; n = 23 feeder locations) from January-March 2014. To test crested tits along with blue, great and coal tits we used feeders in the north-western Cairngorm mountains in Scotland (57.191208, -3.779156; n = 15 feeder locations) from January-March 2015. To test willow tits along with blue, great, and coal tits, we used feeders in Doncaster (53.519235, -1.131355) and Newcastle upon Tyne (55.053305, -1.644546) from January-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, -0.238468; n = 9 feeder locations) from January-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 two weeks before we began the experiment.

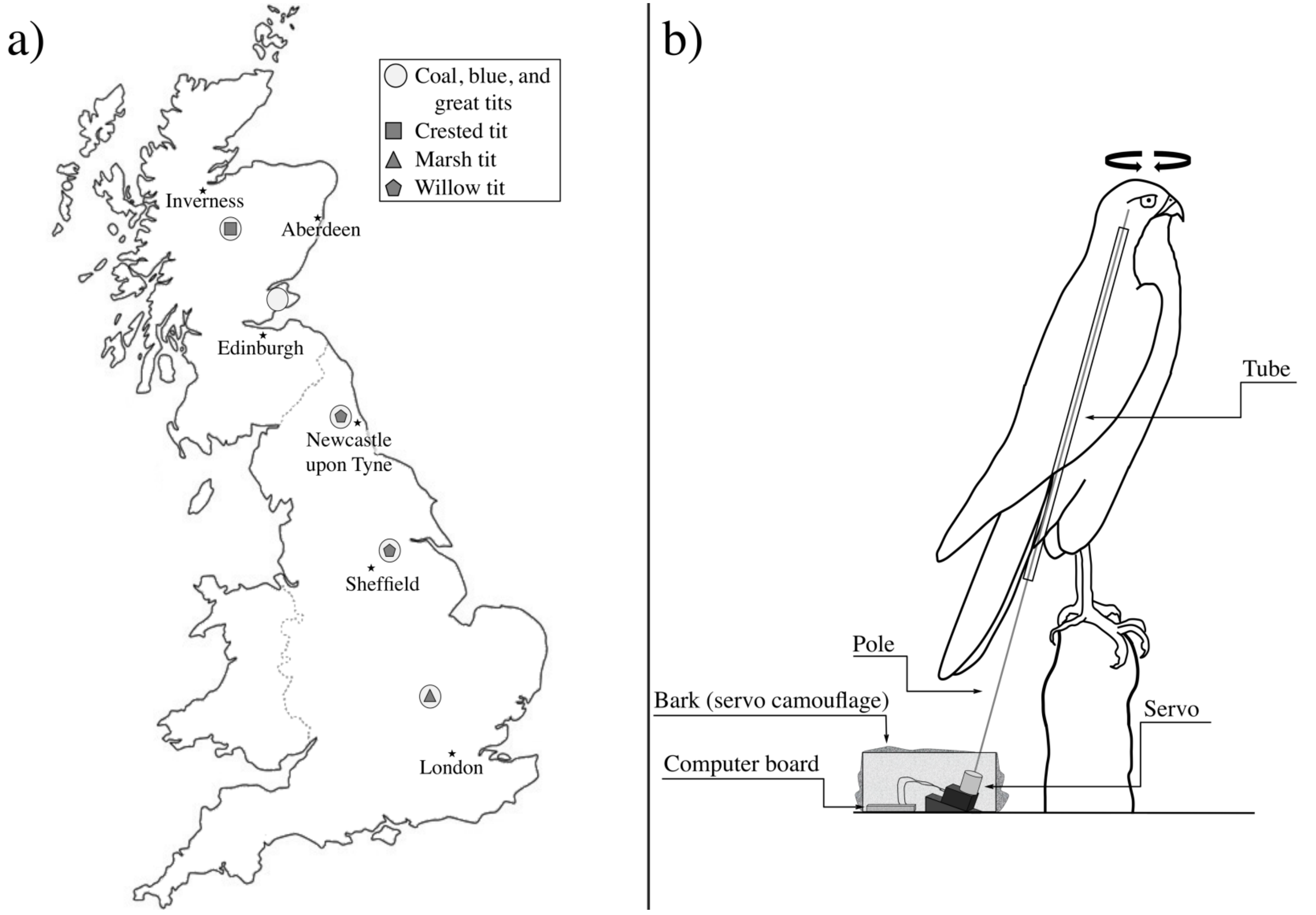
a)
Coal, blue, and great tits
Crested tit
Marsh tit
Willow tit
Inverness
Aberdeen
Edinburgh
Newcastle upon Tyne
Sheffield
London
b)
Tube
Pole
Bark (servo camouflage)
Computer board
Servo

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 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.

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 (~ 73%) made up of mammals and larger birds such as pigeons, buzzards do occasionally eat small passerines (~ 16% of their diet; Graham, Redpath, & Thirgood, 1995), including tit species (Swann & Etheridge, 2009); 3) grey partridges, *Pedrix pedrix*, 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 UK, is similar in size to a sparrowhawk, but as it does not eat birds it poses no threat to tit species (Šálek, Marhoul, Pintíř, Kopecký, & Slabý, 2004).

We used custom-made robotic taxidermy mounts of each species (Carlson et al. submitted; Figure 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, 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 ~ 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 (Figure 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 one hour after dawn to one hour 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 (Jan-March). We separated all buzzard and sparrowhawk presentations and most control and predator presentations by a minimum of 8 hours at each feeder location. Due 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 minutes and then presented a predator trial (sparrowhawk n = 6, buzzard n = 5 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 some locations the focal species were not present for one or more trials and thus we collected data for fewer than three treatments (n = 9 sites).

