ANTI-PREDATOR IN UK TIT SPECIES : INFORMATION ENCODING, PREDATOR RECOGNITION, AND INDIVIDUAL VARIATION

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Anti-predator Behaviour in UK Tit Species: Information Encoding, Predator Recognition, and Individual Variation

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Abstract

To combat the ever-present threat of predation many species produce anti-predator vocalizations and behaviours (mobbing) designed to drive predators away. These vocalizations can encode a predator's threat level, and many species within a community will eavesdrop on this information. To determine how prey species produce, use, and respond to anti-predator information and how individual, social, and phylogenetic factors of different species may influence this behaviour, I conducted a series of robotic-predator presentation and anti-predator vocalization playback experiments in the wild and lab. I predicted that UK Paridae would encode information the same as previously studied species. I found that UK Paridae encode predator information in different ways, and that neither phylogeny nor ecology explained the patterns of similarity in how different species encode predator threat in their calls. Flock structure appeared to affect how species encoded predator threat and while multiple species may be sources of information for familiar flock mates, only blue and great tits met the criteria to be community informants. As blue and great tits need prior experience to recognize novel predators and juvenile great tits avoid novel predators only after seeing adults mob them, tits may use mobbing calls to learn about novel predators. While they responded to mobbing calls, juvenile blue and great tits did not engage in mobbing behaviour although they appear capable of doing so. Furthermore, while individuals varied in their responses to aerial alarm calls this variation was not explained by either their proximity to the call nor their personality. In this close examination of how anti-predator vocalizations are produced and used by UK Paridae, I found variation in these signals. This challenges previous assumptions about how Paridae encode information, raising questions as to the sources of this variation.

1. Candidate's declarations

I, Nora Carlson, hereby certify that this thesis, which is approximately 41,354 words in length, has been written by me, that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

Declaration of collaboration
I collected all of the data in this thesis with the exception of data in Chapters 5 and 6. These data were collected in part by Madeleine Bambridge (Chapter 5) and Helen Pargeter (chapter 6) under my direction for part of an honours project (Chapter 5) and during my absence from the field site (Chapter 6). One quarter of the videos used in Chapter 5 were processed by Madeleine Bambridge. All data I received from Helen Pargeter for Chapter 6 were in raw form and had never been processed, published, or analyzed prior to my receipt of the data and subsequent analysis. I consulted Dr. Michael Morrissey in regards to the linear and generalized linear mixed models used in chapters two and three.

I was admitted as a research student in September 2013 and as a candidate for the degree of PhD in [September 2014; the higher study for which this is a record was carried out in the University of St Andrews between 2013 and [2016].

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Ethical note

All of the experimental procedures described in this thesis were approved by the University of St Andrews School of Biology Ethics Committee (01112013) and Scottish National Heritage. In the case of experiments carried out the at Nederlands Instituut voor Ecologie (NIOO-KNAW) in Wageningen, Netherlands, I had additional permission approved by the Institutional Animal Care and Use Committee: the Koninklijke Nederlandse Akademie van Wetenschappen Dier Experimenten Commissie (KNAW-DEC license NIOO 14.10 to K.V.O.). All research followed the ASAB guidelines for treatment of animals in research.

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Chapter 1

General Introduction

INTRODUCTION

Predation is an important source of mortality for most living organisms. Many species have developed strategies to mitigate the threat of, defend against, or avoid predation (Caro, 2005). One of these strategies is the production of anti-predator vocalizations (Caro, 2005), which are produced by species across the animal kingdom including insects (Connétable, Robert, Bouffault, & Bordereau, 1999; Masters, 1980), amphibians (Hödl & Gollmann, 1986), mammals (Cäsar & Zuberbühler, 2012; Hollén & Radford, 2009; Townsend & Manser, 2013) and one of the most extensively studied taxa, birds (Fallow & Magrath, 2010; Gill & Bierema, 2013; Hollén & Radford, 2009). These anti-predator vocalizations can be categorized into a number of different types, which are often used in different situations (Marler, 1955; Owings & Virginia, 1978).

The two most common types of anti-predator vocalizations are aerial alarm calls and mobbing calls (Ficken, Weise, & Reinartz, 1987; Marler, 1955; Sieving, Hetrick, & Avery, 2010; Templeton, Greene, & Davis, 2005). Production of aerial alarm calls is most often associated with the presence of flying/actively hunting raptors, which represent the greatest immediate threat (Marler, 1955). These calls are often high frequency (Hz) and cover only a narrow frequency band, which makes it difficult for many raptorial predators to detect or localize the caller (Brown, 1982; Jones & Hill, 2001; Klump, Kretzchmar, & Curio, 1989; Marler, 1955). The behavioural response to an aerial alarm call is either that the receiver flees to cover immediately or freezes in place (Hinde, 1952; Owings & Virginia, 1978). This suggests that this call serves both to alert other individuals to highly dangerous situations and to induce behaviour designed to avoid immediate depredation (Marler, 1955; Morse, 1973). Mobbing calls, the main focus of this thesis, are quite different in their acoustic structure, the context under which they are produced, and in the responses of receivers to aerial alarm calls. They are often attention-grabbing and easy to localize (Marler, 1955), are most often associated with low threat, perched raptors or terrestrial predators (Klump & Shalter, 1984) and they induce mobbing behaviour, described below, in the listener(s) (Curio, Ernst, & Vieth, 1978b; Klump & Shalter, 1984).

MOBBING

In response to the discovery of a predator (Curio, Ernst, & Vieth, 1978b; Klump & Shalter, 1984) prey will produce mobbing vocalizations which, aside from harassing the predator, serve to recruit help from both conspecifics and heterospecifics (Gunn, Desrochers, Villard, Bourque, & Ibarzabal, 2000; Marler, 1955). Mobbing vocalizations are often accompanied by a suite of other behaviours, which are designed to harass and to drive off a predator (Altmann, 1956; Curio, 1978; Owings & Coss, 1977). For example, birds will approach the predator, hop between branches or fly close to a predator whilst calling, sometimes even going so far as to attack the predator (Curio, Ernst, & Vieth, 1978b). Mammals will often approach, surround, and even bite the predator (Owings & Coss, 1977).

Mobbing behaviour is not without cost. Mobbing puts individuals within reach of predators, which sometimes results in their death (Sordahl, 1990), and mobbing calls themselves may enable predators to find and attack the individuals producing them (Krams, 2001; Smith, 1968), or locate the very nests the caller is attempting to protect (Krama, 2004). The benefits, however, can be substantial. Mobbing may not only drive predators farther away (Pettifor, 1990), but can also make them less likely to depredate those species known to mob (Ekman, 1986), or to avoid roosting habitat occupied by a higher proportion of mobbing species (Pavey & Smyth, 1998). Additionally, as many of the predators that are mobbed are ambush predators, mobbing also serves as a pursuit-deterrent signal alerting the predator that it has been discovered and is therefore unlikely to catch any prey (Flasskamp, 1994). The combination of repeated discovery (decreasing likelihood of catching prey), predators avoiding depredating or roosting near mobbing species serves to reduce long-term predation pressure for the mobbing species thereby increasing the long-term benefits of mobbing. Mobbing calls also produce short-term benefits such as enhancing survival chances as they serve to alert unaware individuals to the presence of a predator, allowing them a better chance of escape (Griesser, 2013). And, as they also serve to recruit others from the surrounding area into a quick moving more concentrated flock on top of being pursuit-deterrent signals, mobbing calls themselves can increase the chance of the signaller's survival through the selfish herd or confusion effects (Caro, 2005; Crofoot, 2012; Curio, 1978; Hamilton, 1971). These calls can also be used to encode the degree to which a predator is a threat (Fallow & Magrath, 2010; Gill & Bierema, 2013; Hollén & Radford, 2009).

Information encoding

Many species encode information in their mobbing calls about predator threat, but as species differ in their vocalizations, so do the ways they encode information about predator threat, or even in the information they encode. The predator threat information that can be encoded in these calls includes information about a predator's: 1) size (e.g. Carolina chickadees, *Poecile carolinensis,* Soard & Ritchison, 2009, black-capped chickadees, *P. atricapilla,* Templeton et al., 2005, and Gunnison's prairie dogs, *Cynomys gunnisoni,* Slobodchikoff, Briggs, Dennis, & Hodge, 2012), 2) distance (e.g. blue monkeys, *Cercopithecus mitis stuhlmani*, Murphy, Lea, & Zuberbühler, 2013, and crowned plovers, *Vanellus coronatus,* Müller & Manser, 2008), 3) speed of approach (e.g. male domestic chickens, *Gallus gallus,* Evans, Macedonia, & Marler, 1993b), 4) type (e.g. dwarf mongoose, *Helogale parvula,* Beynon & Rasa, 1989, Japanese great tits, *Parus minor,* Suzuki, 2012, and daina monkeys, *Cercopithecus diana diana*, Zuberbühler, Noë, & Seyfarth, 1997), and even 5) behaviour (e.g. Siberian jays, *Perisoreus infaustus,* Griesser, 2008).

Referential vs. graded information

The different types of information regarding a predator threat can be encoded in mobbing calls in two main ways: referentially and graded. Referential signals contain information that refers to a particular object or event outside of the caller, such as a specific type of predator (Gill & Bierema, 2013; Manser et al., 2014; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013; Seyfarth & Cheney, 2010). As we cannot test whether signallers have a mental representation of the object or event they may be referencing with their calls, the true 'meaning' of a given call is unknown. However, calls that are given with high production specificity and that illicit different, adaptive predator-specific responses in receivers across a variety of circumstances are considered functionally referential (Gill & Bierema, 2013; Macedonia & Evans, 1993; Manser et al., 2014; Schel et al., 2013; Townsend & Manser, 2013; Seyfarth & Cheney, 2010). Evidence for functionally referential calls occurs in a wide range of species. Japanese great tits, *Parus minor*, for example, use different calls for Japanese rat snakes, *Elaphe climacophora,* compared to Jungle crows, *Corvus macrorhynchos* (Suzuki, 2011b; 2014; Suzuki & Ueda, 2013), while Siberian jays, *Perisoreus infaustus*, differentiate between owls and hawks (Griesser, 2009), vervet monkeys, *Cercopithecus aethiops*, between leopards, *Panthera pardus*, Martial eagles, *Polemaetus bellicosus*, and pythons, *Python sebae* (Seyfarth, Cheney, & Marler, 1980), and ringtailed lemurs, *Lemur catta*, between carnivores and other threats (Macedonia, 1990) using different types of calls. All of these calls result in categorically different anti-predator search behaviour regardless of the urgency (immediacy or proximity) of the threat, suggesting that the receivers of these calls interpret them as referring to different types of predators.

Unlike functionally referential signals, which are used to describe discrete categories, graded signals change along a continuum in response to differences in threat (Manser et al., 2014). Graded changes in call structure are often thought to be the result of the signaller's internal state (Gill & Bierema, 2013; Suzuki, 2014), size and speed of a predator (Templeton et al., 2005; Wilson & Evans, 2012) or the threat it poses (Templeton et al., 2005). They are most commonly seen within one call type where gross or fine-scale differences create a gradation of threat (Suzuki, 2014). While the gradations in calls are thought to not be functionally referential due to the fine scale changes between gradations resulting in lower production specificity, gradations can be produced in reference to an external threat or event. Many species in the Paridae family (Courter & Ritchison, 2010; Hetrick & Sieving, 2011; Templeton et al., 2005), American crows, *Corvus brachyrhynchos* (Yorzinski & Vehrencamp, 2009), pica, *Ochotona princepes* (Ivins & Smith, 1983), and great gerbils, *Rhombomys opimus* (Randall, McCowan, Collins, Hooper, & Rogovin, 2005), all change elements of their mobbing calls such as increasing or decreasing the length of certain notes or inter-note intervals (Randall et al., 2005; Soard & Ritchison, 2009; Templeton et al., 2005; Yorzinski & Vehrencamp, 2009), or their calling rate/number of notes (Courter & Ritchison, 2010; Hetrick & Sieving, 2011; Ivins & Smith, 1983; Soard & Ritchison, 2009) as predator threat increases. Although graded calls seem less specific than referential calls, they allow transmission of finer detail concerning the current and/or changing level of danger a predator poses, and require the signaller to make and communicate a more detailed assessment of the threat posed by a predator.

As researchers increasingly discover that many species combine both graded and functionally referential calls to create high levels of signal specificity not possible with one method alone, the clear division between referential and graded has broken down (Evans, 1997; Griesser, 2009; Keenan, Lemasson, & Zuberbühler, 2013; Shedd, 1982; Vanderhoff & Eason, 2009a; 2009b; Wilson & Evans, 2012). For example, tufted capuchins, *Cebus apella nigritus*, use discrete calls for aerial and terrestrial predators, and increase their call rate as the predator gets closer (Wheeler, 2010), while Japanese great tits similarly use different calls for Japanese rat snakes compared to Jungle crows and increase the number of elements in their calls as the predator threat increases (Suzuki, 2014). As there is such a diversity of the type of information that can be encoded in calls, it stands to reason that there are a number of different ways these different types of information can be encoded.

Ways of encoding information

Information about a predator's threat can be encoded using both gross differences such as the structure and composition and fine-scale acoustical variations of the signal itself. Many animals that produce different call types or calls made up of discrete elements encode information by varying when or how often they use specific parts of calls or call types. Increasing call rate is thought to be one of the most common ways of encoding information about a predator's threat level and is used by a variety of species of birds and mammals. For example, Japanese great tits (Suzuki, 2014), and yellow-bellied marmots (Armitage & Blumstein, 1997) increase their call rate as predator threat increases. Individuals can also increase the number of notes or elements in their calls to signal differences in predator threat. Black-capped chickadees (Templeton et al., 2005) and California ground squirrels, *Spermophilus beegheyi* (Owings & Virginia, 1978), use this method and increase the number of notes or elements in their calls as a predator's threat increases. As many species produce multiple call, or element, types to warn about predators, they can change the proportion of those calls or elements they produce to different predators. Tufted titmice, *Baeolophus bicolor,* for example, will increase the proportion of certain call or element types in their calls as predator threat increases (Sieving et al., 2010). Finally, individuals can change the production specificity across different mobbing events. Production specificity occurs when an individual produces one call type almost exclusively to one type of threat (e.g. snake) and another call type to a different type of threat (e.g. crow; Seyfarth et al., 1980; Suzuki, 2012). Vervet monkeys, *Ceropithefus aethiops*, (Seyfarth et al., 1980), and Arabian babblers, *Turdoides squamiceps*, produce predator specific calls to eagles vs. leopards (vervet monkeys, Seyfarth et al., 1980), and cats vs. owls (Arabian babblers, Naguib et al., 1999) respectively.

Not all species encode information using gross differences in their vocalizations and instead some change fine-scale acoustic metrics of their calls. Herring gulls, *Larus argentatus*, for example, increase the frequency (kHz) at the end of their calls and include changes in frequency that are larger the higher degree of threat posed by the predator (Shah, Greig, MacLean, & Bonter, 2015), while banded mongoose, *Mungos mungo*, will change aspects of frequency, bandwidth, and modulation to generate more tonal calls vs. harsher broadband calls used in different threat situations (Furrer & Manser, 2009a), and meerkats, *Suricata suricatta*, will change the frequency of the first formant of their calls to differentiate between aerial and terrestrial predators (Townsend, Charlton, & Manser, 2014). Some species will even use a combination of gross and fine scale differences to encode information. Black-capped chickadees (Templeton et al., 2005) and tufted titmice (Sieving et al., 2010), for example, use both gross (number of elements in their calls and call rate) and fine-sale (changes in note length and inter-note interval) acoustic changes to signal varying degrees of predator threat.

While the types of predator threat information and the ways in which different species encode this information is relatively well investigated, the prevalence of this behaviour across related species and the mechanisms driving the evolution of different encoding strategies is still not well understood.

Chapter 1

Information use during mobbing

Why mob?

To understand why individuals produce the information used during mobbing events, first it is necessary to understand why individuals mob at all. While mobbing can benefit other individuals in the social group, it can be risky for the individual(s) that are actively engaging in this behaviour (Caro, 2005; Crofoot, 2012; Garay, 2009; Hughes, Kelley, & Banks, 2012; Sordahl, 1990). Although a number of theories about how and why mobbing behaviour evolved have been proposed, most fall into two main categories: self interest or reciprocal altruism (Curio, 1978).

Self-interest based motivations can be broken further into two groups: direct and indirect (nepotistic) self-interest. Direct benefits to individuals from mobbing behaviour include driving the predator from an area (Pettifor, 1990, Flasskamp, 1994), alerting the predator of its discovery thereby discouraging an attack (Flasskamp, 1994), and reducing local long-term predation pressure by decreasing the likelihood a predator will hunt (Ekman, 1986) or nest (Pavey & Smyth, 1998) near the mobbing species. Mobbing calls are also used to recruit others thereby increasing the group size and therefore decreasing both the likelihood of a successful predator attack (Andersson, 1976; Robinson, 1985) and any potential cost to the signaller through the selfish herd or confusion effects (Caro, 2005; Crofoot, 2012; Curio, 1978; Hamilton, 1971) .

Indirect, or nepotistic, motivation occurs when an individual is altruistic towards kin, thus indirectly increasing their own fitness (Consla & Mumme, 2012; Knight & Temple, 1986). With regard to alarm calls, this requires both that individuals call preferentially to warn their kin and that alarm calling benefits receivers. Many species are more likely to mob and produce mobbing calls when kin are present by either increasing mobbing intensity (e.g. Northern cardinals, *Cardinalis cardinalis,* Gehlbach & Leverett, 1995; Siberian jays, Griesser, 2009, Griesser & Ekman, 2004; and Formosan squirrels, *Callosciurus erythraeus thaiwanensis,* Tamura, 1989), propensity to mob (e.g. superb Fairy-wrens, *Malurus cyaneus,* Colombelli-Négrel, Robertson, & Kleindorfer, 2010; and Gunnison's prairie dogs, *Cynomys gunnisoni,* Hoogland, 1996), or a combination thereof (Black-capped chickadees, Shedd, 1983). Receivers could benefit in a number of ways: (1) if they are more likely to detect and respond more quickly to a predator after hearing an alarm call (Siberian Jays, Griesser, 2013); (2) by learning about a novel threat when naïve (e.g. blackbirds, *Turdus merula,* Curio, Ernst, & Vieth, 1978a, and Tammar wallabies, *Macropus eugenii,* Griffin, Evans, & Blumstein, 2001); (3) by reducing their susceptibility to predation through a pre-emptive response (fleeing to cover, Marler, 1955, by engaging in mobbing, Pettifor, 1990, or making themselves less conspicuous Knight & Temple, 1986). While there are examples that in which kin are the recipients, many individuals engage in mobbing in the presence of unrelated individuals (Barash, 1974), indicating that kin-selection only explains some mobbing behaviour.

In contrast to self-interest based motivations, reciprocal altruism occurs when individuals act in an altruistic and costly way that benefits an unrelated individual, based on the expectation that this individual will then assist them in the future (Campbell & Reece, 2005). Reciprocal altruism can occur in social systems where individuals have a high chance of repeated interactions (Campbell & Reece, 2005) and requires that 'neighbours' are: 1) recognized and share a history with other individuals in the area, which makes their responses reliable and predictable, 2) will continue to have repeated interactions in the future, and 3) that cheaters are punished. Many species show a higher propensity to mob with increased familiarity with their social companions. For example, great tits are more likely to assist in mobbing at a neighbour's nest if they have been neighbours previously (Grabowska-Zhang, Sheldon, & Hinde, 2012), and dominant individuals were more likely to mob with individuals of their own flock than with strangers (Krams, Krama, & Iguaune, 2006b), and migratory chaffinches, *Fringilla coelebs* (Krams & Krama, 2002). Willow tits, *Parus montanus* (Alatalo & Helle, 1990), are more likely to respond to and mob with their neighbours or flock-mates after they have spent time with them. While reciprocal altruism is one explanation given for these examples, increased time spent with others is inherently linked to increased time spent in the same territory. Therefore, what is often explained by reciprocal altruism could also be explained by occupancy: neighbours mob predators to lower predation pressure in the area since mobbing events (individual and group) benefit everyone. While this simpler explanation serves in some cases, there are others where reciprocal altruism may play a part. For example, Pied flycatchers, *Ficedula hypoleuca*, 'punish' cheaters by stopping helping neighbours mob if those neighbours were present during a recent mobbing event but did not help (Krama et al., 2012; Krams, Krama, & Igaune, 2006a). These examples suggest that, although shared occupancy is a more likely explanation for the majority of conspecific and heterospecific mobbing groups, reciprocal altruism may play some part in a few species' propensity and intensity of mobbing.

Although kin-selection and reciprocal altruism seem, at first glance, mutually exclusive explanations, they may act at different scales or time periods within the same communities. For example, during the breeding season when young are present, a given species might be motivated by kin-selection but in the non-breeding season this same species might be motivated instead by reciprocal altruism, potentially altering their mobbing behaviour. To better understand why individuals produce mobbing calls in either situation, we need to understand who the recipients of this information are, intended and otherwise.

Who listens?

Mobbing calls are designed to travel over relatively long distances as they are often used to recruit other individuals (Bloomfield, Farrell, & Sturdy, 2008; Klump & Curio, 1982; Zuberbühler et al., 1997) and are thought to be broadcast primarily to one or a combination of, three types of receivers: conspecifics, predators, and heterospecifics (Branch & Freeberg, 2012). Currently, it is thought that mobbing calls are almost always specifically meant for conspecifics, either individuals related to the caller (Colombelli-Négrel et al., 2010; Griesser, 2009; Griesser & Ekman, 2004; Hoogland, 1996; Tamura, 1989) or individuals who frequently make up the group they occur in (Cresswell, 1994; Curio, 1978; Krams, 2010; Krams, Krama, & Iguaune, 2006b). However, these signals may also be intended for the predator itself (Curio, 1978; Krams, 2010; Zuberbühler, Jenny, & Bshary, 1999). As many of the predators frequently mobbed are ambush or stealth predators, it is thought that these signals may also serve as pursuit-deterrent signals: by indicating to the predator that it has been observed, the predator is more likely to move on because aware prey are generally more difficult to catch (Curio, 1978; Flasskamp, 1994; Zuberbühler et al., 1999). Finally, these calls, whether intended or not, are often received and used by heterospecifics (Carrasco & Blumstein, 2011; Magrath, Haff, Fallow, & Radford, 2014). Although there are very few examples of one species producing mobbing calls specifically to attract other species (e.g. greater racket-tailed drongos, *Dicrurus paradiseus,* Goodale & Kotagama, 2006), many species will eavesdrop on these signals and use the information provided (Carrasco & Blumstein, 2011; Magrath et al., 2014).

