



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

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