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 a minimum distance of 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 seconds more than once in 2 minutes; 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 minutes 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 meters of the mount. We recorded all trials with a Sennheiser ME 66 super-cardioid microphone (Sennheiser Electronics, Hanover, Germany) and a Marantz PMD660 solid-state sound recorder (Marantz America, LLC., Mahwah, N.J., USA) 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. Due to environmental conditions and the variation in flock size (mean ± standard error: 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), and willow: n = 7 locations (control n = 7, buzzard n = 6, sparrowhawk n = 7), as did the average number of conspecifics present during a trial (mean ± standard error): 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, and 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 one hour after sunrise to one hour 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 minutes 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 analyzed all calls produced within three minutes of the onset of mobbing by manually selecting all calls and visually categorizing them by call type and call features (Table 1, Figure 2). All call types were clearly 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, Figure 2). To confirm the reliability of the categorization of calls by NC, we asked six people to categorize the calls. Nearly all of the classifications (89%) had high repeatability across individuals (inter-class correlation (ICC) values > 0.80; Nakagawa & Schielzeth, 2010). The four calls that received scores below 0.80 all included subtle variation, and so were re-scored by an individual familiar with Paridae vocalizations. Repeated scores conducted by this trained individual ranged from 0.77 – 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.

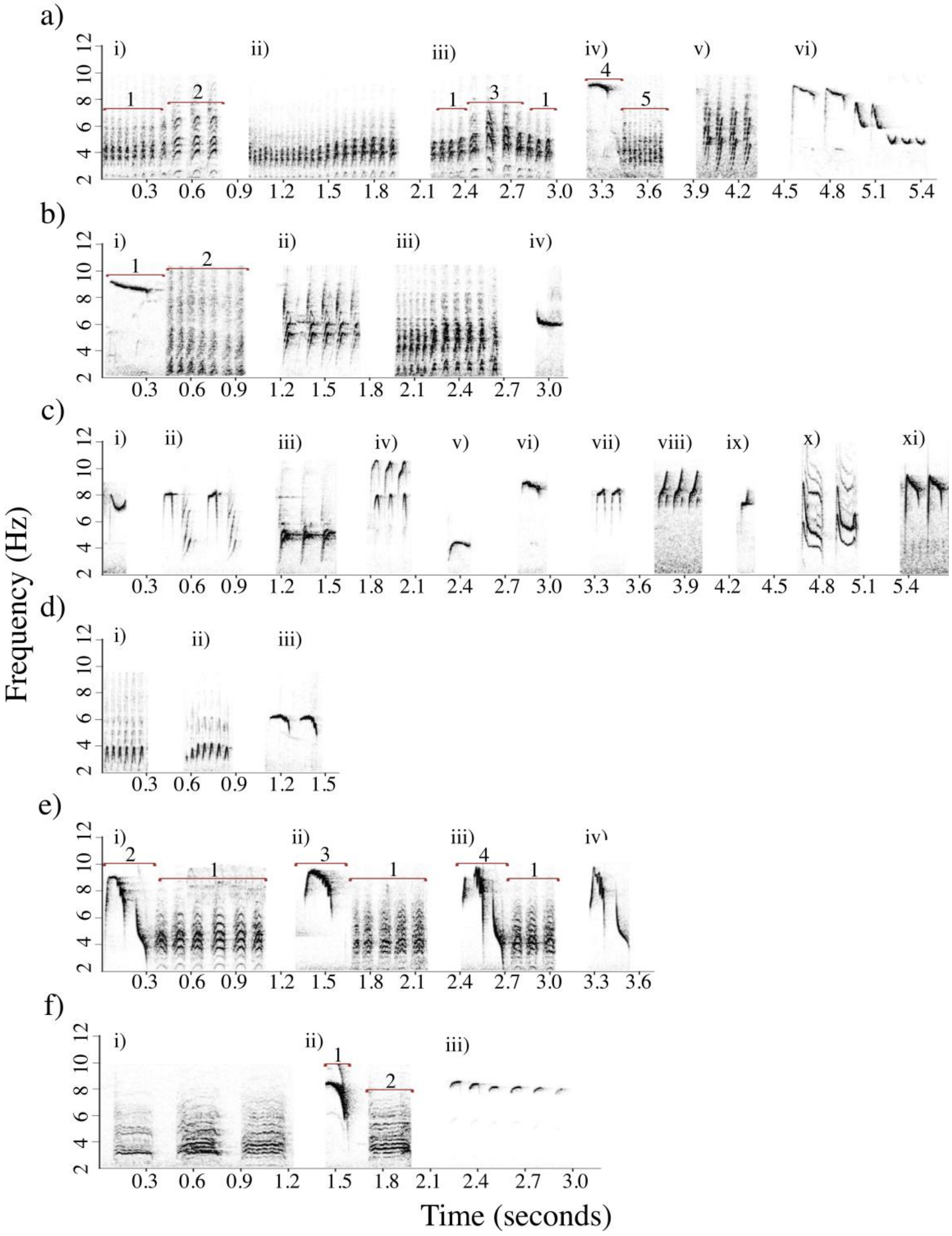

Figure 2. Spectrograms of UK tit mobbing calls. a) Blue tits: i-iv) churr call with 1) normal D elements and 2) exit elements, ii) frequency-modulated call, 3) mid elements, 4) introductory (intro) element (similar to A or B elements in chick-a-dee calls), 5) short D elements, v) chirp call (elements 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, ix) D call, x) 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) dä/D or complete calls with 1) dä/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: (J. P. Hailman, 1989), marsh & willow 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
			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
			intro	narrowband	
	Tonal	Calls containing only tonal elements	tonal	narrowband	2a vi
Great tit	Jar / rattle	Calls containing jar / rattle elements	jar / rattle	broadband with no distinct frequency bands and triangle shape at bottom	2b i 2
			intro	narrowband	2b i 1
	D	Calls containing D elements	D	broadband with distinct peak shaped frequency bands	2b iii
			intro	narrowband	
	Chirp	Calls containing chirp elements	chirp	broadband short call with two distinct dots on right side	2b ii
			intro	narrowband	
	Tonal	Calls containing only tonal elements	tonal	narrowband	2b iv
Coal tit	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
			slide	narrowband decreasing in frequency	2c xi
Crested tit	Trill	Calls containing trill elements	trill	broadband line	2d i & ii
	~Frequency-modulated	Calls containing trill notes that shift in frequency over the course of the call -- Figure 2.2d ii	intro	narrowband	
	Tonal		tonal	narrowband	2d iii
Marsh tit	Complete	Calls containing both dä / D and tonal elements	dä/D	broadband with distinct frequency bands	2e i - iii 1
	Tonal	Non-broadband frequency-modulated notes	whole	peak shape meets at top	2e i 2
			broken	peak shape doesn't meet at top	2e iii 4

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

Statistical analysis

Effect of predator threat on calling behaviour

To test how UK 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/minute), 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 (Figure 2), and as each species had a range of call/note types, we tested if each species employed the encoding mechanisms for each call/note type to differentiate between different threat predators.