While eavesdropping appears common among a number of different communities, and across different species, the extent of these eavesdropping networks often remains unknown. To better understand which species in these communities eavesdrop on others it is necessary to understand why individuals eavesdrop and what the costs may be.

Why eavesdrop?

Acquiring predator threat information can be a costly endeavour, as predator inspection behaviours such as approaching a predator may increase an individual's chance of being eaten, while also taking time away from other necessary behaviours such as foraging (Caro, 2005; Crofoot, 2012; Hughes et al., 2012; Sordahl, 1990). As a result, many species will eavesdrop on predator threat information provided by other individuals (either conspecifics or heterospecifics; Carrasco & Blumstein, 2011; Magrath et al., 2014). Eavesdropping itself is not without potential costs as the information acquired is often less reliable than is personal information (Barrera, Chong, Judy, & Blumstein, 2011; Giraldeau, Valone, & Templeton, 2002; Magrath, Pitcher, & Gardner, 2009; Rieucau & Giraldeau, 2011), but public information also has a number of benefits, which include: reducing the possibility of capture or detection by predators, increasing the ability to detect predators, gaining detailed information about predator threat without being exposed to the predator, gaining spatial information about predators, increased time available for foraging due to lower vigilance rates, and learning about novel predators (Magrath et al., 2014).

For an individual to use public or socially acquired information over personal experience, the information provided needs to meet a number of criteria. First, the eavesdropper must be able to detect and ‘decode’ the signal (Magrath et al., 2014). This can happen in a number of ways, for example, through similarity in call structure or learned associations (Magrath et al., 2014). Second, the information must be salient. Individuals will not pay attention to information about a species that is not threatening. New Holland honeyeaters, *Phylidonyris novaehollandiae*, for example, will preferentially pay attention to and use the information from only those species with which they share predators such as the white-browed scrubwren, *Sericornis frontalis* (Magrath et al., 2009). They will ignore the alarm calls from other species with which they share fewer predators, such as superb fairy-wrens, *Malurus cyaneus* (Magrath et al., 2009). Third, the information needs to be reliable (Magrath et al., 2014). Unreliable alarm calls, both false positives and false negatives are potentially costly: false positives impact fitness through unnecessary and costly anti-predator behaviour (Cresswell, 2008), while false negatives may result in incorrect behaviour resulting in injury or death (Magrath et al., 2014). Adults of many species, Florida scrub jays, *Aphelocoma coerulescens corerulescens* (Francis, Hailman, & Woolfenden, 1989), and Richardson’s ground squirrels, *Spermophilus richardsonii* (Hare & Atkins, 2001; Sloan & Hare, 2006), for example, will not respond, or respond less, to juveniles than to adults as they are often less reliable than are adults. Similarly, vervet monkeys respond less to unreliable than to reliable individuals (Cheney & Seyfarth, 1988), while a number of eavesdropping species will delay their response to less reliable orange-billed babblers, *Turdoides rufescens*, but respond quickly to highly reliable greater racket-tailed drongos (Goodale & Kotagama, 2005a). If these three criteria are met, eavesdropping can be immensely beneficial especially to those species less-capable of detecting predators or that are more vulnerable to predation (Magrath et al., 2014).

Information sources and scroungers

It is generally thought that communities are made up of those species that frequently produce large amounts of information about predator threat regardless of the presence of others and those that eavesdrop on, or scrounge, this information (Dolby & Grubb, 1999; Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Harrison & Whitehouse, 2011; Hetrick & Sieving, 2011).

In the mixed-species flock literature the species that are thought to be the primary producers of predator threat information are often equated with nuclear species (Goodale & Kotagama, 2008; Hetrick & Sieving, 2011). This is primarily due to the fact that of the traits that define a species as nuclear (i.e. 1) key in recruiting and/or maintaining group cohesion, Moynihan, 1962, 2) often found in large numbers, Goodale & Beauchamp, 2010; Hutto, 1994, 3) are gregarious, Hutto, 1994 or, in the case of birds, sallying, Goodale & Kotagama, 2005a, and 4) frequently produce conspicuous anti-predator calls Goodale & Kotagama, 2008; Hetrick & Sieving, 2011; Hutto, 1994), the anti-predator vocalizations they produce are a key driver for mixed-species flock formation and maintenance (Goodale et al., 2010; Goodale & Beauchamp, 2010; Goodale & Kotagama, 2008; Goodale & Ruxton, 2010; Sridhar, Beauchamp, & Shanker, 2009; Sridhar, Jordán, & Shanker, 2013). Additionally, many of the species that appear to eavesdrop on the calls of these nuclear species are negatively affected by their removal (Dolby & Grubb, 1998), which can result in reduced nutritional condition as they spend less time foraging due to increased scanning rates and shifts in microclimate use (Dolby & Grubb, 1998; Sullivan, 1985). Due to the negative effects of the removal of nuclear species or of other gregarious species that produce detailed information about predator threat has on other species, nuclear species are thought to be community informants: individuals that provide detailed information about predator threat for the entire community of species with which they share predators (Hetrick & Sieving, 2011).

The species that are thought to eavesdrop on the information produced by information sources are not as well researched as nuclear species. While species that produce mobbing calls are equated with nuclear species, those that are thought to eavesdrop on mobbing calls are often equated with satellite species from the mixed-species flock literature (Hetrick & Sieving, 2011). This is because satellite species are thought to: 1) be inconsequential to the recruitment and maintenance of mixed-species groups, 2) tend to associate with one other conspecific at most, 3) are more territorial, 4) are more vulnerable to predation and, most importantly, 5) infrequently produce anti-predator vocalizations (Moynihan, 1962; Ridley, Wiley, & Thompson, 2013). In general satellite species are thought to rely on information from the nuclear species as they are unable to, or very infrequently, produce their own detailed information about predator threat (Lea, Barrera, Tom, & Blumstein, 2008; Ridley et al., 2013).

While species in mixed-species groups are often categorized as either nuclear or satellite species, more recently they have been shown to fall on a gradient based on their importance and connectedness to other individuals in the group (Srinivasan, Raza, & Quader, 2010). While this gradation has been addressed in the mixed-species flock literature this is something that has yet to be addressed in the community informant/information scrounger dichotomy.

LEARNING

While many species appear to have un-learned anti-predator behaviour there are just as many examples of species that appear to learn these responses (Caro, 2005; Griffin, 2004). There are costs and benefits to both learned and un-learned anti-predator behaviours. Un-learned anti-predator behaviour has the advantage of providing young with appropriate responses to predator stimuli without the need of experience (Caro, 2005; Griffin, 2004; Hollén & Radford, 2009). However, if this behaviour is fixed it does not allow for modification later in life in response to ecological or situational changes that could alter the composition of the predator population (Caro, 2005; Griffin, 2004). Learned anti-predator behaviour is beneficial specifically because it does allow individuals to adjust their behavioural responses to predators if the composition or differences in predator behaviour or presence across seasons changes (Caro, 2005; Griffin, 2004). The cost is that for young that learn how to respond appropriately to predators during the first or first few encounters with them may respond inappropriately resulting in injury or death (Caro, 2005).

Predator recognition

One of the most important aspects of anti-predator behaviour, learned or un-learned, is the ability to recognize and respond appropriately to a predator, for juveniles and adults alike. Juveniles, particularly those of species that have precocial young, appear to recognize and respond correctly to predators without prior experience. For example, juvenile white-tailed ptarmigan, *Lagopus leucura*, (Ausmus & Clarke, 2013), Richardson's, *Spermophilus richardsonii,* and California, *S. beecheyi,* ground squirrels, (Owings & Coss, 1977; Wilson & Hare, 2006), and tadpoles from three frog species, *Pelophylax perezi, Pelobates cultripes,* and *Bufo calamita* (Polo-Cavia, Gonzalo, López, & Martín, 2010), all respond to predators appropriately when presented with naturally occurring predators for the first time. However, there are just as many examples of juveniles that respond to novel predators very differently from adults (great tits, Kullberg & Lind, 2002, rhesus monkeys, *Macaca mulatta*, Mineka, Davidson, Cook, & Keir, 2004, Japanese macaques, Masataka, 1983, paradise fish, *Macropodus opercularis,* L., Csányi, 1985, Iberian green frog tadpoles, *Rana perezi,* Gonzalo, López, & Martín, 2007, and Belding's ground squirrels, *Spermophilus beldingi,* Robinson, 1981). The lack of recognition in these species suggests that learning is an important part of predator recognition and in developing appropriate responses to these threats.

Juveniles are not the only individuals that exhibit incorrect behaviour in response to novel predators. Adults of species raised in captivity or in populations missing certain types of predators may also exhibit inappropriate behaviour in response to novel predators (Caro, 2005; de Azevedo, Young, & Rodrigues, 2012; Griffin, 2004), indicating that these individuals must learn about novel threats. One way they may do this is through observing anti-predator behaviour associated with a novel predator.

Curio (1978) and Curio et al. (1978a) were the first to show that individuals could learn socially about predators by observing others mobbing a novel predator. They found that one blackbird could learn to mob a novel 'threat' (honeyeater) by observing a demonstrator's apparent mobbing response to the object (Curio, Ernst, & Vieth, 1978a), and could then pass this response down a chain of individuals (Curio, Ernst, & Vieth, 1978a). Vieth et al. (1980) went on to produce similar results using heterospecific mobbing calls. More recently, Griffin & Galef (2005) showed that carib grackles, *Quiscalus lugubris,* after being presented with a novel 'threat' (black-and-yellow pigeon) coupled with grackle mobbing calls, subsequently changed their alarm calling behaviour appropriately in response. And Baker (2004) replicated Curio's 1978 experiment using black-capped chickadees with similar results, while Conover (1987) suggested that ring-billed gulls, *Larus delawarensis*, appear to use mobbing events to learn about predator threats.

Whether or not a species does or does not recognize novel predators as a threat, juveniles may still have to learn either how to engage in mobbing behaviour or to associate the adult mobbing calls with the appropriate predators.

Mobbing behaviour & response to anti-predator vocalizations in juveniles

Learning may be involved not only in predator recognition, but also in both correct mobbing behaviour and response to the information in mobbing calls. Juveniles of many species respond differently to anti-predator vocalizations compared to adults (Lea & Blumstein, 2011). Meerkat, *Suricata suricatta*, juveniles, for example, run towards the nearest adult in response to all alarm calls (Hollén & Manser, 2006), while black-billed magpies, *Pica pica,* stay silent and hidden in response to mobbing calls (Buitron, 1983). Juveniles of yet other species, black-capped chickadees (Ficken et al., 1987), marsh harriers, *Circus aeruginosus* (Sternalski & Bretagnolle, 2010), Siberian jays (Griesser, 2013), and Verreaux's sifakas, *Propithecus verreauxi verreauxi* (Fichtel, 2008) rarely engage in mobbing behaviour at all, even when accompanied by adults. While some of these differences in responses may be a result of predators posing different threats to juveniles (Hollén & Radford, 2009), it may be that juveniles must learn how to perform this behaviour. Juvenile American robins (Shedd, 1982), and Florida scrub jays (Francis et al., 1989), for example, will usually approach silently and observe adult-led mobbing events rather than participate in them, but will begin to exhibit mobbing behaviour upon dispersal or after their first breeding season.

Although there appears to be a role for learning to play in both predator recognition in juveniles and naïve adults, as well as in the acquisition of anti-predator behaviour or the response to the information encoded in alarm calls, little is known about how this behaviour develops over time or what ontogenetic processes may affect the development of this behaviour.

VARIATION IN ANTI-PREDATOR BEHAVIOUR

Responses to predators and anti-predator vocalizations vary across individuals, something that could be a result of differences in vulnerability or costs and benefits. For example, dominant individuals tend to instigate alarm calling (black-capped chickadees, Ficken & Witkin, 1977, Florida scrub-jays, Francis et al., 1989), or spend more time alarm calling than do other individuals (willow tits, *Parus montanus,* Alatalo & Helle, 1990, Northern cardinals, *Cardinalis cardinalis,* Gehlbach & Leverett, 1995, Florida scrub-jays, Francis et al., 1989, and Siberian jays, Griesser, 2013). Some take these risks only when they are accompanied by a female (great tits, Curio, Klump, & Regelmann, 1983, and chickens, Karakashian, Gyger, & Marler, 1988), or when they occupy the most dominant position in a group (great tits, Curio et al., 1983, Florida scrub-jays, Francis et al., 1989). This makes sense given that the age and/or sex of the individuals can differentially affect the costs and benefits they receive/incur from being in a group: dominant males often protect females and have a vested interest in keeping the current territory safe as it will often become their breeding territory in the spring (Alatalo & Helle, 1990), while incurring few costs and all of the benefits through the dilution effect as flock size increases (Griesser & Ekman, 2004). Subordinate individuals, on the other hand, have less invested in the territory and are not usually related, so have little incentive to put themselves in danger by being the first to alarm call (Alatalo & Helle, 1990), especially as they often forage in areas of increased predation risk (Suhonen, 1993a; 1993b; Suhonen, Halonen, & Mappes, 1993) whereby they are at greater risk when calling.

Variation in an individual's general propensity to mob and in their intensity of mobbing behaviour is most often linked with their dominance, but there are examples of species whose phenotype correlates with differences in, not only general mobbing behaviour, but finer levels of specificity during mobbing as well. In marsh harriers, for example, there are two colour morphs (grey and brown), each attributed with a different behavioural type (Sternalski & Bretagnolle, 2010). While both age and sex affect mobbing behaviour, with males and adults mobbing more than females and juveniles (Sternalski & Bretagnolle, 2010), the colour morph of males is also a good predictor of the aspect of a mobbing event in which an individual participates (Sternalski & Bretagnolle, 2010). Grey males mob less but often detect a threat, whereas brown males mob more and recruit others well, with lighter (older and more experienced) individuals being more successful in their recruiting attempts (Sternalski

& Bretagnolle, 2010). This difference may come from differences in ecology/motivation between the morphs. Grey morphs have a higher concentration of eumelanin, a chemical responsible for both pigment in feathers and levels of intraspecific aggression, resulting in increased aggression and less cooperative behaviour (such as mobbing; Sternalski & Bretagnolle, 2010). Similar morphologically-based variation in mobbing occurs in the different morphs of white-throated sparrows, *Zonotrichia albicollis* (Gehlbach & Leverett, 1995). These examples suggest that finer levels of specialization of functional roles may exist in groups of birds in an alarm situation based, not only on general dominance, but on morphology as well.

One other trait that varies across individuals within a species that may impact behaviour is 'boldness' (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2012a). Measures of 'boldness,' often determined through assays testing an individual's responses during stressful situations (Carter et al., 2012a; Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; Kurvers et al., 2010), have been linked to differences in mobbing behaviour. In great tits, for example, 'neophilic' individuals, which were more likely to resume feeding their chicks after a novel object was placed on their nestbox, mobbed a predator longer and approached closer than did 'neophobic' individuals (Vrublevska et al., 2014). As factors such as 'personality', social structure, and degree to which they are a nuclear species, age, and other previously discussed factors, have the potential to affect anti-predator behaviour and the information contained in anti-predator vocalizations, I have designed a number of questions to address how these factors may impact these anti-predator responses across a range of situations.

QUESTIONS

My interest is in the ways in which prey species produce, use, and respond to anti-predator information and how the individual, social, and phylogenetic factors experienced by different species may influence this behaviour.

Species of choice

To answer this question I chose to use the six tit species found in the UK: blue tits, *Cyanistes caeruleus*, great tits, *Parus major*, coal tits, *Periparus ater*, crested tits, *Lophophanes cristatus*, marsh tits, *Poecile palustris*, and willow tits, *Poecile montanus*. I chose these species as my study organisms as they fit a number of behavioural, ecologic, and logistic criteria that allowed me to conduct experimental manipulations of perceived threat, taking advantage of reliable natural behaviour, variation in phylogenetic relatedness, habitat, and range overlaps, and to conduct experiments both in the wild and the lab.

Tits are part of the Paridae family, a family whose ways of encoding information about predator threat in their mobbing calls have been well studied in a number of North American species (Billings, Greene, & La Lucia Jensen, 2015; Courter & Ritchison, 2010; Ficken, Hailman, & Hailman, 1994; Soard & Ritchison, 2009; Templeton et al., 2005), and one Japanese species (Suzuki, 2014). These North American cousins are known to be aggressive mobbers, which respond well to simulated predator encounters as well as to conspecific and heterospecific playbacks (Hetrick & Sieving, 2011; Nolen & Lucas, 2009), and have a highly conserved mobbing call acoustical structure (Hetrick & Sieving, 2011; Randler, 2012). Like their North American cousins, the UK tits also mob predators using vocalizations and behaviours similar to those of North American Paridae (Hailman, 1989; Perrins, 1979; Randler, 2012), suggesting they may encode predator threat information in the same ways. The species in the UK are generally thought to fill the same niche as other Paridae, as nuclear species and /or community informants (Nakamura, 2008; Perrins, 1979; Suzuki, 2011a; 2016a), which makes them an ideal group to study how predator threat information is produced, affected by, and used in mixed-species communities. UK tit species span a wider range of genera (Johansson et al., 2013; Perrins, 1979) than previously studied Paridae, which enables insights into how phylogeny may impact how different species encode information, as well as possibly offering some insight to the ancestral state of mobbing behaviour in Paridae. Tits are quite common where they are found in the UK, with the exception of the marsh and willow tits, allowing for large sample sizes from multiple areas within each species' range (Cramp, 1993; Perrins, 1979). Finally, blue, great, and coal tits occur across the entirety of the UK allowing me to examine variation across their range (Perrins, 1979).

Main questions

In order to address how prey species produce, use, and respond to anti-predator information and how the individual, social, and phylogenetic factors experienced by different species may influence this behaviour, I designed experiments to answer a number of more specific questions:

Are encoding methods conserved across the Family Paridae? (Chapter 2)
Do tits serve as information sources in their community? (Chapter 3)

More explicitly:

Are tits reliable in the information they produce across mobbing events?

Are tits used as a source of information by information scroungers?

Do tits learn about predators?

More explicitly:

Do tits recognize novel predators? (Chapter 4)

Do juvenile tits learn to avoid predators by observing mobbing events? (Chapter 5)

Do juvenile tits mob, or if not, produce any mobbing behaviours? (Chapter 6)

Are individuals variable in their responses to anti-predator signals? (Chapter 7)

To address these questions I used predator presentations in the field at locations across the UK (Question 1), taking advantage of natural range differences of tit species in the UK which resulted in different flock compositions (Questions 2 and 3a). I also conducted predator presentations and simulated mobbing events (Question 3b), and playback experiments in the wild (Question 3c) and in the laboratory (Question 4).

Chapter 2

Ways of encoding information about predators in mobbing vocalizations

INTRODUCTION

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, 1993b; Gill & Bierema, 2013; Griesser, 2008; Marler, 1955; Murphy et al., 2013; Placer & Slobodchikoff, 2000; 2004).

Species vary substantially in the ways they encode information to communicate about predators. Many *Suricate* species, 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 propensity to produce 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, and some may be driven entirely by the signaller's internal state while others reference external stimuli (Gill & Bierema, 2013; Magrath et al., 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 pygerythru,* indicate not only predator type (leopard, eagle, and snake) but degree of danger through both propensity to use different call types (predator types) and to increase the number of elements (degree of danger; Seyfarth et al., 1980). It is not clear why this variability in encoding mechanisms across different taxa and species 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 at least part of the explanation (Hailman, 1989; Latimer, 1977; Randler, 2012)

The North American Paridae have been widely used to study the way in which animals encode predator threat particularly in their mobbing calls. Mobbing calls serve both to harass the predator and to recruit conspecifics and heterospecifics for that harassment (Curio, 1978). In their mobbing calls, North American Paridae not only encode the presence 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 et al., 2015; Hetrick & Sieving, 2011; Templeton et al., 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 et al., 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). Furthermore, as Japanese great tits, *Parus minor*, also use the same four ways to communicate predator threat (Suzuki, 2012; 2014), it has been assumed that all Paridae species encode predator threat information in their mobbing calls using these particular ways of changing their vocalizations (Hetrick & Sieving, 2011).

As only a small number of the Paridae have actually been tested, however, and most of those 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, I 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. I then examined whether each of these species 1) differentiated between predators and non-predators, 2) differentiated between high and low threat predators, and 3) used the same four ways of encoding predator threat in their mobbing calls as the previously-tested Parid species.

I 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 to 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*) should 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

I conducted experiments from January to March 2014 and 2015 in four general geographical regions in the UK (Figure 2.1a), 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 I 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 I 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, I 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 I 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 I began the experiment.

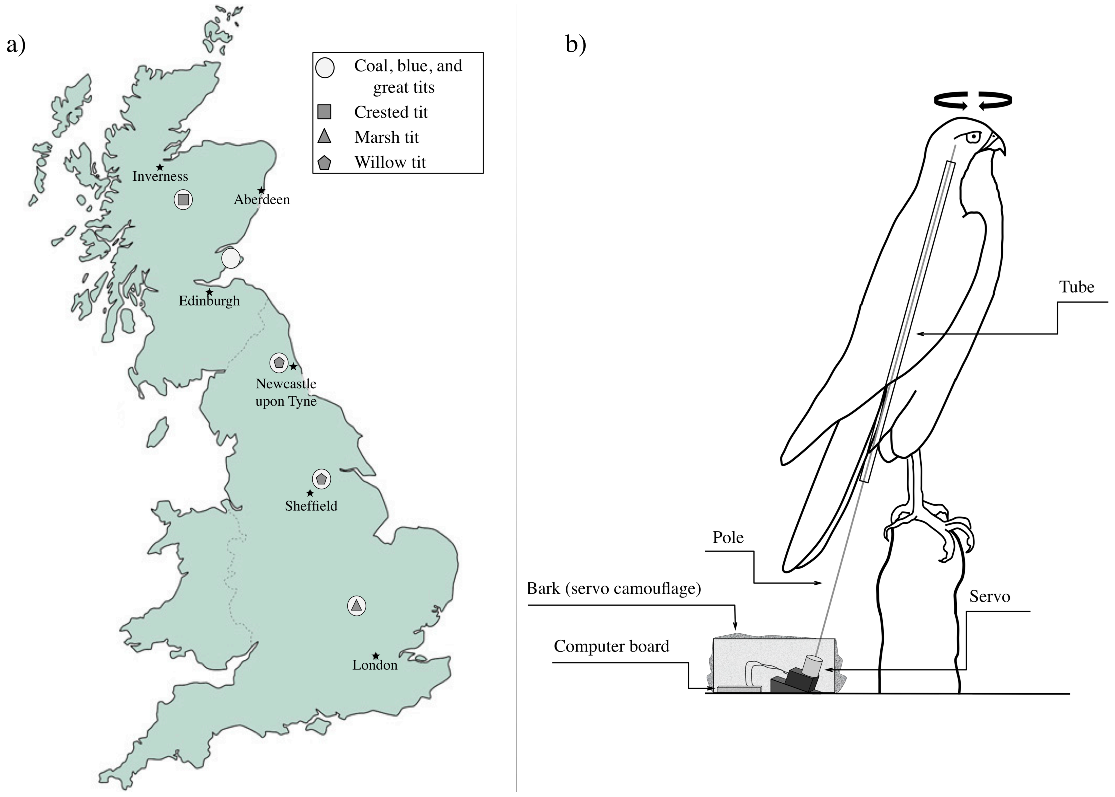


Figure 2.1 a) Feeder locations in the four regions across the UK. Each symbol indicates the species present at each location: circle represents coal, blue, and great tits, square represents crested tits, triangle represents marsh tits, and pentagon represents willow tits. Blue, great, and coal tits were found in all regions as shown by the light grey circle. The additional presence of crested (square), marsh (triangle), or willow tits (pentagon) is indicated by their corresponding dark grey symbol inside the circle. b) Schematic of the robo-raptors used for these experiments.