We used these statistical models to test if 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 geographic 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 boxcox 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 if the effect was different for different predator threats by running a planned comparison between buzzard and sparrowhawk by re-ordering stimulus levels and re-running the model (Table 1). Generalized linear mixed models were fit by maximum likelihood using the Laplace approximation, while linear mixed models were fit 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 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 (Table 2) and 95% confidence intervals for model estimates (Table 3) 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 as follows: 1) call rates are reported as calls/individual/minute, 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 jar/rattle call types some calls have introductory elements, we calculated the proportion of calls that contain introductory elements by dividing the number of calls rattle/jar calls with introductory elements by the total number of rattle/jar calls; Figure 2, Table 1), and 4) propensities as the number of mobbing events where the call or element type occurred/ total number of mobbing events.

Effect of phylogeny on calling behaviour

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

Effect of ecology on behaviour

To determine if 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, 2014; Ekman, 1989; Fisher, 1982; Gimm, 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-predatory behaviour (Goodale et al., 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 spend 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 to eavesdrop on, rather than produce 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, *Turdoide rsufescens* (Goodale & Kotagama, 2005b) and red-cap moustached tamarinds (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 mongoose, *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 if 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 non-threats and to differentiate between different levels of threat (Table 2; Figure 3). Blue tits increased their call rate to predators: they called the least to controls, more to buzzards, and the most to sparrowhawks (mean ± standard error, conditional R^2_{GLMM}; control: 1.06 ± 0.24; buzzard: 2.12 ± 0.37; sparrowhawk: 6.21 ± 0.73; $R^2_{GLMM} = 0.613$). 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, $R^2_{GLMM} = 0.305$; D: control 9.26 ± 0.28, buzzard 11.53 ± 0.33, sparrowhawk 14.05 ± 0.19, $R^2_{GLMM} = 0.699$; mid: control 2.57 ± 0.30, buzzard 1.76 ± 0.17, sparrowhawk 3.22 ± 0.19, $R^2_{GLMM} = 0.478$; Table 2). Blue tits produced a smaller proportion of the churr mobbing calls that include exit notes compared 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, $R^2_{GLMM} = 0.469$; chirp: control 0.31 ± 0.02; buzzard 0.32 ± 0.02, sparrowhawk 0.10 ± 0.01, $R^2_{GLMM} = 0.668$; Table 2). Blue tits also increase the proportion of tonal notes as threat increases (control

0.12 ± 0.01, buzzard 0.15 ± 0.02, sparrowhawk 0.20 ± 0.01, $R^2_{GLMM} = 0.533$). 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, $R^2_{GLMM} = 0.488$; exit: control 0.40 ± 0.08, buzzard 0.40 ± 0.07, sparrowhawk 0.84 ± 0.06, $R^2_{GLMM} = 0.251$; tonal: control 0.24 ± 0.07, buzzard 0.40 ± 0.07, sparrowhawk 0.65 ± 0.07, $R^2_{GLMM} = 0.247$; frequency modulated: control 0.31 ± 0.07, buzzard 0.32 ± 0.07, sparrowhawk 0.67 ± 0.07, $R^2_{GLMM} = 0.607$; short: 0.44 ± 0.08, exit 0.84 ± 0.06, sparrowhawk 0.95 ± 0.03, $R^2_{GLMM} = 0.370$; 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; Figure 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, $R^2_{GLMM} = 0.465$; 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, $R^2_{GLMM} = 0.578$; jar/rattle propensity: control 0.68 ± 0.08, buzzard 0.81 ± 0.06, sparrowhawk 0.95 ± 0.03, $R^2_{GLMM} = 0.271$; 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; Figure 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, $R^2_{GLMM} = 0.347$). Coal tits 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, $R^2_{GLMM} = 0.490$, mt: control 1.43 ± 0.14, buzzard 2.97 ± 0.38, sparrowhawk 1.47 ± 0.12, $R^2_{GLMM} = 0.313$; 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, $R^2_{GLMM} = 0.198$; mound: control 2.50 ± 0.50, buzzard 1.93 ± 0.28, sparrowhawk 1.77 ± 0.14, $R^2_{GLMM} = 0.608$; s-dot: control 2.09 ± 0.34, buzzard 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 ± 0.01=6, 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 different threat predators (Table 2; Figure 3). They increased their call rate as threat increased, produced a higher proportion of frequency modulated calls, and 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; Figure 3).

Marsh tits

Marsh tits used all four ways of encoding information to differentiate both between predators and non-threats and between predators of different threat levels (Table 2; Figure 3). Marsh tits 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; Figure 3). Willow tits increased their call rate in response to predators (mean ± standard error; 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). Willow tits also increased the number of total elements and decreased the number of si intro elements as predator 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.

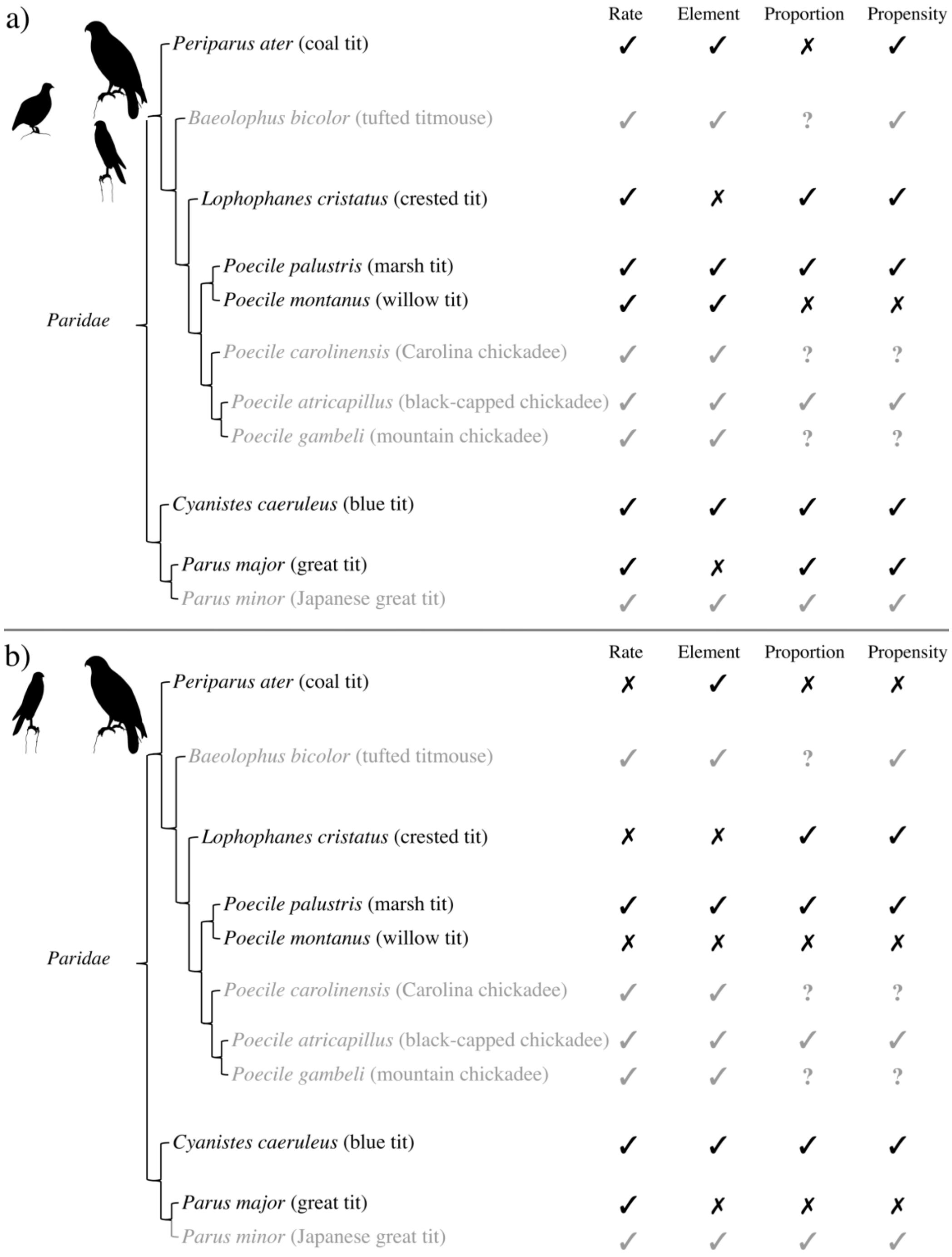

Figure 3. The four ways in which each of the previously studied Paridae encode information differentiating a) predators (sparrowhawk and buzzard) from non-predators (partridge) and b) high (sparrowhawk) from low (buzzard) threat predators. Rate: call rate, Element: number of elements in a call, Proportion: 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, and Xs show mechanisms that are not used. Phylogeny information was based on (Johansson et al., 2013). Published data derived from: black-capped chickadee: (Baker & Becker, 2002; Billings et al., 2015; Clemmons & Lambrechts, 1992; Templeton et al., 2005), tufted titmouse: (Bartmess-LeVasseur et al., 2010; Courter & Ritchison, 2010; Hetrick & Sieving, 2011; Sieving et al., 2010), Carolina chickadee: (Bartmess-LeVasseur et al., 2010; Hetrick & Sieving, 2011; Soard & Ritchison, 2009), Mexican chickadee: (Billings et al., 2015), Japanese great tit: (Suzuki, 2012; 2014; Suzuki & Ueda, 2013).