Stimuli

To test whether and how the tit species encode information about predator threat in their mobbing calls I 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 (~ 97% prey by weight; Newton, 1986) on small to medium sized birds including tit species (Curio et al., 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%) is 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*, are a non-threatening species found across the UK, similar in size to a sparrowhawk, and as it does not eat birds does not pose a threat to tit species (Šálek, Marhoul, Pintíř, Kopecký, & Slabý, 2004). Partridges 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.

I used custom-made robotic taxidermy mounts of each species to elicit mobbing responses by the tits. I constructed these robots either by including the moving parts during the taxidermy process or by taking the head off of the bird post-taxidermy, fitting the robotics, and re-assembling. To construct the robo-raptors I put a hollow tube through the body along the natural plane of head movements. Inside the tube I put a pole that was attached (using either U-POL^{TM} body filler from (U-POL, London, UK), or UHU© all purpose adhesive glue (GmbH & Co. KG, Bühl/Baden, Germany) to the inside of the bird's skull on one end and to a servo motor (Futaba S3003 from Futaba Corporation Oshiba, Japan or Hitec HS-422 Delux from Hitec RCD, Poway, CA, USA), using a 5/32 inch servo shaft coupler (Futaba or Hitec respectively). I controlled the rotation of the head (via the servo) with an Arduino computer (Arduino Duemilanove from Arduino LLC, https://www.arduino.cc) and 9v battery pack. I wrote a simple computer program comprised of a loop of a series of 15 different movements where the head turned between 2-110 degrees. Degree changes and movement delay times were based on natural movements of video-taped accipiters (Erick Greene pers com.). The rotation of the head mimicked natural sparrowhawk, buzzard, or partridge behaviour and did not exceed the natural rotational degree of a live bird. The electronics were hidden in a small box under the bird's perch and concealed by bark and lichens (Figure 1b). I used two different mounts of each species to reduce pseudoreplication and the mounts included: one male juvenile and one female adult sparrowhawk, two adult female buzzards, and two adult male grey partridges.

Predator presentations

At each study site I presented birds with all three treatments (sparrowhawk, buzzard, partridge) in a randomized order; the mount exemplar for each presentation was selected randomly. I 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 (January-March). I 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 I presented the control first and there was no change in behaviour of any of the birds present, I presented a predator trial after waiting at least 15 minutes after the control trial had ended (sparrowhawk $n = 6$, buzzard $n = 5$ trials). I excluded from the analyses those trials in which birds obviously responded to something other than the stimulus (e.g. when I observed a sparrowhawk flying overhead or initial behaviour suggesting birds had encountered a predator just before I arrived; $n = 7$).

When the focal species were not present for one or more trials (n = 9 sites), some locations generated data from fewer than three treatments. I observed some order and mount exemplar effects in the statistical models (see below), however these effects were not consistent across call types, ways of encoding information, stimulus species, or responding tit species and so are not reported.

I began presentations once I had confirmed the presence of the focal species (acoustically or visually) near the feeder. I 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; Carter, Lyons, Cole, & Goldsmith, 2008), I ensured that the mount faced the bird feeder in all trials. I then retreated to a minimum distance of 4 m 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 (Altmann, 1956). Starting at this time point, I recorded all behaviour and vocalizations for 5 minutes before removing the mount.

At each simulated predator encounter I 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.

Acoustic analysis

For all acoustic analyses, I 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. I 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 (Figure 2.2, Table 2.1). 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 (Figure 2.2, Table 2.1). To confirm the reliability of my categorization of calls, I 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.

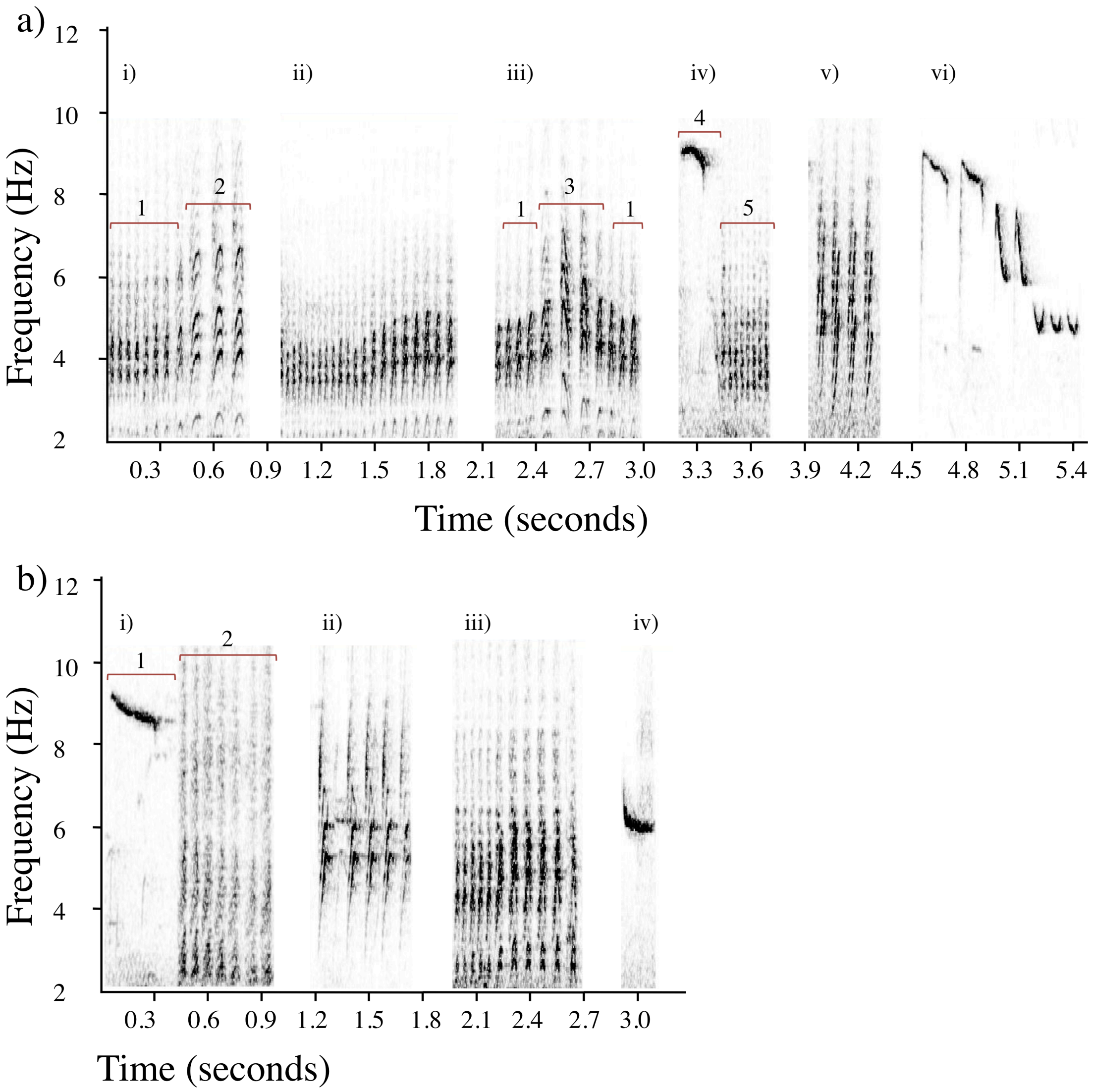


Figure 2.2 Spectrograms of UK tit mobbing calls. a) Blue tits: i-iv) churr call with 1) normal D elements and 2) exit elements, ii) frequency-modulated call, 3) mid elements, 4) introductory (intro) element (similar to A or B elements in chick-a-dee calls), 5) short D elements, v) chirp call (elements 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.

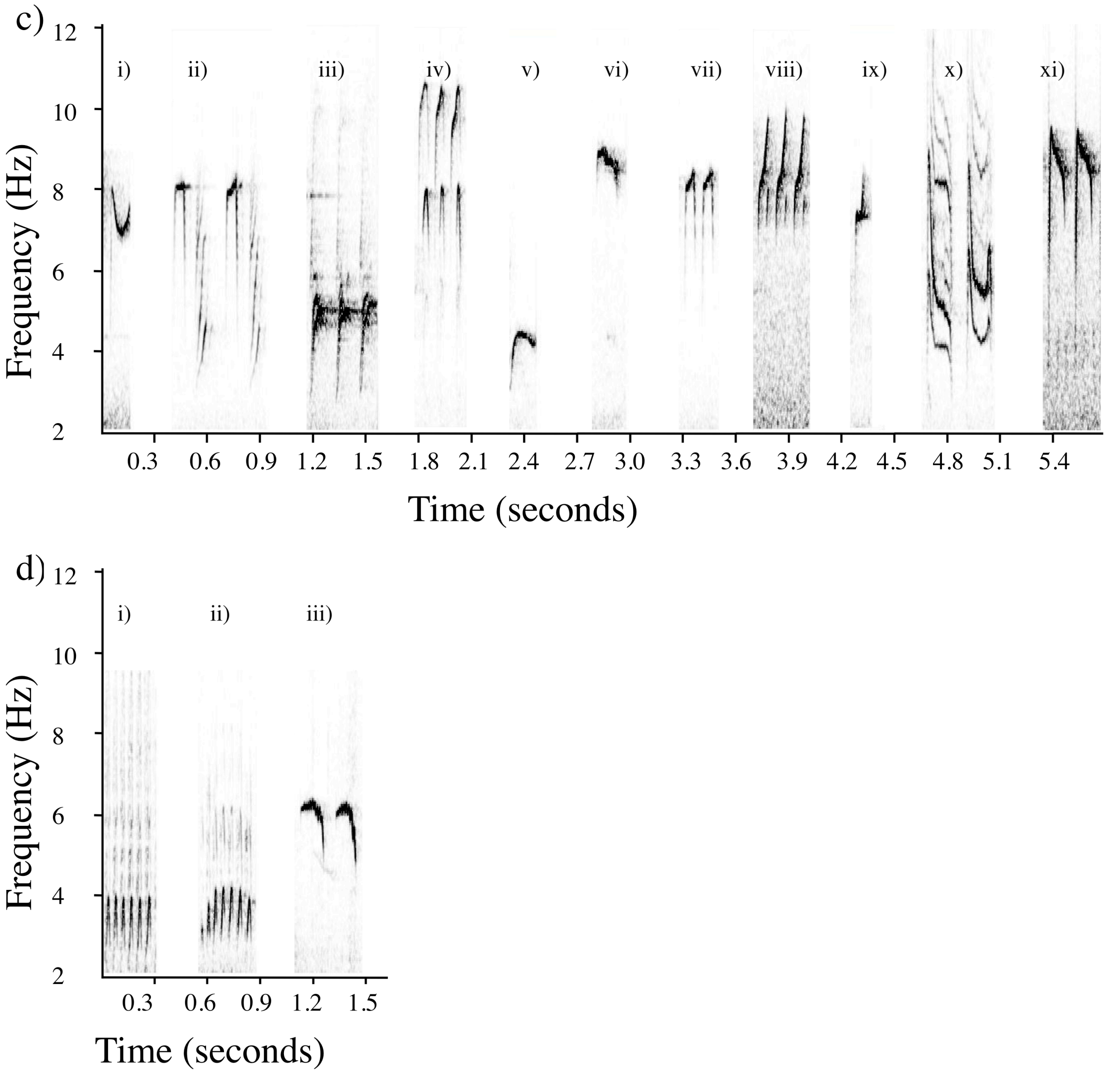


Figure 2.2 cont'd Spectrograms of UK tit mobbing calls. c) Coal tits: i) bowl element, ii) chirp elements (with peak elements), iii) dot elements, iv) hook elements, v) mound elements, vi) mt elements, vii) peak elements, viii) s-dot element, ix), s elements, x) squeak elements, xi) slide elements. d) Crested tits: i) normal trill call, ii) frequency-modulated trill call, iii) tonal call.

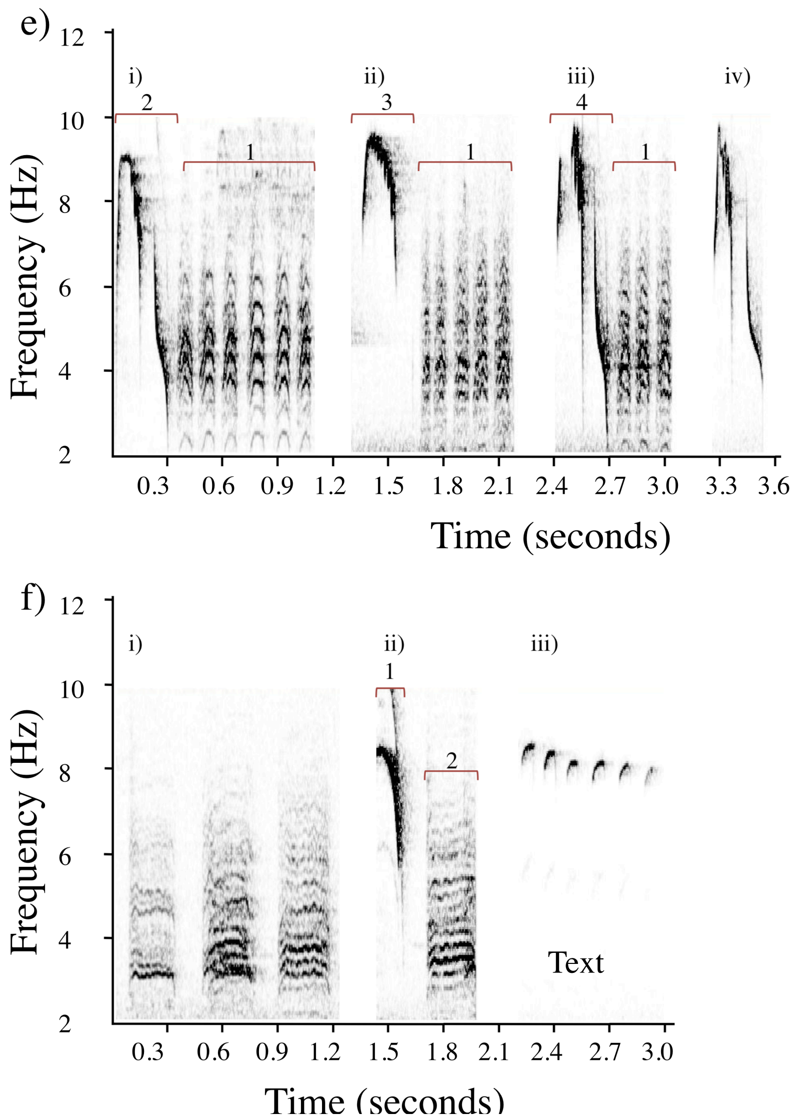


Figure 2.2 cont'd Spectrograms of UK tit mobbing calls. e) Marsh tits: i-iii) dä/D or complete calls with 1) dä/D elements, 2) full whole tonal element, 3) peak whole tonal element, 4) broken whole tonal element, iv) ptew call. f) Willow tits: i) tää-tää call, ii) si-tää-tää call, with 1) si intro element and 2) tää/D element, iii) zizi call. All spectrograms are scaled to one another.

Table 2.1 Definition of call and element types for each tit species with references to spectrogram examples (Figure 2.2). Some call names come from: all species (Hailman, 1989), marsh & willow tits (Goodale et al., 2010; Hetrick & Sieving, 2011; Soard & Ritchison, 2009), (Japanese) great tit (Bartmess-LeVasseur et al., 2010; Fuong, Keeley, Bulut, & Blumstein, 2014; Magrath et al., 2009; Templeton & Greene, 2007).

Call type	Call description	Element type	Element description	Spectrogram figure
a) Blue tit				
Churr	Calls containing D elements	D	broadband with distinct peak shaped frequency bands	2.2a i - iv
~ Short	Churr calls containing short D elements that appear as a stack of dots -- Figure 2.2a iv 5	intro	narrowband element before D elements	2.2a 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	2.2a iii 3
		exit	D elements structurally different from those before	2.2a i 2
Chirp	Calls containing chirp elements	chirp	broadband short call with two distinct dots on right side	2.2a v
		intro	narrowband element before chirp elements	
Tonal	Calls containing only tonal elements	tonal	narrowband elements with no broadband elements	2.2a vi
b) Great tit				
Jar / rattle	Calls containing jar / rattle elements	jar / rattle	Broadband with no distinct frequency bands and triangle shape at bottom	2.2b i 2
		intro	narrowband element before jar/rattle elements	2.2b i 1
D	Calls containing D elements	D	broadband with distinct peak shaped frequency bands	2.2b iii
		intro	narrowband element before D elements	
Chirp	Calls containing chirp elements	chirp	broadband short call with two distinct dots on right side	2.2b ii
		intro	narrowband element before chirp elements	
Tonal	Calls containing only tonal elements	tonal	narrowband elements with no broadband elements	2.2b iv

Call type	Call description	Element type	Element description	Spectrogram figure
c) 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	2.2c i
		chirp	thin broadband line (peak or s often as well)	2.2c ii
		Dot	line with dot on right side	2.2c iii
		Hook	straight line with hook at top	2.2c iv
		Mound	mound shape	2.2c v
		Mt	bumpy mound shape	2.2c vi
		Peak	narrowband increase in frequency	2.2c vii
		S-dot	s shape with dot/dash under	2.2c viii
		S	s shape with no dot/dash under	2.2c ix
		squeak	broadband with frequency bands	2.2c x
		Slide	narrowband decreasing in frequency	2.2c xi
d) Crested tit				
Trill	Calls containing trill elements	trill	broadband line	2.2d i & ii
~Frequency-modulated	Calls containing trill notes that shift in frequency over the course of the call -- Figure 2.2d ii	intro	narrowband element before trill elements	
Tonal		tonal	narrowband elements with no trill elements	2.2d iii
e) Marsh tit				
Complete	Calls containing both dä/D and tonal elements	dä/D	broadband with distinct frequency bands	2.2e i - iii 1
Tonal	Non-broadband frequency-modulated notes	whole	peak shape meets at top	2.2e i 2
		broken	peak shape does not meet at top	2.2e iii 4
		full	has both peak and slide element	2.2e i 2 & iii 4
		peak	only has peak element	2.2e ii 3
Dä/D	Calls containing only dä/D elements.	dä/D	broadband with distinct frequency bands	
Ptew	Calls containing only ptew elements -- Figure 2.2e iv			
f) Willow tit				
Si-tää-tää	Calls containing both D and si intro elements -- Figure 2.2f ii	tää/D	broadband with distinct frequency bands	2.2f i & ii 2
		si intro	narrowband element before tää/D elements	2.2f ii 1
Tää-tää	Calls containing only D elements -- Figure 2.2f i	tää/D	broadband with distinct frequency bands	2.2f i
Zizi	Calls containing only zi elements -- Figure 2.2f iii	zi	narrowband	2.2f 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, I focused on the four ways in which other Parids encode information: 1) call rate (calls/individual/minute), 2) total number of elements in a call (henceforth 'element number'), 3) proportion of all calls produced during a mobbing event that contained particular note types (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 et al., 1994; Hetrick & Sieving, 2011; Soard & Ritchison, 2009; Templeton et al., 2005).

To determine whether the birds used any of these ways of encoding information, I 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. I constructed these models for each species separately as they appeared to differ in their combinations of different call and note types (Figures 2.3), and as each species had a range of call/note types, I tested if each species employed the encoding mechanisms for each call/note type to differentiate between different threat predators.

I used these statistical models to test if each species changed a specific call/note type in response to different predator threat levels for each of the four ways of encoding information. The response variable was the way information was encoded for each call/note type described above, and the 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. The random effects, to control for between feeder variation and to minimize pseudoreplication, were: date, geographic region, and a 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. I transformed the data using a log or boxcox transform for any response variable with non-normal residuals (Appendix 2.1). Although binary call propensity data was tested using binomial GLMMs, some element types consisted of all 1 or 0 for specific combinations of predator and order or predator and exemplar and therefore could not converge. In these instances I used a LMM with a Gaussian error structure instead. I 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 2.1). For models where threat level had a significant effect, I 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 2.1). 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 me to test what call/note types each species used to differentiate between predator threats, and what information encoding mechanisms each species used. Although I, like others, felt that Bonferroni corrections would be too stringent and that the chance of committing type II errors so high that it would likely obscure important biologically meaningful patterns (Feise, 2002; Perneger, 1998; Rothman, 1990), I included sequential Bonferroni corrected P values in the results table (Appendix 2.1). I conducted all statistical analyses in R v3.1.2 (R Core Team, 2014), using the lme4 (Bates, Maechler, Bolker, & Walker, 2014) package. Call rates are reported as calls/individual/minute, element number values are the number of elements/call, all proportions are number of calls that are 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. number of calls with exit elements/total number of D calls; Figure 2.2; Table 2.1), and propensities are 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, I looked for phylogenetic signal using Pagel's lambda (Freckleton, Harvey, & Pagel, 2002; Pagel, 1999). I 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) I am 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, I collected ecological information from the published literature (Alatalo, 1981; Cramp, 1993; Deadman, 2014; Ekman, 1989; Fisher, 1982; Gibb, 1960; Morse, 1978; Perrins, 1979) on foraging niche- as measured by the height and distance from a tree trunk, dominance- as measured by shifts in foraging niche in the presence and absence of heterospecifics (Alatalo, 1981; Perrins, 1979), and gregariousness- as measured as the average size of a conspecific winter flock for each species. I chose these variables because each has been suggested as having an effect on anti-predatory behaviour (Goodale et al., 2010).

To determine if there was a correlation between each species' ecology and the ways in which they encoded predator threat information I ran four generalized linear models with binomial error structure including the ways of encoding information as our response variable. I 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 as well as between different levels of threat (Figure 2.3; Table 2.2a). Blue tits called the least to controls but increased their call rate to predators, more to buzzards, and the most to sparrowhawks (control: 1.06 ± 0.24; buzzard: 2.12 ± 0.37; sparrowhawk: 6.21 ± 0.73). 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; D: control 9.26 ± 0.28, buzzard 11.53 ± 0.33, sparrowhawk 14.05 ± 0.19; mid: control 2.57 ± 0.30, buzzard 1.76 ± 0.17, sparrowhawk 3.22 ± 0.19; Table 2.2a). 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; chirp: control 0.31 ± 0.02; buzzard 0.32 ± 0.02, sparrowhawk 0.10 ± 0.01; Table 2.2a). Blue tits also increased the proportion of tonal notes as threat increased (control 0.12 ± 0.01, buzzard 0.15 ± 0.02, sparrowhawk 0.20 ± 0.01). 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; exit: control 0.40 ± 0.08, buzzard 0.40 ± 0.07, sparrowhawk 0.84 ± 0.06; tonal: control 0.24 ± 0.07, buzzard 0.40 ± 0.07, sparrowhawk 0.65 ± 0.07; frequency modulated: control 0.31 ± 0.07, buzzard 0.32 ± 0.07, sparrowhawk 0.67 ± 0.07; short: mid 0.44 ± 0.08, exit 0.84 ± 0.06, sparrowhawk 0.95 ± 0.03; Table2. 2a).

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 (Figure 2.3; Table 2.2s). 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; Table 2.2s). 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; jar/rattle propensity: control 0.68 ± 0.08, buzzard 0.81 ± 0.06, sparrowhawk 0.95 ± 0.03; Table 2.2s).

Coal tits

Coal tits encoded information in three ways to differentiate between controls and predator threats: call rate, element number, and propensity (Figure 2.3; Table 2.2c). Coal tits used only element number, however, to differentiate between predators of varying threat levels in their mobbing calls (Figure 2.3; Table 2.2c). Coal tits increased their call rate as threat increased (control: 0.45 ± 0.11, buzzard: 2.53 ± 0.56, sparrowhawk: 5.25 ± 1.00). 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, mt: control 1.43 ± 0.14, buzzard 2.97 ± 0.38, sparrowhawk 1.47 ± 0.12; Table 2.2c). 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, mound: control 2.50 ± 0.50, buzzard 1.93 ± 0.28, sparrowhawk 1.77 ± 0.14; s-dot: control 2.09 ± 0.34, buzzard 3.36 ± 0.10, sparrowhawk 4.15 ± 0.17; Table 2.2c). Coal tits decreased their propensity to produce mound or squeak elements in response to controls compared to predator stimuli (mound: control 0.06 ± 0.04, buzzard 0.29 ± 0.08, sparrowhawk 0.51 ± 0.08; squeak: control 0.14 ± 0.01, buzzard 0.47 ± 0.09, sparrowhawk 0.63 ± 0.08; Table 2.2c).

Crested tits

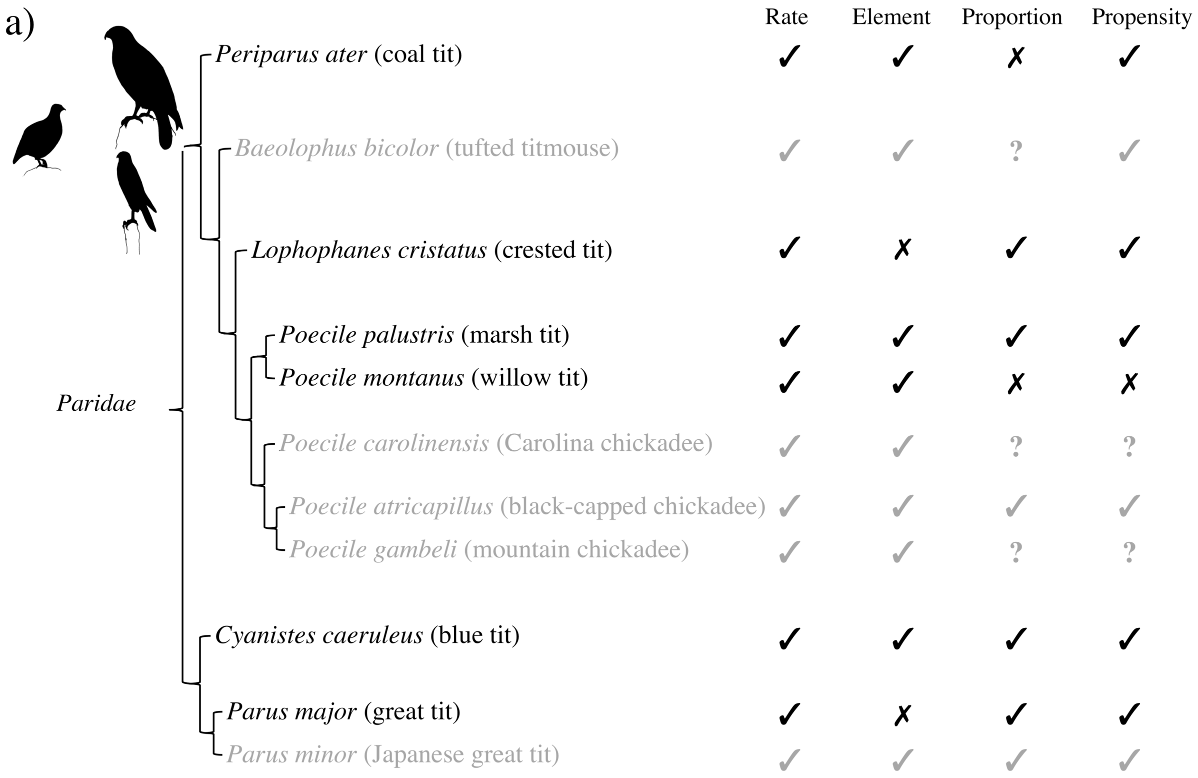
Crested tits differentiated one or both predators from the control in three ways: call rate, proportion, and propensity. However, they only used proportion and propensity to differentiate between different threat predators (Figure 2.3; Table 2.2d). They increased their call rate as threat increased, 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; frequency modulated proportion: control 0.61 ± 0.02, buzzard 0.75 ± 0.01, sparrowhawk 0.73 ± 0.01; tonal propensity: control 0.21 ± 0.11, buzzard 0.08 ± 0.08, sparrowhawk 0.38 ± 0.14; Figure 2.3; Table 2.2d).

Marsh tits

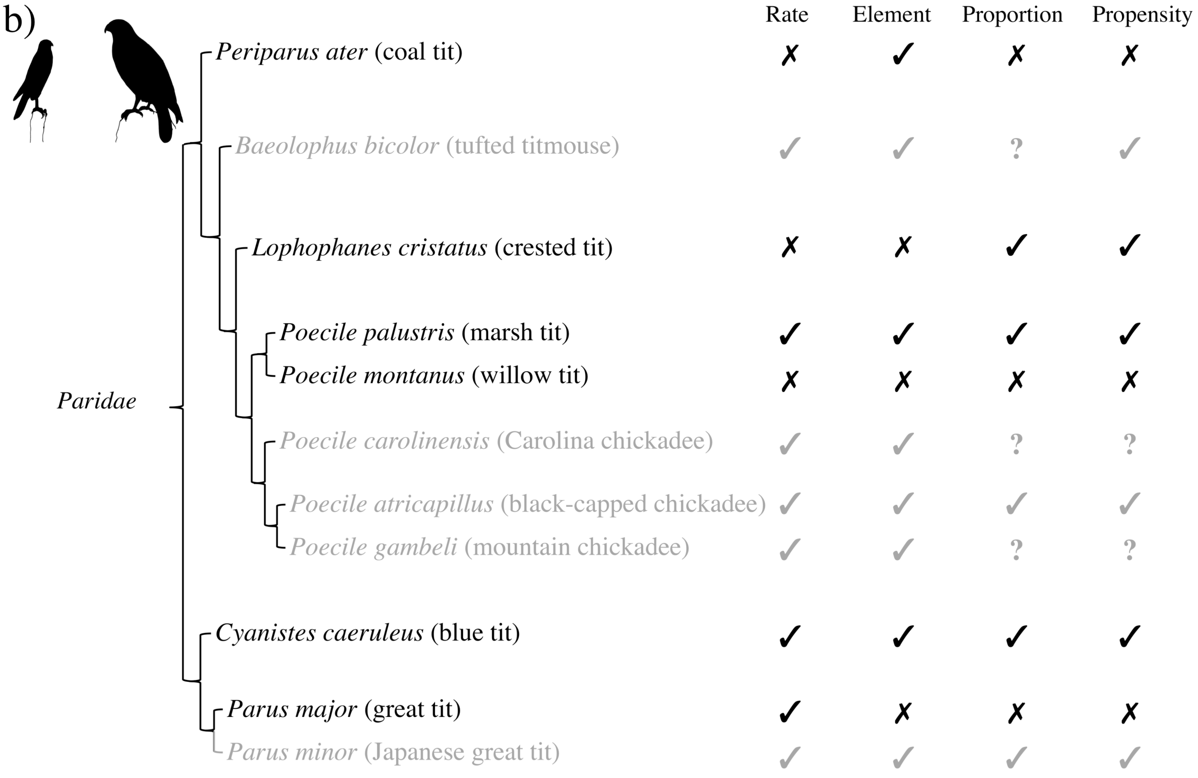
Marsh tits used all four ways of encoding information to differentiate both between predators and non-threats and between predators of different threat levels (Figure 2.3; Table 2.2). Marsh tits increased their call rate to predators compared to controls and decreased the number of dä/D elements and the proportion of full tonal notes in response to buzzards compared to controls or sparrowhawks (rate: control: 1.24 ± 0.35; buzzard: 1.26 ± 0.30; sparrowhawk: 4.56 ± 0.85; dä/D elements: control: 0.21 ± 0.11; buzzard: 0.08 ± 0.08; sparrowhawk: 0.38 ± 0.14; proportion of full tonal notes: control: 0.71 ± 0.07; buzzard: 0.49 ± 0.08; sparrowhawk: 0.53 ± 0.03; Table 2.2e). 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; all tonal: control 0.78 ± 0.15, buzzard 0.89 ± 0.11, sparrowhawk 1.00 ± 0.00; ptew: control 0.78 ± 0.05, buzzard 0.89 ± 0.11, sparrowhawk 1.00 ± 0.00, Table 2.2e).

Willow tits

Willow tits varied several call features between the control and predator treatments but did not differentiate between predators of different threat levels (Figure 2.3; Table 2.2f). Willow tits increased their call rate in response to predators (mean ± standard error; buzzard: 1.72 ± 0.42; sparrowhawk; 2.04 ± 0.25) compared to controls (control: 0.71 ± 0.28; Table 2.2). 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; si intro: control 2.00 ± 0.49, buzzard 2.51 ± 0.19, sparrowhawk 2.83 ± 0.14; Table 2.2f).



	Rate	Element	Proportion	Propensity
Periparus ater (coal tit)	✓	✓	✗	✓
Baeolophus bicolor (tufted titmouse)	✓	✓	?	✓
Lophophanes cristatus (crested tit)	✓	✗	✓	✓
Poecile palustris (marsh tit)	✓	✓	✓	✓
Poecile montanus (willow tit)	✓	✓	✗	✗
Poecile carolinensis (Carolina chickadee)	✓	✓	?	?
Poecile atricapillus (black-capped chickadee)	✓	✓	✓	✓
Poecile gambeli (mountain chickadee)	✓	✓	?	?
Cyanistes caeruleus (blue tit)	✓	✓	✓	✓
Parus major (great tit)	✓	✗	✓	✓
Parus minor (Japanese great tit)	✓	✓	✓	✓



	Rate	Element	Proportion	Propensity
Periparus ater (coal tit)	✗	✓	✗	✗
Baeolophus bicolor (tufted titmouse)	✓	✓	?	✓
Lophophanes cristatus (crested tit)	✗	✗	✓	✓
Poecile palustris (marsh tit)	✓	✓	✓	✓
Poecile montanus (willow tit)	✗	✗	✗	✗
Poecile carolinensis (Carolina chickadee)	✓	✓	?	?
Poecile atricapillus (black-capped chickadee)	✓	✓	✓	✓
Poecile gambeli (mountain chickadee)	✓	✓	?	?
Cyanistes caeruleus (blue tit)	✓	✓	✓	✓
Parus major (great tit)	✓	✗	✗	✗
Parus minor (Japanese great tit)	✓	✓	✓	✓

Figure 2.3 (previous page) The four ways in which each of the studied Paridae encode information differentiating a) predators (sparrowhawk and buzzard) from non-predators (partridge) and b) high (sparrowhawk) and low (buzzard) threat predators. Phylogeny information was based on (Johansson et al., 2013). 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. Black-capped chickadees: (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 2.2. Type III Wald Chi-square test results for predator type (control, buzzard, sparrowhawk) as a significant predictor of variation in vocal response. Planned comparison t and z tests results. Only comparisons with *P* values ≤ 0.05 reported (with the exception of zizi calls); full table is appendix 2.1. Bold text indicates *P* value ≤ 0.05, italicized text indicates model *P* values below sequential Bonferroni values.

Encoding method	Call / element type			Control – Buzzard		Control – Sparrowhawk		Buzzard – Sparrowhawk	
		χ2	P	t/z	P	t/z	P	t/z	P
a) Blue tit									
Call rate	All	3.09	***<0.001***	0.164	0.870	6.345	**<0.001**	5.452	**<0.001**
Number of	Total elements	20.54	***<0.001***	-1.546	0.126	1.914	0.059	3.248	**0.002**
	Mid elements	6.76	**0.034**	-1.279	0.242	0.563	0.584	2.579	0.276
	D elements	28.84	***<0.001***	0.888	0.375	5.346	**<0.001**	3.564	**<0.001**
Proportion of	Exit calls	6.27	**0.044**	-1.060	0.289	1.677	0.094	2.435	**0.015**
	Chirp calls	17.04	***<0.001***	2.511	**0.012**	-1.878	0.060	-4.104	**<0.001**
	Tonal calls	14.17	***0.001***	1.105	0.269	3.649	**<0.001**	2.587	**0.010**
Propensity to use	Mid elements	33.01	***<0.001***	-0.389	0.698	5.280	**<0.001**	5.044	**<0.001**
	Exit elements	14.78	***0.001***	3.604	**<0.001**	-0.694	0.489	3.264	**0.001**
	Tonal calls	14.35	***0.001***	0.490	0.625	3.695	**<0.001**	2.925	**0.004**
	Frequency-modulated calls	9.63	**0.008**	-1.538	0.124	2.200	0.028	2.981	**0.003**
	Short calls	17.27	***<0.001***	0.368	0.713	4.014	**<0.001**	3.312	**0.001**
b) Great tit									
Call rate	All	44.00	***<0.001***	1.822	0.071	6.569	**<0.001**	4.489	**<0.001**
Proportion of	Chirp calls	7.55	**0.023**	-1.162	0.249	-2.723	**0.008**	-1.740	0.086
Propensity to use	Jar/rattle calls	0.96	**0.004**	2.625	**0.010**	2.870	**0.005**	0.346	0.730
c) Coal tit									
Call rate	All	15.46	***<0.001***	2.093	**0.039**	3.856	**<0.001**	1.216	0.227
Number of	Hook elements	11.19	**0.004**	3.098	**0.004**	0.625	0.537	-2.700	**0.012**
	Mound elements	7.05	**0.029**	0.307	0.761	-1.557	0.128	-2.258	**0.033**
	Mt elements	21.84	***<0.001***	3.993	**<0.001**	0.049	0.961	-4.667	**<0.001**
	S-dot elements	11.97	**0.003**	1.771	0.083	1.343	0.187	-0.773	0.446
	Squeak elements	7.27	**0.026**	-2.656	**0.008**	-2.663	**0.008**	0.193	0.848
Propensity to use	Mound elements	9.75	**0.008**	2.137	**0.035**	2.889	**0.005**	0.393	0.695
	Squeak elements	18.58	***<0.001***	3.703	**<0.001**	3.331	**0.001**	-0.651	0.517

Encoding method	Call / element type			Control – Buzzard		Control – Sparrowhawk		Buzzard – Sparrowhawk	
		X^2	P	t/z	P	t/z	P	t/z	P
d) Crested tit									
Call rate	All	6.21	**0.045**	-0.047	0.963	2.432	**0.022**	1.602	0.121
Proportion of	Frequency-modulated calls	6.32	**0.042**	2.496	**0.013**	0.456	0.648	-2.207	**0.027**
Propensity to use	Tonal calls	6.45	**0.040**	-1.173	0.251	1.940	0.063	2.318	**0.028**
e) Marsh tit									
Call rate	All	10.39	**0.006**	-1.732	0.108	2.816	**0.013**	3.140	**0.006**
Number of	dä/D elements	12.69	***0.002***	0.061	0.952	-3.491	**0.001**	-3.084	**0.004**
Proportion of	Full tonal elements	6.88	**0.031**	-1.996	**0.046**	0.834	0.404	2.482	**0.013**
Propensity to use	Tonal elements	8.28	**0.016**	-0.636	0.534	2.703	**0.016**	2.519	**0.023**
	Peak tonal elements	12.37	***0.002***	3.091	**0.008**	2.316	**0.036**	0.144	0.888
	Ptew calls	8.29	**0.016**	-0.636	0.534	2.703	**0.016**	2.519	**0.023**
f) Willow tit									
Call rate	All	46.36	***<0.001***	3.721	**0.007**	1.994	0.086	0.602	0.561
Number of	Total elements	7.90	**0.019**	-0.222	0.826	2.803	**0.025**	1.634	0.167
	Si intro elements	16.46	***<0.001***	0.360	0.719	-4.053	**<0.001**	-1.685	0.093
Propensity to use	Zizi calls	5.96	0.051	2.420	**0.036**	-1.234	0.246	-0.446	0.665

Phylogeny and ecology

Neither phylogenetic signal nor ecology explained which species used which ways of encoding information about predator threat in their mobbing calls (rate: χ^2_1 = -0.03, P = 1; number of elements: χ^2_1 = -1.37, P = 1; proportion: χ^2_1 = -6.36, P = 1; propensity: χ^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 $F_2 < 0.01$, $P > 0.999$; propensity: foraging niche F_2 = 0.52, P = 0.657, dominance F_2 = 2.77, P = 0.265, gregariousness $F_2 < 0.01$, $P > 0.999$; Table 2.3).

Table 2.3 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

I found that the UK tit species varied in both the types and degree to which they encoded 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, with the exception of willow tits, all differentiated between low and high threat predators (Figure 2.3). 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 that are more closely related should be more similar in terms of the number and ways of encoding information they use to encode information about predators. Alarm calling as a behaviour in rodents, for example, appears to be well explained by phylogeny, though this says little of the ways these animals encode information in these calls (Shelly & Blumstein, 2005). However, I found no correlations between relatedness and ways of encoding information used by the species I tested (Figure 2.3; Table 2.3). 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. This lack of phylogenetic patterns is similar to that 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 et al., 2010). There are at least three plausible ecological variables that might explain the variation in ways of encoding information: foraging niche, gregariousness, and dominance. For example species that forage high up in trees or on insects in the air spend more time scanning the sky and may, therefore, be more likely to see an aerial predator and respond to it, while species, that forage near to or on the ground may not (Goodale et al., 2010; Goodale & Kotagama, 2005a; Lima, 1993; Magrath et al., 2014). For example, greater racket-tailed drongos, *Dicrurus paradiseus*, (Goodale & Kotagama, 2005a) and red-cap moustached tamarins, *Saguinus mystax pileatus*, (Peres, 1993) both forage high up of the ground (sallying and upper canopy respectively) and are the species in their mixed-species groups that best detect aerial predators. If this was also the case for the Paridae, then species that spend time foraging in the outer/upper canopy (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). Counter to this possibility, however, blue and marsh tits are 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 (Table 2.3).

Gregariousness could also affect the number or ways of encoding information used as the chance of seeing a predator (Goodale et al., 2010), the propensity to produce calls (Goodale et al., 2010; Magrath et al., 2014), and the complexity of signalling (Freeberg & Harvey, 2008; Goodale et al., 2010; Manser et al., 2014) might increase with increased group size. Orange-billed babblers, *Turdoide rsufescen*, (Goodale & Kotagama, 2005b) and red-cap moustached tamarinds (Peres, 1993) are the most abundant species in their mixed species groups and tend to spend more time scanning and respond to more potential threats, respectively, than do their flock mates. Downy woodpeckers, *Picoides pubescen*; (Sullivan, 1985) and yellow mongoose, *Cynictis penicillata*; (le Roux, Cherry, & Manser, 2008) tend to produce alarm calls only when heterospecifics are present, while mongoose species', *Herpestidae*, anti-predator vocal repertoire size increases with that species' group size and social complexity (Manser et al., 2014). If winter conspecific flock size, similarly, was to explain the number of ways in which the Paridae encode information the gregarious blue, great, and coal tits should produce more ways of encoding information relative to those produced by the less gregarious species (crested, marsh, and willow tits; Deadman, 1973; 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 (Table 2.3).

We can also dismiss dominance as a suitable explanation. 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, 2009b; Marler, 1967). However, the more dominant great and blue tits are no more similar in the ways they encode information than are the more subordinate coal or willow tits (Alatalo, 1981; Cramp, 1993; Perrins, 1979; 2012; Table 2.3). 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 (though the sample of species still provides little power to confirm this conclusion), 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 used in relevant literature. The first is that the multiplicity is an artefact of the signaller's internal state: as the animal's internal state affects a suite of aspects of its vocal response via arousal, an increase in that animal's arousal (fear) will result in an increase in the call rate, number of elements, or even different call types (Blumstein, 2007; Blumstein & Armitage, 1997; Hailman & Ficken, 1996; Marler, Evans, & Hauser, 1992; Seyfarth & Cheney, 2003). This explanation presupposes that the information provided to receivers is redundant but that the variety in the ways the information is provided leads to a stronger or more urgent signal (Blumstein & Armitage, 1997; Marler et al., 1992).