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. Planed comparison t and z test results. Only comparisons with P values ≤ 0.05 shown here (with the exception of zizi calls); full table is included in supplemental material.

			R^2_{GLMM}				Control-Buzzard		Control-Sparrowhawk		Buzzard-Sparrowhawk	
Species	Encoding Method	Element Type	Margianl	Conditional	χ^2	*P*	T	*P*	T	*P*	T	*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**
		Tonal calls	0.153	0.533	14.17	**0.001**	1.105	0.269	3.649	**<0.001**	2.587	**0.010**
	Propensity to use	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
Crested Tit	Call rate	All	0.321	0.479	6.21	**0.045**	-0.047	0.963	2.432	**0.022**	1.602	0.121
	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	**0.004**
	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
		Ptew calls	0.398	0.398	8.29	**0.016**	-0.636	0.534	2.703	**0.016**	2.519	**0.023**
Willow Tit	Call rate	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

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

					95% Confidence interval	
Species	Encoding Method	Element Type	Stimulus	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

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

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

DISCUSSION

We found that the UK tit species varied in both the types and degree to which they encode information about predators. UK 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 of encoding information they use to encode information about predators. The presence or absence of alarm calling as a behaviour in rodents appears to be well explained by phylogeny, though this says nothing concerning 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, encode information in the same ways as do blue tits, one of their more distant relatives, while they share 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 fails to explain the variation in the number and mechanisms across the rest of the phylogeny. These patterns are similar to those found in marmots, 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 UK tits, aspects of their natural history might. Some species may be pre-disposed 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, Beauchamp, Magrath, Nieh, & Ruxton, 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 are, however, more similar in the ways in which they respond to predators (both presence and threat) than are 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 those less gregarious species (crested, marsh, and willow tits; Deadman, 2014; Ekman, 1979; 1989; Fisher, 1982; Morse, 1978). As the more gregarious tit species are, 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 encode information than are the more subordinate coal or willow tits (Alatalo, 1981; Cramp, 1993; Perrins, 2012). Given that neither phylogeny or any of the more plausible natural history traits provide an explanation for the variation in the number or ways that the UK 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; J. P. 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 thereat, 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: A, B and C notes elicit scanning behaviour, while D notes elicit approach behaviour (Suzuki, 2016). In order to address why related species use different ways to encode 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 to encode different types of information, predatory category using propensity and distance using call rate (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 UK tit species each 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 of encoding information 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.

REFERENCES

Alatalo, R. V. (1981). Interspecific Competition in Tits *Parus* spp. and the goldcrest *Regulus regulus*: Foraging Shifts in Multispecific Flocks. *Oikos*, *37*(3), 335–344.

Baker, M. C., & Becker, A. M. (2002). Mobbing calls of black-capped chickadees: Effects of urgency on call production. *The Wilson Bulletin*, *114*(4), 510–516.

Bartmess-LeVasseur, J., Branch, C. L., Browning, S. A., Owens, J. L., & Freeberg, T. M. (2010). Predator stimuli and calling behavior of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology and Sociobiology*, *64*(7), 1187–1198. http://doi.org/10.1007/s00265-010-0935-y

Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2014, September 30). lme4: Linear mixed-effects models using “Eigen” and S4.

Billings, A. C., Greene, E., & La Lucia Jensen, De, S. M. (2015). Are chickadees good listeners? Antipredator responses to raptor vocalizations. *Animal Behaviour*, *110*, 1–8. http://doi.org/10.1016/j.anbehav.2015.09.004

Bioacoustics Research Program. (2014, September 30). Raven Pro: Interactive Sound Analysis Software (Version 1.5). Ithaca, NY: The Cornell Lab of Ornithology.

Blumstein, D. T. (2007). The Evolution, Function, and Meaning of Marmot Alarm Communication. In *Advances in the Study of Behavior Vol. 37* (Vol. 37, pp. 371–401). Elsevier. http://doi.org/10.1016/S0065-3454(07)37008-3

Blumstein, D. T., & Armitage, K. B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, *53*, 143–171.

Book, D. L., & Freeberg, T. M. (2015). Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats. *Animal Cognition*, *18*(5), 1155–1164. http://doi.org/10.1007/s10071-015-0888-7

Clemmons, J. R., & Lambrechts, M. M. (1992). The waving display and other nest site anti-predator behavior of the black-capped chickadee. *The Wilson Bulletin*, *104*(4), 749–756.

Courter, J. R., & Ritchison, G. (2010). Alarm calls of tufted titmice convey information about predator size and threat. *Behavioral Ecology*, *21*(5), 936–942.

Cramp, S. (1993). Handbook of the birds of Europe the Middle East and North Africa. (C. M. Perrins, D. J. Brooks, E. Dunn, R. Gillmor, J. Hall-Craggs, B. Hillcoat, et al., Eds.) Oxford, New York: Oxford University Press.

Curio, E. (1978). The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Zeitschrift Fur Tierpsychologie*, *48*, 175–183.

Curio, E., Klump, G. M., & Regelmann, K. (1983). An anti-predator response in the great tit (*Parus major*): is it tuned to predator risk? *Oecologia*, *60*(1), 83–88.

Deadman, A. J. (1973). *A population study of the coal tit (Parus ater) and crested tit (Parus cristatus) in a Scottish pine plantation* (Doctoral thesis). Aberdeen, U.K.: University of Aberdeen.

Ekman, J. (1979). Coherence, composition and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *P. cristatus*. *Ornis Scandinavica*, *10*(1), 56–68.

Ekman, J. (1989). Ecology of non-breeding social systems of *Parus*. *The Wilson Bulletin*, *101*(2), 263–288.

Evans, C. S., Macedonia, J. M., & Marler, P. (1993). Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Animal Behaviour*, *46*, 1–11.

Feise, R. J. (2002). Do multiple outcome measures require p-value adjustment. *BMC Medical Research Methodology*, *2*(8), 1–4.

Ficken, M. S., Hailman, E. D., & Hailman, J. P. (1994). The chick-a-dee call system of the Mexican chickadee. *Condor*, *96*(1), 70–82.

Fisher, D. J. (1982). Report on roving tit flocks project. *British Birds*, *75*, 370–374.

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. *American Naturalist*, *160*(6), 712–726. http://doi.org/10.1086/343873

Freeberg, T. M., & Harvey, E. M. (2008). Group size and social interactions are associated with calling behavior in Carolina chickadees (*Poecile carolinensis*). *Journal of Comparative Psychology*, *122*(3), 312–318. http://doi.org/10.1037/0735-7036.122.3.312

Furrer, R. D., & Manser, M. B. (2009). The evolution of urgency- based and functionally referential alarm calls in ground- dwelling species. *American Naturalist*, *173*(3), 400–410. http://doi.org/10.1086/596541

Gibb, J. A. (1960). Populations of tits and goldcrests and their food supply in pine plantations. *Ibis*, *102*(2), 163–208.

Gill, S. A., & Bierema, A. M. K. (2013). On the meaning of alarm calls: a review of functional reference in avian alarm calling. *Ethology*, *119*, 449–461.

Gill, S. A., & Sealy, S. G. (2004). Functional reference in an alarm signal given during nest defense: seet calls of yellow warblers denote brood-parasitic brownheaded cowbirds. *Behavioral Ecology and Sociobiology*, *56*(1), 71–80.

Goodale, E., & Kotagama, S. W. (2005a). Alarm calling in Sri Lankan mixed-species bird flocks. *Auk*, *122*(1), 108–120.

Goodale, E., & Kotagama, S. W. (2005b). Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology*, *21*(6), 669–676.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, *25*(6), 354–361. http://doi.org/10.1016/j.tree.2010.01.002

Graham, I. M., Redpath, S. M., & Thirgood, S. J. (1995). The diet and breeding density of Common Buzzards *Buteo buteo* in relation to indices of prey abundance. *Bird Study*, *42*(2), 165–173. http://doi.org/10.1080/00063659509477162

Griesser, M. (2008). Referential calls signal predator behavior in a group-living bird species. *Current Biology*, *18*(1), 69–73.

Haftorn, S. (1993). Ontogeny of the vocal repertoire in the willow tit *Parus montanus*. *Ornis Scandinavica*, *24*(4), 267–289.

Hailman, J. P. (1989). The Organization of Major Vocalizations in the Paridae. *The Wilson Bulletin*, *101*(2), 305–343.

Hailman, J. P., & Ficken, M. S. (1996). Comparative Analysis of Vocal Repertoires, with Reference to Chickadees. In D. E. Kroodsma & E. H. Miller (Eds.), *Ecology and Evolution of Acoustic Communication in Birds* (pp. 136–159). Ithaca.

Hetrick, S. A., & Sieving, K. E. (2011). Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behavioral Ecology*, *23*(1), 83–92.

Johansson, U. S., Ekman, J., Bowie, R. C. K., Halvarsson, P., Ohlson, J. I., Price, T. D., & Ericson, P. G. P. (2013). A complete multilocus species phylogeny of the tits and chickadees (Aves: Paridae). *Molecular Phylogenetics and Evolution*, *69*(3), 852–860. http://doi.org/10.1016/j.ympev.2013.06.019

Klump, G. M., & Shalter, M. D. (1984). Acoustic behaviour of birds and mammals in the predator context. *Zeitschrift Fur Tierpsychologie - Journal of Comparative Ethology*, *66*, 189–226.

Langham, G. M., Contreras, T. A., & Sieving, K. E. (2006). Why pishing works: Titmouse (Paridae) scolds elicit a generalized response in bird communities. *Ecoscience*, *13*(4), 485–496.

Latimer, W. (1977). A comparative study of the songs and alarm calls of some *Parus* species. *Zeitschrift Fur Tierpsychologie*, *45*, 414–433.

le Roux, A., Cherry, M. I., & Manser, M. B. (2008). The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*. *Animal Behaviour*, *75*(3), 943–949. http://doi.org/10.1016/j.anbehav.2007.07.014

Lima, S. L. (1993). Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *The Wilson Bulletin*, *105*(1), 1–47.

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2014). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews*, *90*(2), 1–27. http://doi.org/10.1111/brv.12122

Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B:Biological Sciences*, *268*(1483), 2315–2324.

Manser, M. B., Jansen, D. A. W. A. M., Graw, B., Hollén, L. I., Bousquet, C. A. H., Furrer, R. D., & le Roux, A. (2014). Vocal Complexity in Meerkats and Other Mongoose Species. *Advances in the Study of Behavior* (1st ed., Vol. 46, pp. 281–310). Elsevier Inc. http://doi.org/10.1016/B978-0-12-800286-5.00006-7

Marler, P. (1955). Characteristics of some animal calls. *Nature*, *176*(4470), 6–8.

Marler, P. (1967). Animal communication signals. *Science*, *157*(3790), 769–774.