The second explanation is that each way of encoding information is used to communicate different information about the threat, enabling a signaller to increase the amount of information it can deliver (Marler et al., 1992; Suzuki, Wheatcroft, & Griesser, 2016). Here the information, while pertaining to the same threat, is not redundant. In order to address why related species use different ways and different numbers of ways to encode predator threat, we need to establish what specific information it is that they encode (Templeton et al., 2005). Unlike California ground squirrels, *Spermophilus beecheyi*, which use changes in their calls to redundantly signal state of arousal (Owings & Virginia, 1978), signallers might use different ways of encoding information to encode different types of information: predator category using propensity and distance using call rate for example (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 the UK tit species show considerable variation in the encoding strategies they employ to communicate predator threat, they may provide a fruitful system for investigating which of these explanations is the more appropriate.

Chapter 3

Variation in information encoding strategies and the value of predator threat information

INTRODUCTION

Information about predators is vital for the survival of prey species, and many species, across a wide range of taxa, produce anti-predator vocalizations that help to defend themselves and others (Gill & Bierema, 2013; Townsend & Manser, 2013). These signals not only warn about predators, but can contain information about the predator's level of threat such as size (Evans, Macedonia, & Marler, 1993b; Templeton et al., 2005), speed (Evans, Macedonia, & Marler, 1993b), distance (Baker & Becker, 2002; Murphy et al., 2013), type (Griesser, 2009; Placer & Slobodchikoff, 2000; 2004), and even behaviour (Gill & Bierema, 2013; Griesser, 2008; Marler, 1955; Townsend & Manser, 2013). As this information can be costly to acquire and produce, however, many species eavesdrop on the anti-predator signals of others (Clucas, Freeberg, & Lucas, 2004; Fuong et al., 2014; Lea et al., 2008; Magrath et al., 2014; Munoz, Brandstetter, Esgro, Greene, & Blumstein, 2014; Sherman, 1977; Templeton et al., 2005).

Given that not all species produce this anti-predator information, communities are thought to be made up of informants, those species that frequently produce copious amounts of reliable and detailed information about predator threat, and scroungers, those species that eavesdrop on this information (Goodale et al., 2010; Hetrick & Sieving, 2011; Soard & Ritchison, 2009). To be considered a community informant, a species must not only produce otherwise unavailable or detailed information but they must also be consistently reliable in the ways in which they encode this information between mobbing events. Most importantly, however, the information they produce must be used by other species in the community.

Because those species assumed to be community informants supply detailed information about predator threat and conspecifics and heterospecifics respond to this information (Bartmess-LeVasseur et al., 2010; Fuong et al., 2014; Goodale & Kotagama, 2008; Magrath et al., 2009; Templeton & Greene, 2007), it is thought that the information provided is reliable across events (Bartmess-LeVasseur et al., 2010; Fuong et al., 2014; Magrath et al., 2009; Templeton & Greene, 2007). However, each mobbing event is different (e.g. different species in attendance, different numbers of individuals (conspecific and heterospecific), different investment in mobbing by each species). These differences in local group structure may introduce variability into the ways 'information sources' encode predator threat information if their vocalizations are sensitive to group structure (Fichtel & Manser, 2010; Townsend, Rasmussen, Clutton-Brock, & Manser, 2012). This variability may then impact the usefulness of these signals to heterospecifics.

Variability in ways of signalling due to social factors not related to the pertinent threat (e.g. flock size and species composition) would be unlikely to impact a conspecific's ability to 'decode' the information. However, this variability could make it more difficult for heterospecifics to interpret these signals if they are only temporarily or peripherally part of the stable group structure. Effective community informants should, then, produce signals that are largely unaffected by factors external to the pertinent threat. Much of the current research focus is not on the impact of this variability in signal production or receipt. Instead, typical data are averages across predator encounters, which, while showing how 'community informants' encode information, they do not address the amount, or causes, of variation. There are a number of factors that might lead to variation in ways of encoding, but here I will focus on just three: group size, conspecific number, and presence of heterospecifics.

Group dynamics could affect the ways species encode information about predators in a number of ways. Increased group size, for example, could decrease an individuals perceived threat or arousal through the selfish herd (Hamilton, 1971) or confusion effects (Blumstein, Evans, & Daniel, 1999; Caro, 2005; Curio, 1978; Goodale & Ruxton, 2010). This might cause them to produce vocalizations indicating lower threat than a predator might pose if it were encountered by a smaller group. Audience effects can impact alarm calling as well (Fitchel & Manser, 2010; Townsend et al. 2012). For example, some bird (Karakashian et al., 1988; Marler, 1956; Sullivan, 1985) and mammal (Cheney & Seyfarth, 1985; Sherman, 1985; Townsend et al., 2012; Wich & Sterck, 2003) species are less likely to call or to encode detailed information unless conspecifics, such as kin or mates, are present. The presence of heterospecifics can also result in one species changing their calling behaviour in the presence of another (Griesser & Ekman, 2005; Karakashian et al., 1988; Ridley, Child, & Bell, 2007), which may mean that species that comprise mixed-species flocks are more susceptible to variation in the ways they encode information.

Not only would community informants be expected to produce consistent signals about predator threat regardless of group structure, the information they produce must also be used by heterospecifics in the community. There are data that show that sympatric nuclear species (Hetrick & Sieving, 2011) or species that produce detailed predator threat information (Fallow & Magrath, 2010; Shriner, 1998) will eavesdrop on each other. For example when played tufted-titmouse mobbing calls produced in response to different threat predators, Carolina chickadees responded to calls given to higher, compared to lower, threat predators appropriately (i.e. increased number of D elements in their mobbing calls and increased call rate; Hetrick & Sieving, 2011). Scrub-wrens and fairy-wrens, when presented with each other's alarm calls, were more likely to flee to alarm calls indicating a more imminent threat (Fallow & Magrath, 2010), and both golden-mantled ground squirrels and yellow-bellied marmots responded to one another's alarm calls as they did to their own (Shriner, 1998). However, few studies have examined whether species thought to be information scroungers respond appropriately to the information produced by information sources (Templeton & Greene, 2007).

While vocal production between eavesdropping nuclear species has been examined, the vocal production by proposed eavesdroppers in the presence of information sources has been overlooked. However, the vocal interplay between proposed eavesdropper and information source species may provide further evidence to support each species role. The mobbing calls of many species are similar, both in their broadband quality and frequency ranges (Ficken et al. 1996; Marler, 1957) possibly resulting in mobbing vocalizations of different species masking one another (Magrath 2014). Masked or degraded anti-predator vocalizations elicit less of a response (Damsky & Gall, 2016; Morris-Drake, Bracken, Kern, & Radford, 2017; Murray & Magrath, 2015; Templeton, Zollinger, & Brumm, 2016) possibly increasing the chance of capture by a predator. To avoid masking the information contained in the calls produced by information sources, eavesdroppers may avoid calling when information source species do. In this way eavesdroppers may appear to 'pay attention' to the calls of information sources by not overlapping their calling bouts with those of information source species. Additionally, as eavesdroppers are necessarily listening to and using the information provided by information sources, they may either not mob at all, or, if they do engage in mobbing behaviour, should not produce detailed information about predator threat when it is already being produced (Moynihan, 1962; Ridley et al., 2013).

To address whether those species thought to be community informants produce reliable information and are used by eavesdroppers in their community, I simulated predator encounters to all six species of tit (Paridae) found in the UK. I used tits because they respond to the presence of predators by engaging in mobbing behaviour, and five out of these six species encode detailed information about predator threat using at least one way of encoding information, which suggests they may be community informants (Chapter 2). These species are, then, good candidates to be community informants. To confirm this, I made two predictions I addressed with two different experiments: 1) community informant species should reliably differentiate between predators of different threat using vocalizations that are uninfluenced by flock size (conspecific or heterospecific) or composition, and 2) that in the presence of community informant species, information scrounging-species (such as European robins, *Erithacus rubecula,* and dunnocks, *Prunella modularis*) should 'pay attention' to community informant species (i.e. avoid overlapping their calling with those of community informants) and would not produce vocalizations differentiating between predators of different threat.

METHODS

Stimuli

I used robotic taxidermy mounts to simulate a predator encounter to our focal species. These mounts varied in threat level from a no-threat control to low and high-threat predators (for details see Methods in Chapter 2).

Predator presentations

I simulated predator encounters by presenting the study species with the taxidermy mounts during the winters of 2014 and 2015 at 40 feeders in gardens and forests throughout the UK (for details see Methods section of Chapter 2). These presentations were done in winter as it is the season tit-led mixed species flocks form (Perrins, 1979). All predator presentations followed the predator presentation methods from Chapter 2.

EXPERIMENT 1: INFORMATION RELIABILITY

Study Sites & Species

I carried out predator presentations during the winters on the six Paridae species found in the UK. Blue tits, *Cyanistes caeruleus*, great tits, *Parus major*, coal tits, *Periparus ater*, are found throughout the UK (Perrins, 1979). Blue and great tits prefer primarily broad leaved deciduous woodland while coal tits prefer more conifer dense habitats (Perrins, 1979). Crested tits, *Lophophanes cristatus*, are located in the northwest of Scotland in new Caledonian or Scots pine forests (Perrins, 1979), while

Marsh tits, *Poecile palustris*, and willow tits, *Poecile montanus*, are found in England. Marsh tits prefer open broad leaf forests while willow tits prefer damp peat bogs and willow thickets (Perrins, 1979), and are often not found in the same areas. I was able to take advantage of the different regional flock compositions created by this natural variation in species distribution to test the effects of different flock compositions on the production of mobbing calls.

Acoustic Analysis

I analysed all the calls using Raven Pro v 1.5 acoustical software (Bioacoustics Research Program, 2014) using a Hann window function, a frequency grid resolution of 23.04 Hz, and a fast fourier transformation (FFT) of 1050 samples. I manually categorized all calls by species and type and selected each call by hand (for specifics see Chapter 2).

Statistical Analysis

To test the effect of community/flock composition on encoding methods of different tit species, I ran linear mixed and generalized linear mixed models on element/call types for all four encoding methods used by tit species: call rate (calls/individual/minute), number of elements/notes in a call: element number, proportion of calls during a mobbing event of one type: proportion, and propensity for a call type to be used across mobbing events: propensity. To test how the number of conspecifics affected encoding methods I included a fixed effect of conspecific number; to test how the presence of other species affected encoding methods I included terms for the presence/absence of blue tits, great tits, and coal tits, however due to experimental design, I could test only the blue, great, coal, and crested tit data as blue and great tits were always present and coal tits were almost never present when marsh or willow tits were present; to test how the size of the flock affected encoding methods I included flock size as a fixed effect. As, however, flock size and number of conspecifics were positively correlated for blue, great, and coal tits I included only the number of conspecifics in the models for these three species; I included mount presentation order, and mount exemplar as fixed effects as they were part of the experimental design. I did see order and exemplar effects in the models, but as none of these effects were consistent across responding species, element/call type, stimulus species, or encoding methods they are not reported here. I also included random effects of geographic area, date, and a term (trial) that accounted for multiple calls produced at each location to reduce pseudoreplication. For any models that had non-normal residuals, I used a log or boxcox transform to normalize the residuals. In several instances models could not converge if stimulus:order or stimulus:mount exemplar levels were all 1 or 0 so I fitted these using linear models instead. For each model I tested for an effect of the number of conspecifics, the presence of blue, great, and/or coal tits, and the flock size using III Wald Chi squared tests.

EXPERIMENT 2: INFORMATION USE

Study species

I chose dunnocks and European robins as typical ‘information scrounger’ species because they are commonly found at feeders all over the UK and their ecology is that of satellite species that eavesdrop on community informants (Moynihan, 1962): they are solitary (robin) or found in small groups (dunnocks) during the winter and defend relatively small territories through which other mixed-species flocks travel (Birkhead, 1981; Dunn, Copelston, & Workman, 2004). Both of these species give alarm calls in response to predators (Cramp, 1993; Davies, Madden, & Butchart, 2004), share predators (e.g. sparrowhawks *Accipiter nisus*, merlins, *Falco columbarius*, kestrels, *Falco tinnunculus,* and domestic/feral cats, *Felis catus,* etc.) with 'community informant' species (tits in the case of this study) in their community (Birkhead, 1981; Cramp, 1993; Zawadzka & Zawadzki, 2001). As different tit species use a different number of ways of encoding information in their calls, each species has the potential to encode varying amounts of information (more ways of encoding information could indicate more information about a predator's threat; see Chapter 2 for details). Therefore I chose three information source species: blue tits, great tits, and coal tits.

The number of simulated encounters for both species differed as both dunnocks and robins were not always present at all locations during all trials (dunnock: sparrowhawk n = 19 feeders, buzzard n = 25 feeders, partridge n = 17 feeders; robin: sparrowhawk n = 28 feeders, buzzard n = 28 feeders, partridge n = 27 feeders). As willow, crested, or marsh tits were present in all flocks tested (within each species' respective geographical range), I did not examine how their presence and absence affected the calling behaviour of dunnocks or robins. Similarly, as blue tits were present during all sparrowhawk presentations when dunnocks were present, I could not test the effect of presence and absence of blue tits on dunnock vocal behaviour.

Acoustic analysis

To determine whether robins or dunnocks encoded information about predator threat into their calls, I measured three call features for dunnocks and two for robins: 1) call rate: the number of calls/individuals present; 2) peak frequency (kHz): the frequency at which the most energy occurs; and 3) the call length (seconds) during the three minutes after the onset of mobbing. As robin 'tick' calls are very short in duration, collecting accurate measurements on call length was not possible so I recorded only the first two call features (Figure 3.1a).

I took these measurements from spectrograms generated using Raven Pro v1.5 acoustical software (Bioacoustics Research Program, 2014) by visually identifying calls belonging to each species (Figure 3.1). To keep all peak frequency and call length measurements consistent across each recording, all spectrograms used a fast Fourier transform (FFT) size of 1050 sample, a spectrogram frequency grid resolution of 23.04 kHz, and a Hann window function.

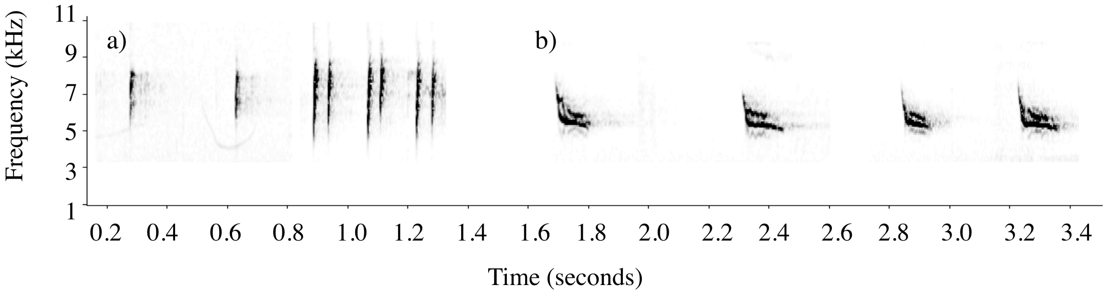


Figure 3.1 Spectrogram of a) European robin tick calls and b) dunnock calls

Statistical analysis

To test whether robins or dunnocks 'pay attention' to community informants, I determined whether dunnocks or robins overlapped their calls with calls produced by nuclear species I used a program called song overlap null model generator (SONG, Masco, Allesina, Mennill, & Pruett-Jones, 2015). This program takes the total call length and inter-call interval of both species and randomizes them in order to generate a distribution of the number of calls that should overlap for each species by chance . This method takes into account the species-specific differences in call rate, length, and inter-call interval when determining and producing the overlap matrix for all species. This allowed me to test whether the number of calls that robins and dunnocks produced that overlapped blue, great, or coal tit, and each other's calls were likely to be due to avoidance or to overlap. For each species pair, I only included calling data where I had visual confirmation of the presence of both species being compared.

To test whether robins or dunnocks encoded information about predator threat in their own calls, and if their ways of doing so were affected by the presence of information producing species, I generated linear mixed models with a Gaussian error structure. I constructed separate models for robins and dunnocks as each had a different call (Figure 3.1). I generated a separate model for each possible way of encoding information (call rate, peak frequency, and length) to test each method separately, as they may not be correlated with one another. I included the call feature (call rate, peak frequency, or length) as the response variable and predator threat level, the presence of each information source species (blue, great, coal tits) as fixed effects. I also included the interaction between predator threat and the presence of blue, great, and coal tits separately as fixed effects. To account for experimental design, I included the mount exemplar and order, the number of conspecifics, and the flock size as fixed effects and included date, location, and a term (trial) to account for multiple calls at each location as random effects. I ran type III Wald Chi-square tests on each model to test for significant effects of stimulus, or the presence of information source species on call feature. I used R v3.1.2 (R Core Team, 2014) and the lme4 package (Bates et al., 2014) to conduct all of the statistical analyses.

RESULTS

EXPERIMENT 1: INFORMANTS

Blue tits

Increase in the number of conspecifics

Blue tits varied their calling behaviour in two ways in response to increases in the number of conspecifics present: 1) they changed their call rate (calls/individual/minute) and the proportion of chirp elements differently depending on the predator presented (significant interaction between the number of conspecifics and predator threat; rate: $\chi^2 = 21.00$, $P < 0.001$; chirp: $\chi^2 = 6.28$, $P = 0.043$; Table 3.1a), and 2) they increased the number of calls per minute, the proportion of tonal calls, and the propensity to produce intro, exit, and tonal calls (call number: $\chi^2 = 5.57$, $P = 0.018$; tonal (proportion): $\chi^2 = 9.00$, $P = 0.003$; intro: $\chi^2 = 6.13$, $P = 0.013$; exit: $\chi^2 = 5.21$, $P = 0.0$; tonal (propensity): $\chi^2 = 5.28$, $P = 0.022$). All other ways of encoding information were unaffected by the number of conspecifics (Table 3.1a).

Presence of heterospecific tits

Blue tits decreased their propensity to produce intro elements and varied the proportion of chirp and propensity to produce exit calls differently in response to different predators when great tits were present (significant interaction between the presence of great tits and predator threat; chirp: $\chi^2 = 9.81$, $P = 0.007$; intro: $\chi^2 = 3.83$, $P = 0.050$; exit: $\chi^2 = 6.30$, $P = 0.043$; Table 3.1a). They varied the proportion of chirp elements differently in response to different predators when coal tits were present (significant interaction between the presence of coal tits and predator threat; $\chi^2 = 6.44$, $P = 0.040$; Table 3.1a). All other ways of encoding information were unaffected by the presence of heterospecifics (Table 3.1a).

Stable signals

Blue tits changed the number of total elements in their calls as well as their propensity to produce mid, frequency modulated, and short elements in response to stimuli of different threat levels, but these ways of encoding information were not affected by either the number of conspecifics nor the presence of heterospecifics (element number: $\chi^2 = 18.30$, $P < 0.001$; mid: $\chi^2 = 25.93$, $P < 0.001$; frequency-modulated: $\chi^2 = 9.72$, $P = 0.008$; short: $\chi^2 = 20.54$, $P < 0.001$; Table 3.1a). All other ways of encoding information were influenced by flock structure (Table 3.1a).

Great tits

Increase in the number of conspecifics

Great tits increased the total number of calls and the proportion of chirp calls as the number of conspecifics increased (call number: $\chi^2 = 8.15$, $P = 0.017$; chirp: $\chi^2 = 6.21$, $P = 0.013$; Table 3.1b). All other ways of encoding information were unaffected by the number of conspecifics (Table 3.1b)

Presence of heterospecific tits

Great tits did not vary any of the ways of encoding information in their calls in response to the presence of heterospecifics (Table 3.1b).

Stable signals

Great tits increased their call rate to higher threat predators but this response was not affected either by the number of conspecifics nor the presence of heterospecifics ($\chi^2 = 21.63$, $P < 0.001$; Table 3.1b). All other ways of encoding information were influenced by flock structure (Table 3.1b).

Coal tits

Increase in the number of conspecifics

Coal tits varied the number of hook elements they produced as the number of conspecifics increased, but the number of hook elements varied differently in response to different predators (significant interaction between the number of conspecifics and predator threat; hook: $\chi^2 = 6.81$, $P = 0.033$; Table 3.1c). All other ways of encoding information were unaffected by the number of conspecifics (Table 3.1c)

Presence of heterospecific tits

Coal tits varied the number of calls in response to the presence of blue tits and the number of mound notes in response to the presence of great tits but differently to different predators (significant interaction between the presence of blue or great tits and predator threat; calls: $\chi^2 = 6.32$, $P = 0.042$; mound: $\chi^2 = 5.92$, $P = 0.015$; Table 3.1c). All other ways of encoding information were unaffected by the presence of heterospecifics (Table 3.1c)

Stable signals

Coal tits increased their call rate, changed the number of mt and s-dot elements, as well as their propensity to produce mound and squeak notes in response to different predators, but these were not affected by either the number of conspecifics or the presence of heterospecifics (call rate: $\chi^2 = 19.92$, $P < 0.001$; mt: $\chi^2 = 14.44$, $P = 0.001$; s-dot: $\chi^2 = 6.67$, $P = 0.036$; mound: $\chi^2 = 6.43$, $P = 0.040$; squeak: $\chi^2 = 7.86$, $P = 0.020$; Table 3.1c). All other ways of encoding information were influenced by flock structure (Table 3.1c).

Crested tits

Increase in the number of conspecifics

Crested tits varied the total number of calls and the proportion of frequency-modulated calls as the number of conspecifics increased but differently in response to different predators (significant interaction between number of conspecifics and predator threat; call number: $\chi^2 = 14.77$, $P < 0.001$; frequency-modulated: $\chi^2 = 14.74$, $P = 0.001$; Table 3.1d). All other ways of encoding information were unaffected by the number of conspecifics (Table 3.1d)

Increase in the flock size

Crested tits varied the call rate and number of calls and the proportion of frequency-modulated calls as the number of conspecifics differently in response to different threat predators (significant interaction between flock size and predator threat; call rate: $\chi^2 = 15.63$, $P < 0.001$; call number: $\chi^2 = 31.62$, $P < 0.001$; Table 3.1d). All other ways of encoding information were unaffected by the flock size (Table 3.1d)

Presence of heterospecific tits

Crested tits decreased the number of calls and proportion of frequency-modulated calls, and varied the call rate differently to different predators in response to the presence of blue tits (significant interaction between blue tit presence and predator threat; call rate: $\chi^2 = 8.27$, $P = 0.016$; call number: $\chi^2 = 25.44$, $P < 0.001$; frequency-modulated: $\chi^2 = 10.12$, $P = 0.001$; Table 3.1d). Crested tits also varied their call rate, the number of calls, and the proportion of frequency-modulated calls differently to different predators when great tits were present (significant interaction between presence of great tits and predator threat; call rate: $\chi^2 = 13.65$, $P = 0.001$; call number: $\chi^2 = 42.24$, $P < 0.001$; frequency-modulated: $\chi^2 = 8.00$, $P = 0.018$; Table 3.1d). All other ways of encoding information were unaffected by the presence of heterospecifics (Table 3.1d)

Stable signals

All crested tits' calls were affected by either the number of conspecifics, flock size, and/or the presence of heterospecifics (Table 3.1d).

Marsh tits

Increase in the number of conspecifics

Marsh tits increased the number of D elements and the propensity to produce peak tonal elements as the number of conspecifics increased (D: $\chi^2 = 6.65$, $P = 0.010$; peak tonal P: $\chi^2 = 8.15$, $P = 0.004$). All other ways of encoding information were not affected by the number of conspecifics (Table 3.1e)

Increase in flock size

Marsh tits increased the proportion of calls that contained full tonal elements as flock size increased and varied the propensity of calls that contained peak tonal elements differently to different predators as flock size increased (significant interaction between flock size and predator threat; full intro: $\chi^2 = 5.22$, $P = 0.022$; peak intro: $\chi^2 = 7.27$, $P = 0.026$; Table 3.1e). All other ways of encoding information were not affected by flock size (Table 3.1e).

Stable signals

All marsh tits' calls were affected by the number of conspecifics or flock size (Table 3.1e).

Willow tits

Increase in the number of conspecifics

Willow tits increased their call rate as the number of conspecifics increased ($\chi^2 = 5.29$, $P = 0.021$; Table 3.1f). All other ways of encoding information were not affected by the number of conspecifics (Table 3.1f)

Increase in the flock size

Willow tits varied their call rate, the number of calls, and their propensity to produce zizi calls as flock size increased, but differently in response to different predators (significant interaction between flock size and predator threat; call rate: $\chi^2 = 23.00$, $P < 0.001$; call number: $\chi^2 = 7.81$, $P = 0.019$; zizi: $\chi^2 = 19.61$, $P < 0.001$; Table 3.1f). All other ways of encoding information were not affected by the flock size (Table 3.1f)

Stable signals

Willow tits increased the number of total elements and D elements in response to predators, and these responses were not affected either by the number of conspecifics nor the flock size (total elements: $\chi^2 = 14.10$, $P < 0.001$; D elements: $\chi^2 = 7.60$, $P = 0.022$; Table 3.1f). All other ways of encoding information were influenced by flock structure (Table 3.1f).

Table 3.1 Type III Wald Chi-square test results for generalized and linear mixed models testing for predator type, group size (conspecific and heterospecific) and composition (presence of blue, great, and coal tits) on ways of encoding information about predator threat for a) blue tits, b) great tits, c) coal tits, d) crested tits, e) marsh tits, and f) willow tits. § indicates the model residuals were not normally distributed. Bonferroni corrected p-values for each respective species based on the number of models are as follows: blue tits = 0.005, great tits = 0.017, coal tits = 0.006, crested tits = 0.017, marsh tits = 0.017, willow tits = 0.010, p-values ≤ 0.05 are bold and p-values ≤ Bonferroni corrected p-values are italicized. Direction column indicates whether the element/call type increases (+), decreased (-), is an interaction, or is not significant (NA).

Encoding method		Element / call type			Number of conspecifics			Great tits present			Coal tits present		
			χ^2	*P*	χ^2	*P*	Direction	χ^2	*P*	Direction	χ^2	*P*	Direction
a) Blue tit													
Rate		All	62.94	***<0.001***	21.00	***<0.001***	**Interaction**	1.17	0.280	NA	1.50	0.221	NA
Call		All	25.65	***<0.001***	5.57	*0.018*	**+**	0.01	0.910	NA	0.87	0.352	NA
Number		Element	18.30	***<0.001***	1.25	0.264	NA	0.13	0.714	NA	0.38	0.540	NA
Proportion		Chirp	13.03	**0.001**	6.28	*0.043*	**Interaction**	9.81	**0.007**	**Interaction**	6.44	**0.040**	**Interaction**
		Tonal	8.06	**0.018**	9.00	*0.033*	**+**	0.47	0.492	NA	2.78	0.095	NA
Propensity		Intro	3.29	**0.193**	6.13	*0.013*	**+**	3.83	*0.050*	**-**	1.85	0.174	NA
		Mid	25.93	***<0.001***	2.11	0.146	NA	0.66	0.418	NA	0.49	0.485	NA
		Exit	15.92	***<0.001***	5.21	*0.022*	**+**	6.30	**0.043**	**Interaction**	0.00	0.954	NA
		Tonal	4.09	**0.130**	5.28	*0.022*	**+**	0.07	0.787	NA	0.85	0.357	NA
		Frequency-modulated	9.72	**0.008**	1.71	0.191	NA	0.41	0.521	NA	0.98	0.323	NA
		Short	20.54	***<0.001***	3.16	0.075	NA	1.89	0.169	NA	0.54	0.464	NA

Encoding method		Interaction direction of Element / call type * number of conspecifics			
			CO	BZ	SH
a) Blue tit					
Rate		All	**~**	**~**	**-**
Proportion		Chirp	**~**	**+**	**++**

Encoding method		Element / call type			Number of conspecifics			Blue tits present			Coal tits present		
			χ^2	*P*	χ^2	*P*	Direction	χ^2	*P*	Direction	χ^2	*P*	Direction
b) Great tit													
Rate		All	21.63	***<0.001***	0.07	0.788	NA	0.37	0.541	NA	0.02	0.876	NA NA
Call		All	5.51	0.064	8.15	***0.017***	**+**	0.28	0.597	NA	0.03	0.863	NA NA
Proportion		Chirp	0.91	0.633	6.21	***0.013***	**+**	0.82	0.366	NA	2.60	0.107	NA NA

Encoding method		Element / call type			Number of conspecifics			Blue tits Present			Great tits present		
			χ^2	*P*	χ^2	*P*	Direction	χ^2	*P*	Direction	χ^2	*P*	Direction
c) Coal tit													
Rate		All	19.92	***<0.001***	0.07	0.789	NA	0.60	0.439	NA	0.01	0.926	NA
Call		All	16.77	***<0.001***	0.79	0.375	NA	6.32	**0.042**	**Interaction**	0.06	0.815	NA
Number		Hook	7.81	**0.020**	6.81	**0.033**	**Interaction**	0.94	0.332	NA	0.48	0.487	NA
		Mound	6.04	**0.049**	0.18	0.675	NA	1.93	0.165	NA	5.92	**0.015**	**Interaction**
	§	Mt	14.44	***0.001***	0.16	0.693	NA	0.38	0.383	NA	0.06	0.813	NA
		S-dot	6.67	**0.036**	0.42	0.516	NA	1.94	0.164	NA	0.16	0.391	NA
Propensity		Mound	6.43	**0.040**	0.64	0.425	NA	2.61	0.107	NA	0.40	0.530	NA
		Squeak	7.86	**0.020**	0.13	0.719	NA	0.00	0.975	NA	0.01	0.939	NA

Encoding method		Interaction direction of Element / call type * number of conspecifics			
			CO	BZ	SH
c) Coal tit					
Number		Hook	~	~	-

Encoding method		Element / call type			Number of conspecifics			Blue tits present			Great tits present		
			χ^2	*P*	χ^2	*P*	Direction	χ^2	*P*	Direction	χ^2	*P*	Direction
d) Crested tit													
Rate		All	23.50	***<0.001***	0.42	0.516	**NA**	8.27	***0.016***	**Interaction**	13.65	***0.001***	**Interaction**
Call		All	46.06	***<0.001***	14.77	***<0.001***	**Interaction**	25.44	***<0.001***	**-**	42.24	***<0.001***	**Interaction**
Proportion	§	Frequency-modulated	13.64	***0.001***	14.74	***0.001***	**Interaction**	10.12	***0.001***	**-**	8.00	**0.018**	**Interaction**

Encoding method		Element / call type			Flock size		
			χ^2	*P*	χ^2	*P*	Direction
d) Crested tit							
Rate		All	23.50	***<0.001***	15.63	***<0.001***	**Interaction**
Call		All	46.06	***<0.001***	31.62	***<0.001***	**Interaction**
Proportion	§	Frequency-modulated	13.64	***0.001***	0.71	0.401	NA

Encoding method		Interaction direction of Element / call type * number of conspecifics			Interaction direction of Element / call type * flock size		
			CO	BZ	SH	CO	BZ	SH
d) Crested tit								
Rate		All				**+**	**~**	**-**
Call		All	**-**	**+**	**+**	**+**	**~**	**-**
Proportion	§	Frequency-modulated	**~**	**+**	**++**			

Encoding method		Element / call type			Number of conspecifics			Flock size		
			χ^2	*P*	χ^2	*P*	Direction	χ^2	*P*	Direction
e) Marsh tit										
Number		Dä/D elements	2.09	0.352	6.65	***0.010***	**+**	0.01	0.934	NA
Proportion	§	Full tonal	3.21	0.201	0.07	0.786	NA	5.22	**0.022**	**+**
Propensity		P tonal	0.99	0.611	8.15	***0.004***	**+**	7.27	**0.026**	**Interaction**

Encoding method		Interaction direction of Element / call type * flock size			
			CO	BZ	SH
e) Marsh tit					
Proportion	§	Full tonal	**-**	**+**	**+**
Propensity		P tonal	**~**	**+**	**++**

Encoding method		Element / call type			Number of conspecifics			Flock size		
			χ^2	*P*	χ^2	*P*	Direction	χ^2	*P*	Direction
f) Willow tit										
Rate		All	2.43	0.296	5.29	**0.021**	**-**	23.00	***<0.001***	Interaction
Call		All	2.03	0.362	0.23	0.635	NA	7.81	**0.019**	**Interaction**
Proportion	§	**Element**	14.10	***<0.001***	0.03	0.855	NA	0.98	0.322	NA
		D elements	7.60	**0.022**	0.01	0.923	NA	2.00	0.157	NA
		Zizi calls	9.63	***0.008***	0.36	0.552	NA	19.61	***<0.001***	**Interaction**

Encoding method		Interaction direction of Element / call type * flock size			
			CO	BZ	SH
f) Willow tit					
Rate		All	**-**	**+**	**+**
Call		All	**-**	**+**	**+**
Proportion		Zizi calls	**-**	**1**	**-**

EXPERIMENT 2

Robins avoided overlapping their calls with blue, great, and coal tits more often than by chance given their respective call lengths, rates, and inter-call intervals, and neither avoided nor overlapped calling with dunnocks (blue tit: $P < 0.01$; great tit: $P < 0.01$; coal tit: $P < 0.01$; dunnock: $P = 0.17$). There was a significant interaction between predator threat and tit presence. When blue tits were absent, robins called with a higher peak frequency and differentiated sparrowhawks from buzzards and controls by increasing call rate (rate: $\chi^2 = 18.99$, $P < 0.001$; peak frequency $\chi^2 = 5.02$, $P = 0.025$; Figure 3.2a). When great tits were absent, robins increased call rate in response to buzzards and sparrowhawks ($\chi^2 = 8.57$, $P = 0.014$; Figure 3.2b). They did not change their calling behaviour in response to the presence or absence of coal tits ($\chi^2 = 0.07$, $P = 0.793$).

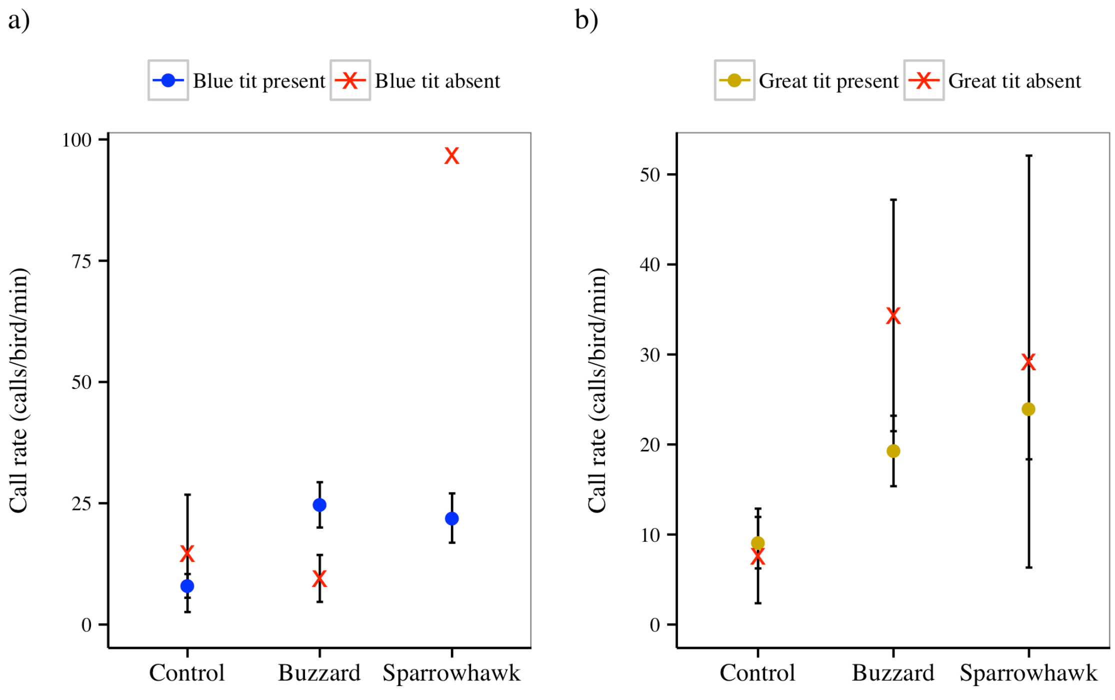


Figure 3.2 Mean ± standard error of robin call rate in response to the presence (•) and absence (x) to a) blue tits and b) great tits.

Dunnocks did not avoid or overlap their calls with those of blue tits, coal tits, or robins, but they did avoid calling when great tits were calling (blue tit: $P = 0.45$; coal tit: $P = 0.09$; robin: $P = 0.65$; great tit: $P < 0.01$). There was no interaction between predator threat and the presence of any community informant (tit) species (great tits: $\chi^2 = 3.10$, $P = 0.078$; coal tits: $\chi^2 = 1.23$, $P = 0.268$). However, dunnocks increased their call rate to predators compared to controls, and decreased their call length to buzzards compared to controls or sparrowhawks, but did not change their peak frequency in response to predator threat (call rate: $\chi^2 = 9.37$, $P = 0.009$; call length: $\chi^2 = 6.60$, $P = 0.037$; peak frequency: $\chi^2 = 1.47$, $P = 0.480$, Figure 3.3).

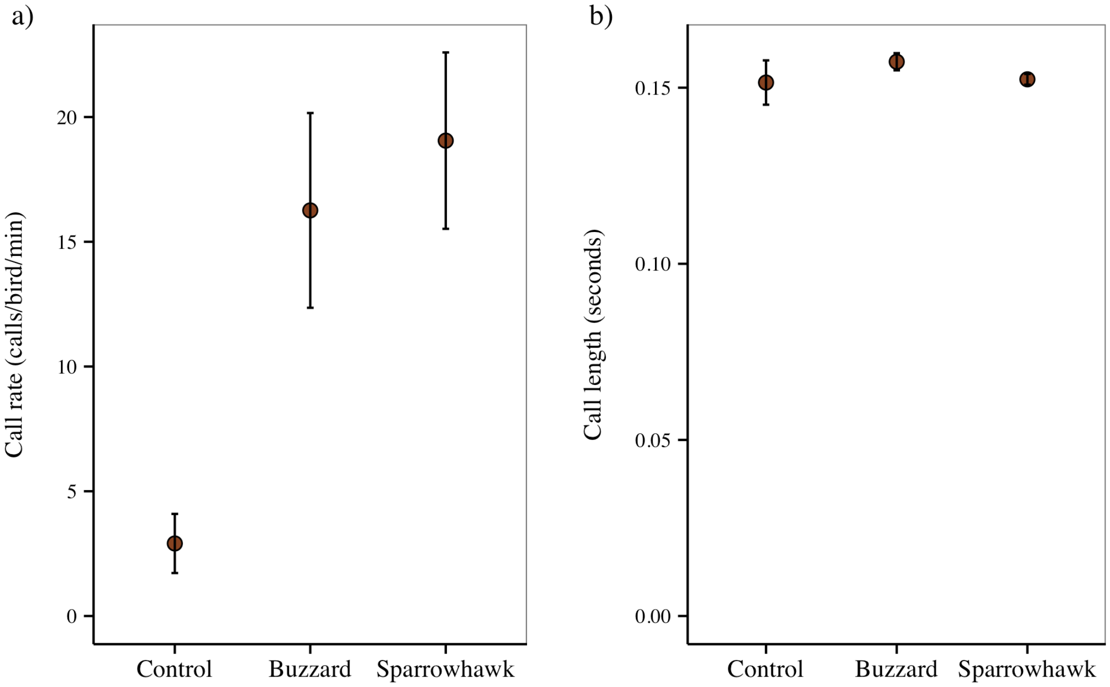


Figure 3.3 Mean ± standard error of dunnock a) call rate and b) call length in response to different threat predators.

DISCUSSION

In response to stimuli that represented different levels of predator threat, blue, great, coal, and willow tits produced at least one reliable way of encoding information that was unaffected by flock size or composition. In their responses blue, great and coal tits differentiated between stimuli of different threat levels, while willow tits differentiated only the un-threatening stimulus from the predator stimuli. All of the responses made by marsh and crested tits, and most of those made by blue, great, coal, and willow tits were dependent on group size (conspecific and/or flock), and/or composition. Both ‘information scrounger’ species ‘paid attention’ to at least one of the three tit species that produced accessible predator threat information, although robins appeared to use only the information produced by blue and great tits, and dunnocks from none of the tit species.

The responses of three of the six species to the predators fit the production criteria of community informants: they produced calls that were independent of flock size (conspecific or heterospecific) or composition. The second criteria, that information scrounging species would ‘pay attention’ to (i.e. avoid calling over and adjust their calling behaviour) community informant species was supported in only two of the species: blue and great tits. These two species, therefore, are the best candidates for being community informants. These two species also highlight the fact that the number of ways in which a species encodes predator threat in their calls is not necessarily correlated with whether a species is a community informant as, while blue tits use many ways, great tits use only one (Chapter 2).

Because coal tits produce reliable information about predator threat regardless of flock structure, they could also be classified as a community informant based simply on the available information in the calls they produced. However, confidence in assigning the label of community informant to coal tits is reduced by the lack of response (not changing their vocalizations in the presence of coal tits) by robins. There are at least three different reasons coal tits may still be considered community informants. 1) coal tits may encode information in a way (e.g. changes in number of elements) robins do not decode, while great and blue tits do (e.g. changes in call rate); 2) because robins and coal tits have different habitat preferences (Cramp, 1993; Lack, 1948), they may come into contact with coal tits during mobbing events relatively rarely and so are unfamiliar with coal tit information encoding (Magrath et al., 2009); 3) finally, robins are unlikely to be the only information scrounger in the wider community and coal tit mobbing calls may be used as sources of information by other species (Chapter 2).

The remaining three species (crested, marsh, and willow tits) do not meet either of the criteria necessary for being community informants. Like many other species (buff-streaked chats, *Oenanthe bifasciata,* Seoraj-Pillai & Malan, 2014, Thomas languars, *Presbytis thomasi,* Wich & Sterck, 2003, and drongos, *Dicrurus adsimilis,* Ridley et al., 2007), the information that crested and marsh tits produce about predators varies with flock structure and would not be readily interpretable by itinerants. However, an individual that is more familiar with the flock structure would probably be able to interpret their calls appropriately. Crested and marsh tits do not, therefore, meet the community informant criteria although they may still be sources of information for familiar conspecific and heterospecific individuals within their flocks. By producing a call that is unaffected by flock composition, willow tits might, at first, appear to meet the first criterion of community informant. However, they do not conform to the specifications of a community informant because they did not differentiate between predators with their calls (Chapter 2).

To determine that a species is a community informant one must demonstrate not only that it produces calls uninfluenced by flock structure, but, more importantly, that heterospecifics use this information (information scroungers). Given this criterion, robins seem to fit the description of an information scrounger. Surprisingly, on the other hand, dunnocks do not. Although the dunnocks in my study did not overlap their calling with great tits, in the presence of source species they encoded information differentiating between predators, robins did not. This difference in response by dunnocks and robins might have been expected because although dunnocks and robins are both commonly found with tit flocks, there are potential differences in the vulnerability of both satellite species to shared predators: robins and dunnocks vary in their relative predation risk from sparrowhawks compared to blue and great tits across seasons and years (Cresswell, 1995; Götmark & Post, 1996). Although both dunnocks and robins forage primarily low to and on the ground (Cramp, 1993; Davies, 1992; Lack, 1948), robins sing year round from perches at heights that are similar to those on which blue tits tend to forage (Cramp, 1993; Götmark & Post, 1996; Lack, 1948). As a bird's position on the ground or lower vegetation increases predation risk, more time spent perched at higher positions engaging in high vigilance behaviours, (i.e. singing) may decrease predation risk (Götmark & Post, 1996). This year-round singing behaviour may mean that the predation risk robins face more closely matches that of foraging blue tits than dunnocks. Although sparrowhawks frequently hunt tits, dunnocks, and robins, sparrowhawks prey upon tits and robins more often than dunnocks (Newton, 1986). This difference in vulnerability may make the information from blue tits less pertinent or reliable to dunnocks (Magrath et al., 2014), resulting in differences in information use across species (Forsman & Mönkkönen, 2001; Magrath et al., 2009; Rainey, Zuberbühler, & Slater, 2004b; 2004a). Just as it is not as straightforward to determine which species are community informants, deciding which species are information scroungers may require more information than just their peripheral or temporary position in a flock.

In conclusion, my data show that some of those species thought to be community informants may not be after all. Before assigning a species as a community informant or a scrounger, it would seem useful to determine whether they produce calls that differentiate between predator threat, calls that are independent of flock structure and calls that are used by at least one satellite species. Given that it is not typical to collect all of these data, it plausible that some of the species currently presumed to be community informants or information scroungers may be incorrectly classified. Additionally, as there appears to be variation in the amount and quality of information produced and used across species, I suggest that, similar to discussions of nuclearity in mixed-species flock literature (Farley, Sieving, & Contreras, 2008; Harrison & Whitehouse, 2011; Srinivasan et al., 2010), we should shift our focus from a dichotomy of community informants and scroungers to a continuum of information production based not only the production of reliable information but also on the use of that information by other species in the community.