Marler, P., Evans, C. S., & Hauser, M. D. (1992). Animal signals: Motivational, referential, or both? In H. Papoušek, U. Jürgens, & M. Papoušek (Eds.), *Nonverbal Vocal Communication: Comparative and Developmental Approaches* (pp. 64–84). Cambridge: Cambridge University Press.

Millon, A., Nielsen, J. T., Bretagnolle, V., & Møller, A. P. (2009). Predator-prey relationships in a changing environment: the case of the sparrowhawk and its avian prey community in a rural area. *Journal of Animal Ecology*, *78*(5), 1086–1095. http://doi.org/10.1111/j.1365-2656.2009.01575.x

Morse, D. H. (1978). Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. *Ibis*, *120*(3), 298–312. http://doi.org/10.1111/j.1474-919X.1978.tb06790.x

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, *3*(4), 743–756. http://doi.org/10.1111/j.2041-210X.2012.00196.x

Murphy, D., Lea, S. E. G., & Zuberbühler, K. (2013). Male blue monkey alarm calls encode predator type and distance. *Animal Behaviour*, *85*(1), 119–125. http://doi.org/10.1016/j.anbehav.2012.10.015

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, *85*, 935-956.

http://doi.org/10.1111/j.1469-185X.2010.00141.x

Nakagawa, S., & Schielzeth, H. (2012). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. http://doi.org/10.1111/j.2041-210x.2012.00261.x

Nakamura, T. (1970). A study of Paridae community in Japan, 141–169.

Owings, D. H., & Virginia, R. A. (1978). Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Zeitschrift Fur Tierpsychologie*, *46*(1), 58–70.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884.

Peres, C. A. (1993). Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica; International Journal of Primatology*, *61*(2), 61–76.

Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *British Medical Journal*, *316*(7139), 1236–1238. http://doi.org/10.1136/bmj.316.7139.1236

Perrins, C. M. (1979). British Tits. (M. Davies, J. Gilmour, K. Mellanby, & E. Hosking, Eds.) (1st ed.). London, U.K.: William Collins Sons & Co. Ltd.

Petty, S. J., Patterson, I. J., Anderson, D. I. K., Little, B., & Davison, M. (1995).

Numbers, breeding performance, and diet of the sparrowhawk *Accipiter nisus* and merlin *Falco columbarius* in relation to cone crops and seed-eating finches. *Forest Ecology and Management*, *79*, 133–146.

Placer, J., & Slobodchikoff, C. N. (2000). A fuzzy-neural system for identification of species-specific alarm calls of Gunnison's prairie dogs. *Behavioural Processes*, *52*, 1–9.

Placer, J., & Slobodchikoff, C. N. (2004). A method for identifying sounds used in the classification of alarm calls. *Behavioural Processes*, *67*(1), 87–98. http://doi.org/10.1016/j.beproc.2004.03.001

R Core Team. (2014). *R: A language and environment for statistical computing* (3rd ed.). Vienna, Austria: R Foundation for Statistical Computing.

Randler, C. (2012). A possible phylogenetically conserved urgency response of great tits (*Parus major*) towards allopatric mobbing calls. *Behavioral Ecology and Sociobiology*, *66*(5), 675–681.

Rothman, K. J. (1990). No adjustments are needed for multiple comparisons. *Epidemiology*, *1*(1), 43–46.

Seyfarth, R. M., & Cheney, D. L. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology*, *54*, 145–173.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094.

Shelly, E. L., & Blumstein, D. T. (2005). The evolution of vocal alarm communication in rodents. *Behavioral Ecology*, *16*(1), 169–177. http://doi.org/10.1093/beheco/arh148

Sieving, K. E., Hetrick, S. A., & Avery, M. L. (2010). The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. *Oikos*, *119*(2), 264–276.

Slobodchikoff, C. N. (2010). Alarm calls in mammals and birds. *Encyclopedia of Animal Behavior*, 40–43.

Soard, C. M., & Ritchison, G. (2009). Chick-a-dee calls of Carolina chickadees convey information about degree of threat posed by avian predators. *Animal Behaviour*, *78*(6), 1447–1453.

Sullivan, K. (1985). Selective alarm calling by downy woodpeckers in mixed-species flocks. *Auk*, 184–187.

Suzuki, T. N. (2012). Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. *Animal Behaviour*, *84*(1), 53–57.

Suzuki, T. N. (2014). Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. *Animal Behaviour*, *87*, 59–65.

Suzuki, T. N. (2016). Semantic communication in birds: evidence from field research over the past two decades. *Ecological Research*, 1–14.

Suzuki, T. N., & Ueda, K. (2013). Mobbing calls of Japanese tits signal predator type: field observations of natural predator encounters. *The Wilson Journal of Ornithology*, *125*(2), 412–415.

Suzuki, T. N., Wheatcroft, D. J., & Griesser, M. (2016). Experimental evidence for compositional syntax in bird calls. *Nature Communications*, *7*, 1–7. http://doi.org/10.1038/ncomms10986

Swann, R. L., & Etheridge, B. (2009). A comparison of breeding success and prey of the Common Buzzard *Buteo buteo* in two areas of northern Scotland. *Bird Study*, *42*(1), 37–43. http://doi.org/10.1080/00063659509477146

Šálek, M., Marhoul, P., Pintíř, J., Kopecký, T., & Slabý, L. (2004). Importance of unmanaged wasteland patches for the grey partridge *Perdix perdix* in suburban habitats. *Acta Oecologica*, *25*(1-2), 23–33. http://doi.org/10.1016/j.actao.2003.10.003

Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, *308*(5730), 1934–1937.

Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: the past, present and the future. *Ethology*, *119*(1), 1–11. http://doi.org/10.1111/eth.12015

Wilson, D. R., & Mennill, D. J. (2011). Duty cycle, not signal structure, explains conspecific and heterospecific responses to the calls of black-capped chickadees (*Poecile atricapillus*). *Behavioral Ecology*, *22*(4), 784–790.

Yorzinski, J. L., & Vehrencamp, S. L. (2009). The effect of predator type and danger level on the mob calls of the American crow. *Condor*, *111*(1), 159–168. http://doi.org/10.1525/cond.2009.080057

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

Species	Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	χ2	p value
Blue Tit	Call rate	All			lmer	identity	log	43.10	**<0.001**
	Number of	Total elements			lmer	Gaussian	identity	20.54	**<0.001**
		Intro elements		log	lmer	Gaussian	identity	2.38	0.305
		Mid elements			lmer	Gaussian	identity	6.76	**0.034**
		Exit elements		log	lmer	Gaussian	identity	0.18	0.912
		D elements		boxcox: 0.29	lmer	Gaussian	identity	28.84	**<0.001**
		Chirp elements			lmer	Gaussian	identity	0.92	0.630
		Tonal elements			lmer	Gaussian	identity	1.26	0.553
	Proportion of	Intro calls			glmer	binomial	logit	1.68	0.432
		Mid calls	§		lmer	Gaussian	identity	3.25	0.197
		Exit calls			glmer	binomial	logit	6.27	**0.044**
		D calls			glmer	binomial	logit	4.18	0.124
		Ciurp 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
	Propensity to use	Intro elements			glmer	binomial	logit	1.59	0.451
		Mid elements			lmer	Gaussian	identity	33.01	**<0.001**
		Exit elements			lmer	Gaussian	identity	14.78	**0.001**
		D elements	§		lmer	Gaussian	identity	3.06	0.217
		Chirp elements	§		glmer	binomial	logit	4.78	0.092
		Tonal elements			lmer	Gaussian	identity	14.35	**0.001**
		Frequency-modulated calls			glmer	binomial	logit	9.63	**0.008**
		Short elements			lmer	Gaussian	identity	17.27	**<0.001**
Great Tit	Call rate	All			lmer	identity	log	44.00	**<0.001**
	Number of	Total elements		log	lmer	Gaussian	identity	0.65	0.721
		Intro elements			lmer	Gaussian	identity	0.38	0.827
		Jar/rattle elements		log	lmer	Gaussian	identity	0.05	0.975
		D elements	§	log	lmer	Gaussian	identity	3.44	0.179

		Chirp elements			lmer	Gaussian	identity	0.40	0.819
		Tonal elements			lmer	Gaussian	identity	5.11	0.078
	Proportion of	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
		Chirp calls			lmer	Gaussian	identity	7.55	**0.023**
		Tonal calls			lmer	Gaussian	identity	0.48	0.789
	Propensity to use	Intro elements			glmer	binomial	logit	3.71	0.157
		Jar/rattle elements	§		lmer	Gaussian	identity	10.96	**0.004**
		D elements			lmer	Gaussian	identity	1.87	0.393
		Chirp elements	§		lmer	Gaussian	identity	0.50	0.779
		Tonal elements	§		lmer	Gaussian	identity	4.25	0.119
Coal tit	Call rate	All			lmer	identity	log	15.46	**<0.001**
	Number of	Total elements		log	lmer	Gaussian	identity	3.68	0.159
		Bowl elements		boxcox:-8.41	lmer	Gaussian	identity	0.53	0.766
		Churp 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**
	Proportion of	Bowl elements			lmer	Gaussian	identity	0.34	0.844
		Churp 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
		Multi calls	§		glmer	binomial	logit	5.42	0.067

	Propensity to use	Bowl elements			lmer	Gaussian	identity	1.64	0.440
		Churp 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
		Tonal elements		log	lmer	Gaussian	identity	2.83	0.243
	Proportion of	Trill calls	§		lmer	Gaussian	identity	0.49	0.784
		Tonal calls	§		lmer	Gaussian	identity	0.50	0.778
		Frequency-modulated calls			glmer	binomial	logit	6.32	**0.042**
	Propensity to produce	Trill calls			lmer	Gaussian	identity	4.72	0.094
		Frequency-modulated calls			lmer	Gaussian	identity	6.45	**0.040**
		Tonal calls			lmer	Gaussian	identity	4.72	0.094
Marsh Tit	Call rate	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
		dä/D elements			lmer	Gaussian	identity	12.69	**0.002**
	Proportion of	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
		Complete calls	§		lmer	Gaussian	identity	0.08	0.960
	Propensity to use	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
Willow Tit	Call rate	All			lmer	Gaussian	identity	46.36	**<0.001**
	Number of	Total elements		log	lmer	Gaussian	identity	7.89	**0.019**
		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
		Tää elements		log	lmer	Gaussian	identity	5.73	*0.057*
	Proportion of	Si intro elements			glmer	binomial	logit	0.13	0.938
		Zi elements			glmer	binomial	logit	0.17	0.919
		Tää elements			glmer	binomial	logit	0.46	0.795
		Tää-tää calls			glmer	binomial	logit	0.13	0.938
		Si-tää-tää calls	§		lmer	Gaussian	identity	1.88	0.391
		Zizi calls			lmer	Gaussian	identity	0.76	0.684
	Propensity to use	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*
		Si-tää-tää calls			lmer	Gaussian	identity	3.65	0.162
		Zizi calls			lmer	Gaussian	identity	5.96	*0.051*

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