Chapter 4

Hoo are you? Tits do not respond to novel predators as threats

INTRODUCTION

Predation is a major source of mortality for most animals and even when not the cause of loss of life it has multiple negative indirect effects on prey (Caro, 2005; Cresswell, 2008; Preisser, Bolnick, & Benard, 2005). Rapid and accurate identification of predators allow prey both to reduce immediate predation risk and appropriately modulate their anti-predator responses without unnecessarily reducing time spent on other important behaviours, such as foraging or searching for mates (Caro, 2005; Creel, Schuette, & Christianson, 2014; Cresswell, 2008; Lima, 1998). When individuals encounter a novel species they need to determine whether it poses a threat and the degree of threat it poses before responding appropriately. Recognizing and responding appropriately to a novel species as a non-predator and not engaging in costly anti-predator behaviours may be similarly important as recognizing a novel species as a predator and avoiding being injured or eaten (Caro, 2005; Creel et al., 2014; Cresswell, 2008; Lima, 1998). Due to the importance of predator recognition for survival, considerable effort has been invested in examining how different species respond to novel predators (Griffin, 2004; Sih et al., 2010). The literature provides evidence for a variety of responses by naïve prey. For example, captive-born greater rheas, *Rhea Americana*, do not discriminate between predators and non-predators (de Azevedo et al., 2012), and captive-born rhesus monkeys, *Macaca mulatta*, do not respond appropriately to snakes (Mineka et al., 2004). Similarly, many conservation programs have succeeded in training naïve prey to respond appropriately to novel predators they previously did not view as a threat (Griffin, Blumstein, & Evans, 2000). For example, with training, naïve New Zealand robins, *Petrocia australis*, mobbed mammalian predators (Maloney & McLean, 1995). Conversely, captive-born Atlantic salmon, *Salmo salar* L., increase their opercular rate, a sign of increased stress in response to predators (Hawkins, Armstrong, & Magurran, 2004a), even when they had no prior experience of the predator (Hawkins, Magurran, & Armstrong, 2004b), and both zoo-reared black tailed prairie dogs, *Cynomys ludovicianus*, and naïve wild-living California ground squirrels, *Spermophilus beecheyi*, engage in stereotyped snake-directed behaviour in response to moving snakes (Owings & Coss, 1977; Owings & Owings, 1979).

Anti-predator behaviour in captive animals (Hinde, 1954b) or by juveniles (Francis et al., 1989; Hinde, 1954a; Rajala, Ratti, & Suhonen, 2003; Shedd, 1982) may not, however, be representative of the way in which free-living adults recognize and respond to predators particularly if prior experience of other predators shapes responses to novel predators. But if a novel predator shares similar ‘predatory features’ with known predators, a prey species may be able to generalize those features across predators and identify a novel predator appropriately (Beránková, Veselý, Sýkorová, & Fuchs, 2014; Davies & Welbergen, 2008). Most of the experiments in which predator recognition has been investigated have been conducted on young juveniles in the laboratory, or in captive situations where the test animals have never been exposed to predators of any kind (Beránková et al., 2014; Ferrari, Messier, & Chivers, 2007; Göth, 2001; Griffin et al., 2001; Kullberg & Lind, 2002; Veen, Richardson, Blaakmeer, & Komdeur, 2000).

To test whether wild-living adults that have experienced predators can recognize a novel predator as a threat, I presented three tit species that are found throughout the UK (blue tits, *Cyanistes caeruleus,* great tits, *Parus major*, and coal tits, *Periparus ater*) with two different species of predators: sparrowhawks, *Accipiter nisus*, a high threat predator that specializes in hunting small birds, and little owls, *Athene noctua*, a predator that, while only infrequently eats small birds (Altringham, OBrien, & Sydney, 1994; Hounsome, O'Mahony, & Delahay, 2010; Cramp, 1993), is of similar size to a sparrowhawk and could therefore pose a threat as a predator (Dial, et al 2008; Templeton et al., 2005). Sparrowhawks are both currently and historically common throughout the UK (Cramp, 1993; Gordon, 2007; Perrins, 1979; 2012). Little owls, in contrast, are present across England and Wales, but are mostly absent from Scotland, found only below the 56th parallel, south of Glasgow and Edinburgh (Cramp, 1993; Gordon, 2007; Perrins, 1979; 2012; Figure 4.1). In response to predators, blue and great tits engage in an anti-predator behaviour called mobbing, which is accompanied by vocalizations that contain information about the degree of predator threat (Chapter 2). I used these vocalizations to assess the level of threat that blue, great, and coal tits perceived the sparrowhawk and little owl mounts to represent. If the tits do not recognize novel predators as a threat, the inexperienced birds (those in Scotland) should respond to the familiar predator much more strongly than to the novel model (with increased call rate etc.; Chapter 2). However, if the birds in Scotland recognize the threat of the novel predator, their response to the little owl compared to the sparrowhawk should not differ between England and Scotland. No difference in response to the little owl compared to the sparrowhawk in England and Scotland could be taken as evidence that birds generalize from familiar predators to novel stimuli.

METHODS

Study sites & species

I conducted predator presentations to blue, great, and coal tits at 56 feeders in 5 locations across the UK, 3 of these locations were in England and 2 were in Scotland, from January to March of 2014 and 2015 (Figure 4.1). The 2 locations in Scotland were all located outside the known range of little owls. The feeders were all placed within 0.5 m of dense leafy cover, and feeders were filled with black-oil sunflower seeds.

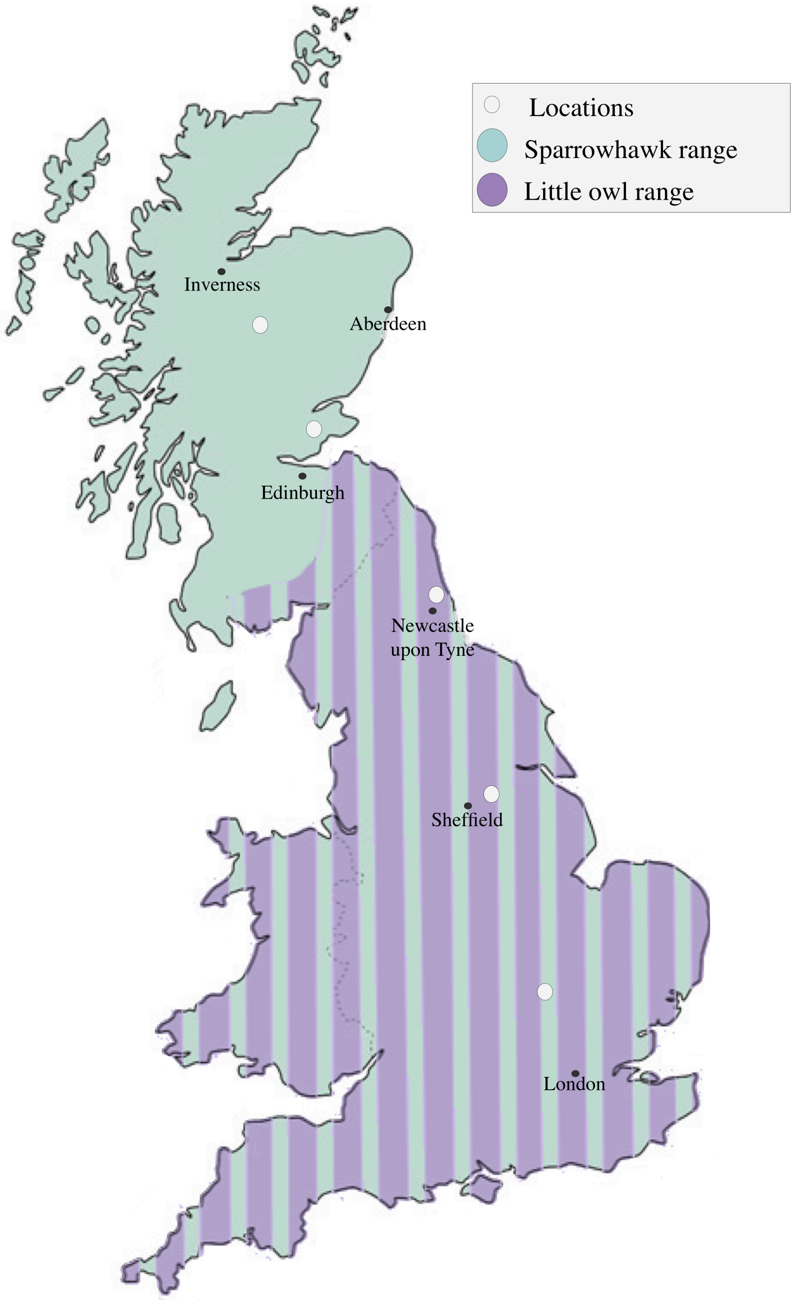


Figure 4.1 Map showing the locations of field sites as well as the ranges of sparrowhawks and little owls.

Stimuli

I used two different species of predators to simulate predator encounters: a species present throughout the range of blue, great, and coal tits, and one present in only part of their range. I used the sparrowhawk as the familiar high-threat predator as it is found throughout the whole of the UK. I used a little owl as the partially novel high-threat predator as it is only found below the 56th parallel (south of Edinburgh) in the UK and therefore was unfamiliar for those tits in my study sites above the 56th parallel (Brehm, 2007; Cramp, 1993; Gordon, 2007). Both predators are small, making them especially dangerous to the small birds (Dial, Greene, & Irschick, 2008; Templeton et al., 2005), including tits, which are known to make up part of their diet (Glue & Scott, 1980; Zawadzka & Zawadzki, 2001). Although crepuscular, little owls are often out during the day (Cramp, 1993; Glue & Scott, 1980; Gordon, 2007) so are likely to be encountered by tits.

I used taxidermy mounts for the predator simulations, each fitted with robotics that allowed the head to rotate in an approximation of natural head movement for predatory birds (Chapter 2). I used two exemplars of each species (one juvenile male & one adult female sparrowhawk and two adult little owls of unknown sex) to help mitigate the effects of pseudoreplication.

Predator presentation

I presented the model predators at feeders located in nature reserves and private gardens in English and Scottish countryside and forests. All feeders were stocked with food for at least two weeks prior to trials to allow the local birds to find and grow accustomed to them. After I confirmed the presence of any of the three target species (blue, great, or coal tits), I placed a 1.5 m high platform 2 m from the feeder and placed the mount on the platform with its body and head oriented towards the feeder, as head orientation can affect perceived predator threat (Book & Freeberg, 2015; Carter et al., 2008). Once I exposed the mount I began recording, but the trial proper began when a bird of the target species either: displayed mobbing behaviour towards the mount (Altmann, 1956), was within 5 meters of the mount, or came within 7 meters of the mount and had its body and head oriented towards the mount for more than 20 seconds within 2 minutes. I assigned the specific mount exemplar used at and the order of predator presentation each feeder randomly. To reduce any stress associated with recovering from or preparing to overnight I conducted all predator presentations from 1 hour after sunrise to 1 hour before sunset.

I conducted 48 trials where blue tits were present, (n = 15 England, n = 33 Scotland). I conducted 51 trials where great tits were present (n = 18 England, n = 33 Scotland). Lastly, I conducted 48 trials where coal tits were present (n = 13 England, n = 35 Scotland).

Acoustic Analysis

I used Raven Pro v1.5 (Bioacoustics Research Program, 2014) to analyze my recordings, using a frequency grid resolution of 23.04 Hz, a fast Fourier transformation (FFT) of 1050 samples, and a Hann window function. I selected all calls by hand and assigned them to species using visual identification based on a catalogue of known vocalizations (Chapter 2, Figure 2.2). To test whether a species responded differently to little owls in Scotland compared to England, I compared the differences in the known methods of information encoding used by tit species to encode information about predators for each element/call type each species produces (Chapter 2; Figure 2.2a-c). Specifically, for blue tits during the three minutes after they began mobbing, I examined 1) the call rate (calls/individual/minute), 2) the element number (total number of elements in each call), 3) the proportion (proportion of all calls during a mobbing event that were of particular call types), and 4) the propensity (likelihood of producing particular call types across all mobbing events), for great tits only call rate; and for coal tits only element number (Chapter 2; Figure 2.2a-c; Table 2.2).

Statistical Analysis

To test whether tit species responded differently to familiar and unfamiliar predators, I tested for an interaction between predator type (sparrowhawk and little owl) and experience (England and Scotland). Because sparrowhawks are common throughout the study population and should be familiar, high-threat predators at all study sites, I used them as a positive control for a 'high-threat' response for which I could compare the response of each flock to the little owl, thereby controlling for any regional differences in overall mobbing response. I generated generalized linear mixed models with a Poisson distribution to test for the interaction of area and predator on call rate (calls/individual/minute), and included mount exemplar and order as fixed effects and number of blue tits as well as each test site as random effects. To test for the interaction of area and predator for other ways of encoding information I used linear mixed models as the binomial generalized linear mixed models for testing proportion and propensity would not converge. However, this resulted in non-normal distributions for residuals in most proportion and propensity models (see Table 4.1). In these models I included area, predator, and the interaction of area and predator as well as mount exemplar and order as random effects. I also included a random effect to account for the number of calls at each location to help mitigate pseudoreplication due to multiple calls. To check for a significant interaction of experience (England and Scotland) and predator (sparrowhawk and little owl), I ran type III Wald Chi-squared tests. For each species, I focused on call parameters known to vary in response to predators (Chapter 2). I used R statistical software (R Core Team, 2014) and the lme4 package (Bates et al., 2014) for all statistical tests and all p-values I report are two-tailed. To control for running multiple tests, I calculated a Bonferroni corrected p-value for each species (blue tit: 0.001, great tit: 0.05, coal tit: 0.006); I reported all results that trended towards significance of models that and had normal residuals. All model results and normality as well as all Bonferroni corrected p-values are included in Table 4.1.

RESULTS

Blue, great, and coal tits showed an interaction between experience (England and Scotland) and predator (sparrowhawk and little owl): their response to a predator mount depended on whether they were experienced English tits or naïve Scottish tits. Blue tits responded to both sparrowhawks and little owls similarly in England but called at a lower rate in response to little owls than compared to sparrowhawks in Scotland ($\chi^2 = 9.64$, $P = 0.002$; Figure 4.2a; Table 4.1a). Blue tits calls in response to little owls had more elements than to sparrowhawks in England, but did not differ in Scotland ($\chi^2 = 6.56$, $P = 0.010$; Figure 4.1b; Table 4.1a). Great tits responded to both sparrowhawks and little owls similarly in England but tended to call at a lower rate in response to little owls than they did to sparrowhawks in Scotland ($\chi^2 = 3.26$, $P = 0.071$; Figure 4.2c; Table 4.1b). Coal tits produced fewer squeak elements to little owls as they did to sparrowhawks in England but produced more squeak elements to little owls as they did to sparrowhawks in Scotland (Figure 4.2c; Table 4.1c).

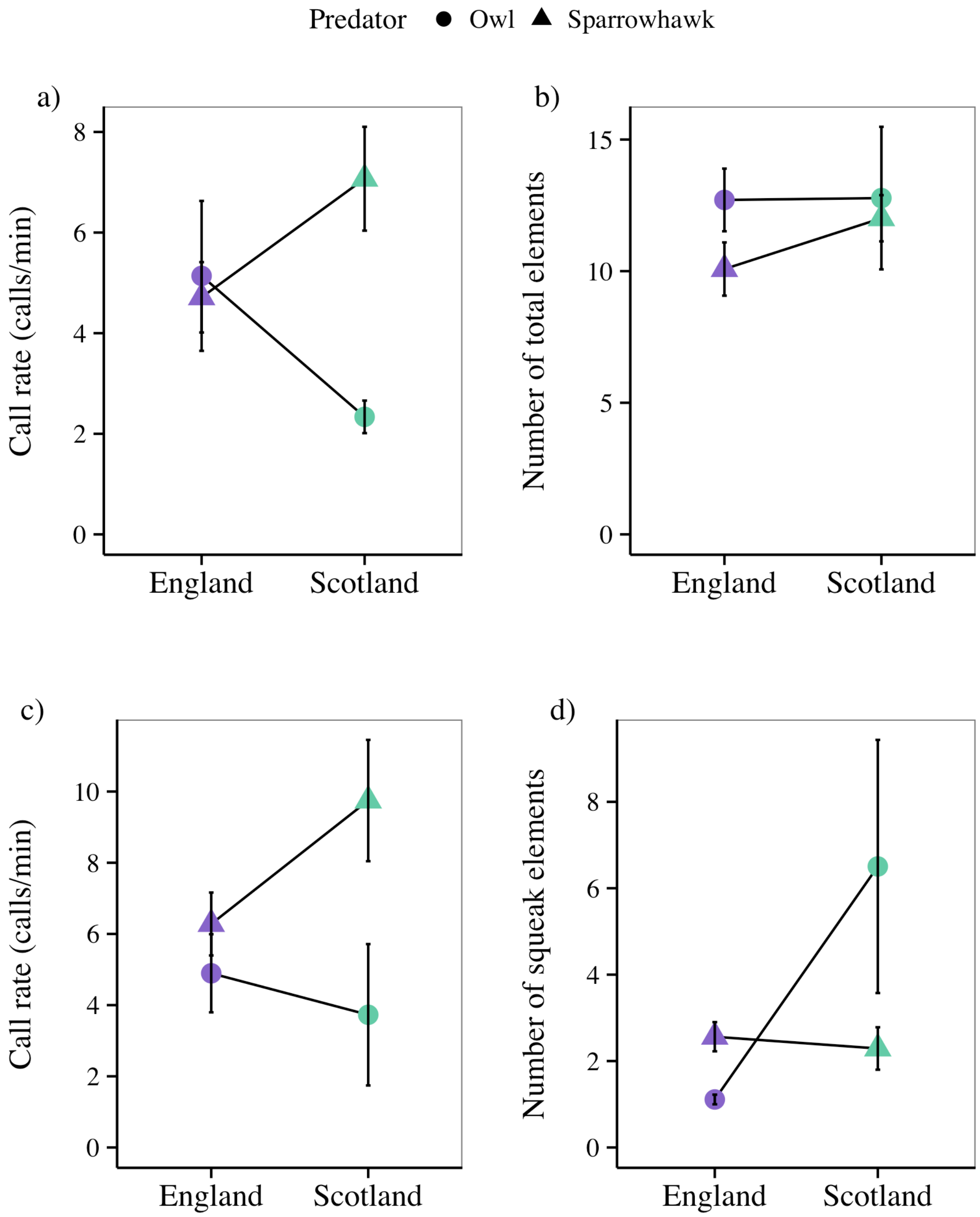


Figure 4.2 Mean (± standard error) difference in blue tit a) call rate (calls/individual/minute) and b) number of total elements, c) great tit call rate (calls/individual/minute), and d) number of coal tit squeak elements in response to little owls (●) and sparrowhawks (▲) in England (purple) and Scotland (teal).

Table 4.1 Type III Wald Chi-square test results for the interaction between prey experience (England, Scotland) and predator type (sparrowhawk, little owl) as a significant predictor of variation in ways of encoding information in mobbing calls. Bold type indicates p-values ≤ 0.05, italic type indicates p-values ≤ sequential Bonferroni corrected p-values. Sequential Bonferroni corrections were calculated using the total number of models run for each species respectively.

Encoding method	Call / element type	Transform	Normal	Interaction		Adjusted
				$\chi 2$	*P*	*P*
a) Blue tit						
Calls	All		normal	9.64	***0.002***	0.004
Number of	Total elements	boxcox:0.47	normal	6.56	**0.010**	0.005
	Mid elements		normal	NA	NA	0.050
	D elements		normal	0.00	0.989	0.025
Proportion of	Exit calls		bimodal	4.99	**0.025**	0.007
	Chirp calls		bimodal	11.79	***0.001***	0.005
	Tonal calls		bimodal	0.94	0.333	0.010
Propensity to use	Mid elements		bimodal	5.49	**0.019**	0.006
	Exit elements		bimodal	5.12	**0.024**	0.006
	Tonal calls		bimodal	0.01	0.922	0.017
	Frequency-modulated calls		bimodal	0.08	0.773	0.013
	Short calls		bimodal	1.13	0.287	0.008
b) Great tit						
Call rate	All		normal	3.26	0.071	0.05
Proportion of	Chirp calls		NA	NA	NA	NA
Propensity to use	Jar/rattle calls		NA	NA	NA	NA
c) Coal tit						
Call rate	All		normal	0.54	0.465	0.010
Number of	Hook elements		skewed	0.99	0.320	0.008
	Mound elements		normal	0.13	0.720	0.025
	Mt elements		skewed	1.79	0.181	0.007
	S-dot elements		skewed	0.06	0.814	0.050
	Squeak elements	boxcox:0.42	normal	3.921	**0.048**	0.006
Propensity to use	Mound elements		bimodal	0.21	0.646	0.017
	Squeak elements		skewed	0.53	0.466	0.013

DISCUSSION

In England, blue and great tits called at similar call rates in response to the two predators (little owl and sparrowhawk), both of which were probably familiar to them. In Scotland, however, blue tits responded differently to the unfamiliar predator (little owl) than they did to the familiar predator (sparrowhawk) and great tits showed a similar trend: blue and great tits called at a lower call rate to the little owl than they did to the sparrowhawk.

A decrease in call rate for blue and great tits suggests that they considered the little owl to be of lower threat than the sparrowhawk (Chapter 2). This also suggests that the tits may need experience with a novel predator before they can recognize it as such. As blue and great tits responded to little owls as they did to sparrowhawks in England they may therefore perceive them as a similar threat. This raises the question, however, as to why tits in England respond to little owls as they do to a high threat species.

Little owls are much less of a threat to tits than are sparrowhawks as, like many other owl species found in the UK, tits only make up a small portion of the little owl's diet (little owls: 4-15% frequency, short-eared owls: 0.1-14.5 % total prey weight, long-eared owls: 0.4-12.8 % total prey weight, barn owls: 0.1-14.5 % total prey weight, tawny owls: 0-50 % total prey weight; Cramp, 1993; Glue, 1967; 1974; 1977; Glue & Scott 1980; Jedrzejewski, Jedrzejewska, Szymura, & Zub, 1996; Marti, 1976; Roberts & Bowman, 1986; Southern, 1953; Tome, 1994), whereas tits make up a substantial portion of the sparrowhawk diet (~ 97% prey by weight; Newton, 1986). So why did the tits respond to the little owl as to a high threat predator? This could be a result of a combination of two factors: 1) while little owls do not hunt small birds often, they will take small birds. Some individual tits may then have some experience of little owls as a predator; 2) little owls fit the size criteria of a high threat predator (Dial, et al 2008; Templeton et al., 2005). These two features could have led to the tits responding in a way that exceeded the predator's actual threat. Regardless, naïve and experienced tits responded to little owls compared to sparrowhawks differently suggesting that tits need some form of experience in order to ‘recognize’ a predator as a threat.

More than one strategy used to ‘recognize’ a novel species as a predator might lead to misidentification of a novel predator. First, tits may need to learn to identify each new predator. Naïve blue and great tits misidentify the level of threat posed by the little owl similarly to many other species that learn about novel predators from other individuals. Naïve rhesus monkeys, *Macaca mulatta*, for example, learn to exhibit a fear response to snakes after observing this response in others (Mineka et al., 2004). Other Paridae species can learn about novel predators by observing other individuals mobbing the novel predator (Baker, 2004), and there is evidence that black-capped chickadees in areas with resident screech-owls, *Megascops asio*, alter their mobbing vocalizations by producing a shorter first D element than in areas without resident screech-owls (Saborse & Renne, 2012).

Second, tits may not be able to recognize a new predator if that predator does not share salient ‘predatory features’ with other, familiar predators. The lack of apparent recognition of the little owl as a predator threat may be because any ‘predatory features’ (e.g. eye colour, beak shape, coloration, etc.) that are shared between little owls and sparrowhawks were not sufficiently similar to allow the tits to generalize from sparrowhawks to little owls. Although this is a plausible explanation, a number of other prey species have been shown capable of generalizing from one predator to another. Tammar wallabies, *Macropus eugenii*, for example, which, after learning to fear a fox, *Vulpes vulpes*, were exposed to two unfamiliar animals, a cat, *Felis catus*, and a goat, *Capra hircus*, (Griffin et al., 2001). Wallabies responded to the cat much as they responded to the fox, but not to the goat, which suggests that they generalized predatory features from the fox to the cat but not to the goat (Griffin et al., 2001). Tits may also use certain features to identify known predators (Beránková et al., 2014): wild adult great tits brought into captivity, for example, exhibited the same high-stress in response to a sparrowhawk dummy with a pigeon beak as they did to a normal wooden sparrowhawk dummy (Beránková et al., 2014). However, like Siberian jays, *Perisoreus infaustus*, blue and great tits may classify hawks and owls as belonging to different classes of predators (Griesser, 2009).

Finally, as great and blue tits do not generalize from sparrowhawks to little owls, yet appear to be capable of using 'predatory features' to recognize a threat (Beránková et al., 2014), it is likely that tits generalize a novel predator's threat from familiar morphologically similar predators that are of a different threat level than the novel predator. The response of naïve blue and great tits to little owls was similar to their response to familiar low threat predators like buzzards or non-threats like partridges (Chapter 2), which may be due to their generalizing from previous experience with other owls. There are a number of other owl species in Scotland (e.g. short-eared, *Asio flammeus*, long-eared, *A. otus*, barn, *Tyto alba*, and tawny, *Strix aluco*, owls), none of which feed primarily on tits or other small birds (Cramp, 1993), but which may have been known or familiar to the birds I tested.

Although it is unclear why the blue and great tits in England responded to the little owls as they did to the sparrowhawks, in Scotland they did treat the two predators differently. This difference in response of naïve Scottish tits to a novel predator suggests that prior experience with predators is important for individuals to associate novel predators with their appropriate level of threat. What still remains unclear, however, is how this association is formed. This association could be formed as a result of personal experience of a predation event, or through social or observational learning as is found in some species (Baker, 2004; Curio, Ernst, &

Vieth, 1978b). Tits, due to their high propensity to mob and with their tendency to differentiate between predators of different threat levels, provide an ecologically and logistically useful system to examine the mechanisms by which species learn about novel predators.

Chapter 5

Great tit mobbing calls communicate novel predator threat to juveniles

INTRODUCTION

Tit species appear to need to experience a novel predator before they respond appropriately (Chapter 4). One way this may occur is by learning about predators either through personal experience or through watching others (Curio, Ernst, & Vieth, 1978a; 1978b; Vieth et al., 1980). Because it is difficult to ascertain the experience wild adults have had with predators, juveniles might be a more useful group of individuals to investigate whether individuals learn about predators through observing mobbing events. Evidence that juveniles might learn about predators at all comes from a range of sources: 1) juveniles of some species do not differentiate between predator and harmless species (e.g. great tits Kullberg & Lind, 2002), 2) others do not distinguish between levels of threat (e.g. two-year-old Japanese macaques Masataka, 1983), 3) in yet other species, juveniles do not respond appropriately to the information contained in anti-predator vocalizations (e.g. mobbing calls). For example, young Florida scrub jays, *Aphelocoma coerulescens* (Francis et al., 1989), black-billed magpies, *Pica pica* (Buitron, 1983), and American robins, *Turdis migratorius* (Shedd, 1982) all retreat to cover and remain quiet in response to adult mobbing calls, while California ground squirrel, *Otospermophilus beecheyi*, juveniles respond more urgently and spend less time out of view on hearing chatter calls and respond less urgently to whistle calls than do adults (Hanson & Coss, 2001).

Some species can learn to associate novel animals with an appropriate fear response such as avoidance behaviour. For example, paradise fish, *Macropodus opercularis* L., can be trained to avoid common goldfish, *Carassius auratus* (Csányi, 1985; Kelley & Magurran, 2003), birds such as New Zealand robins, *Petroica australis*, can be trained to be frightened of stoats, *Mustela erminea* (Griffin, 2004; Maloney & McLean, 1995), and mammals like tammar wallabies, *Macropus eugenii*, can be trained to be wary of foxes, *Vulpes vulpes* (Griffin, 2004; Griffin & Evans, 2003). It is thought that one component of such predator recognition learning is the observation by naïve prey of the novel stimulus as a recipient of anti-predator behaviour by another individual (Conover, 1987; Curio, Ernst, & Vieth, 1978a; 1978b; Griffin & Galef, 2005; McLean, Hölzer, & Studholme, 1999; Mineka & Cook, 1988; Vieth et al., 1980). Most of the evidence that individuals can learn about predators, however, comes from adult-to-adult transmission (McLean et al., 1999; Mineka & Cook, 1988).

The specific experiences that young birds need in order to learn appropriate mobbing behaviours, is still unclear. To test whether juveniles might learn about novel predators by observing an adult mobbing event, I presented a taxidermy sparrowhawk, *Accipiter nisus*, combined with audio and audio-video playbacks of an adult great tit mobbing a sparrowhawk to juvenile hand-reared great tit fledglings. I expected that after observing a mobbing event, juvenile great tits would mob sparrowhawks as the adult did (approach the sparrowhawk while producing mobbing calls), or avoid the sparrowhawk (spend more time further from it or exhibit escape flying behaviour).

METHODS

Study site & animals

I ran the experiments from the beginning of June to mid July 2014 at Nederlands Instituut voor Ecologie (NIOO-KNAW), Wageningen, Netherlands (latitude, longitude; 51.987718, 5.672721). I chose juvenile great tits as they do not recognize sparrowhawks as predators without prior experience (Kullberg & Lind, 2002). Because the peak in mobbing behaviour in adult chaffinch, *Fringilla coelebs* (Hinde, 1954a), and black-capped chickadees (Shedd, 1983) occurs shortly after their offspring fledge, I chose to present these playbacks as soon after fledgling as permitted.

I tested 48 fledgling great tits in four cohorts of 12, starting between 18 and 32 days post fledging. All of the great tits were brought in from nest boxes from a local long-term study population near Arnhem, the Netherlands at 10 days old. They were hand reared in natural nests in small topless wooden boxes (30 x 14 cm and 10 cm high) which were kept in incubators during this time and only removed for feeding (for diet specifics see Verbeek, Drent, & Wiepkema, 1994). Approximately 20 days after hatching, when the nestlings would normally leave the nest, birds were placed in fledgling cages and moved from the nestling room to the fledgling room where they were kept until they could be transferred to individual cages. In the fledgling metal wire cages (0.4 x 0.5 x 0.4 m) containing two perches they were housed with no more than three other individuals and no less than one other. They were given water *ad libitum* and fed a diet of beef heart mixture supplemented with insect larva (for specifics see Verbeek et al., 1994). Once they were able to feed themselves (~25-30 days), the birds were moved into individual housing (testing and holding cages), which was set up in rooms with two banks of 12 cages (3 high x 4 long; Figure 5.1a). Testing and holding cages were 0.9 m x 0.4 m x 0.5 m, with solid top, bottom, back and side walls and wire bar front, two ‘doors’ one on which a water dish was hung, and three horizontal perches. The testing cages were connected to a light-tight testing room by a 20 x 20 cm sliding door in the back of the cage, which could be opened from inside the testing room; holding cages were identical to testing cages except they lacked the door in the back of the cage (Figure 5.1b).

As the cage banks were situated on opposite walls, all birds were in both visual and auditory contact with other great tit fledglings. Birds had access to food (a combination of sunflower seeds and a protein rich commercial seed mixture) and water *ad libitum* (van Oers, Drent, Dingemanse, & Kempenaers, 2008). They were also given a few live mealworms daily and water and food was checked, filled, or replaced twice daily. As the cages were located in rooms with large windows they were kept under natural light conditions. Husbandry followed protocols set out in Drent, Van Oers & van Noordwijk (2003) and Verbeek et al. (1994).

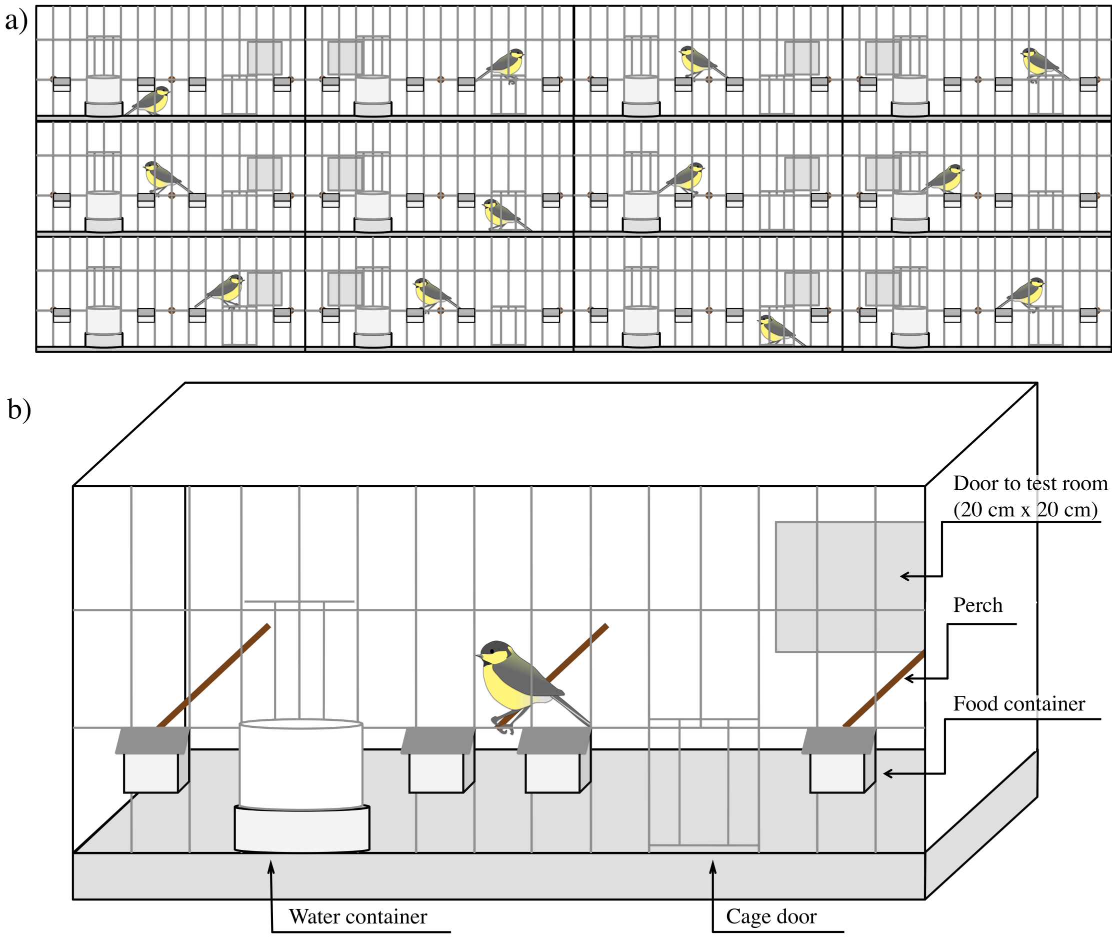


Figure 5.1 Schematic of a) cage bank arrangement, and b) a testing cage (0.9 x 0.4 x 0.5 meters). Holding cages did not share their back wall with testing room and therefore did not have the sliding door in the back, otherwise the holding and testing cages were identical.

Stimuli

I used a sparrowhawk, as the model predator because it is a high-threat predator that specializes in foraging on small birds (like tits; Curio et al., 1983; Millon et al., 2009; Perrins, 1979; Petty et al., 1995). Indeed, sparrowhawks kill a large number of juvenile tits during the breeding season (up to 44% of all great tit deaths over one month and kill up to 34% of great and 28% of blue tit juveniles; Millon et al., 2009; Newton, 1986; Petty et al., 1995). To make the mount appear more realistic

I used robotic raptors (details in the Methods in Chapter 2). To reduce the effects of pseudoreplication I used two sparrowhawk mounts: a juvenile male, and an adult female.

To test for the effect of adult mobbing vocalizations or behaviour and vocalizations coupled with a sparrowhawk I used three mobbing stimuli: 1) control – no audio or video of adults mobbing a sparrowhawk, 2) audio – audio only of adult great tits mobbing a sparrowhawk; 3) audio and video – video with audio of adult great tits mobbing a sparrowhawk. I used video as there is evidence that many bird species will respond to videos as they would to conspecifics (e.g. chickens, *Gallus domesticus,* Evans & Marler, 1991; McQuoid & Galef, 1993, zebra finch, *Taeniopygia guttata,* Swaddle, McBride, & Malhotra, 2006, and rooks, *Corvus frugilegus,* Bird & Emery, 2008; D'eath, 1998; Oliveira et al., 2000), but more importantly because video would allow us to control the mobbing demonstration experienced by all individuals. Audio and video mobbing stimuli were generated from video recordings of mobbing events induced by a sparrowhawk mount near the nest box of wild adult great tits at NIOO. Videos were pieced together from clips of adults mobbing and the image was zoomed in on the mobbing individual (as only one individual mobbed in all videos) to make the individual appear close to the mount during the presentation. The calling rates were approximately equal in all exemplars (mean ± std.error: 0.48 ± 0.01 calls/minute, range: 0.45 – 0.53 calls/minute). The audio and audio-video treatments had the same audio component, the screen in the audio treatments was turned off so as to not show the accompanying video. There were five exemplars of the video (and by extension audio) to help to reduce the effects of pseudoreplication.

In each cohort individuals were randomly assigned to one treatment for a total of four individuals per treatment. Half of the individuals from each cohort treatment were randomly assigned to sparrowhawk model A or B. Each individual was randomly assigned a playback exemplar for each training session.

Training & trials

All of the training and testing took place in the testing room. This room was approximately 4.0 m x 2.4 m x 2.3 m high, and contained three perches (1.5 meter high with a main trunk of 4 cm x 4 cm and four 'branches' each 20 cm long with the upper 2 branches 5 cm below the top and the lower 2 branches 25 cm below the top and on the side perpendicular to the top branches), the sparrowhawk and a monitor and speakers from which all audio and audio-video were played in the far left corner from the door, and a video stand in the near right corner from the door (Figure 5.3). The video screen sat slightly above the sparrowhawk, mimicking the position from which mobbing normally occurs (personal observation). The sparrowhawk was initially covered by a black cloth, which was placed on a square frame to keep the cloth from touching the mount or knocking it over when the cloth was removed (Figure 5.3). To expose the sparrowhawk I pulled on a line to remove the cloth (Figure 5.3). Birds entered and left the testing room through the sliding doors on the back of their cages (Drent et al., 2003; Verbeek et al., 1994).

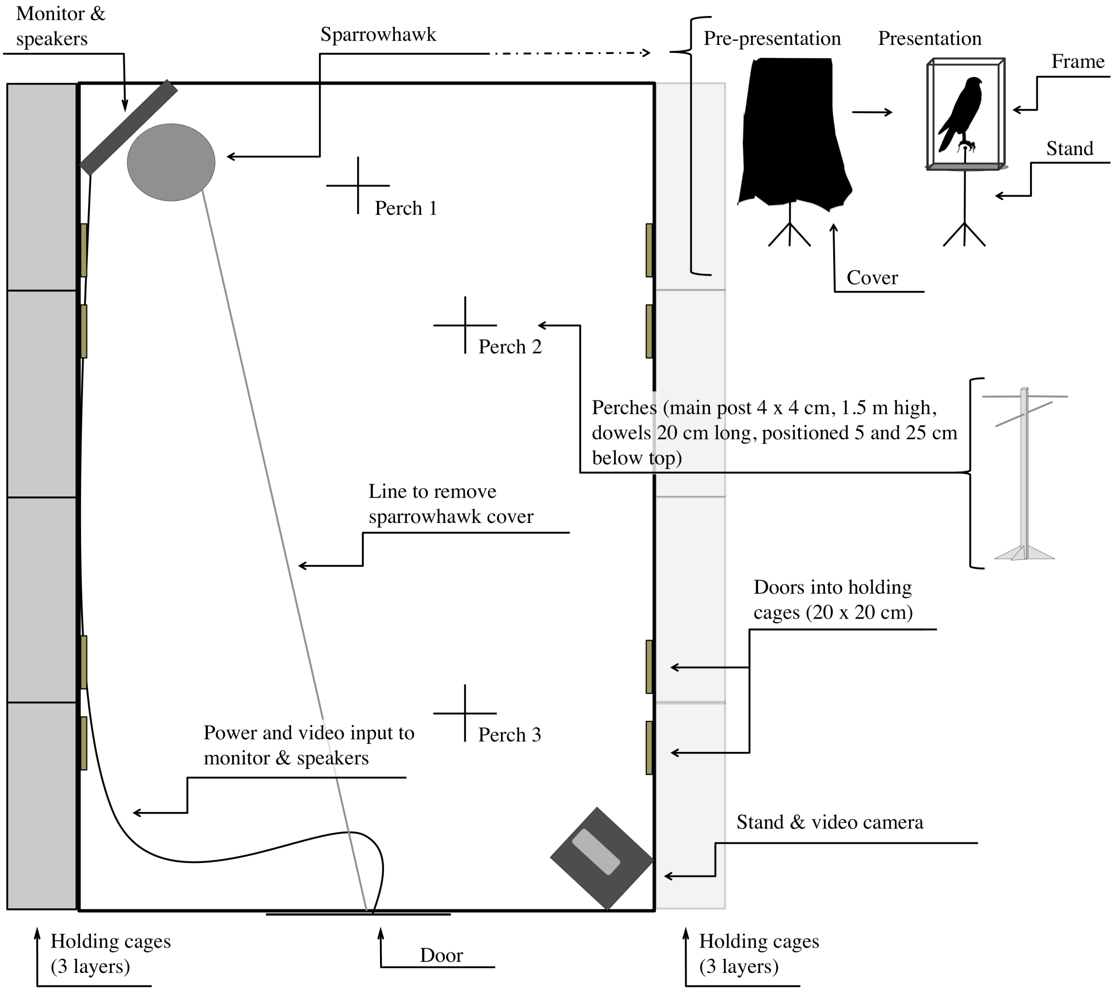


Figure 5.3 Testing room (4.0 x 2.4 x 2.3 meters)

During the first presentation, I tested whether juvenile great tits with no experience of predators responded to sparrowhawks by either mobbing or fleeing. During this initial presentation I allowed an individual to enter the testing room. I then allowed the bird 5 minutes or, in the case of two of the four cohorts, until they approached the closest perch to the covered sparrowhawk (mean ± std.error; 1.78 ± 0.42 minutes, range: 9 sec - 6.93 minutes), to acclimate to the test room before I removed the cloth covering the sparrowhawk. The trial with the sparrowhawk uncovered lasted two minutes and then I turned off the lights to end the trial, allowing the bird to return to its home cage.

To test whether juveniles became more wary of sparrowhawks (seen as an increase in the time spent farther from the sparrowhawk or in flight) after witnessing adults mobbing, I conducted pairs of training sessions followed by a test session. Each cohort received an initial presentation to test how they responded to the sparrowhawk mount, followed by two training sessions, a test, two more training sessions, a test, two final training sessions (three in the case of the first cohort) followed by a final test. This resulted in an initial presentation, six (seven for cohort 1) training sessions and three tests. All training sessions and tests were separated by a minimum of one day with two exceptions: the first cohort had three training sessions and a trial back-to-back during the last set of training sessions and test, and the final trial for all cohorts occurred the day after the final training. Training and test sessions followed the same protocol as the initial presentation, but the initial acclimatization period was only three minutes. For training sessions, when the cloth was removed from the sparrowhawk the mobbing treatment (control, audio, or audio-video) would begin. For tests, the protocol was the same as for the training sessions, but there was no mobbing treatment. All birds experienced a novel environment test in the testing room with a different setup (five perches in different positions) either the day before the initial trial, or the same day as the initial trial using the protocol followed in Baugh, van Oers, Naguib, & Hau (2013), Dingemanse et al. (2002), and Drent et al. (2003).

Behavioural Analysis

I watched all of the training sessions live as well as recording them on video. I scored the videos of the trials using Solomon coder software v 16.06 (www.solomoncoder.com). The data extracted from the videos were the total number seconds a bird spent on each perch, which allowed me to calculate the proportion of the total test each bird spent on each perch as well as flying (e.g. seconds flying/trial length). Due to the recorder's field of view, I was able to see all of the perches but not the wall close to the door or the floor. When the bird was out of sight, I coded the bird being on the wall/floor if there was no sound of flying, and as flying if I could hear wing beats. Videos for cohort four were processed by an undergraduate student, Madeleine Bambridge, and a random sample of those videos were re-sampled by me to check for accuracy and consistency. I processed all videos for the remaining three cohorts (one, two, and three). Due to time constraints only the data from the initial test before training and the first test after the first two training sessions are included in this chapter.

Statistical Analysis

To test if individuals changed their behaviour in response to the sparrowhawk training with either the control (no stimulus), the mobbing audio-only (henceforth audio), or the mobbing audio + video (henceforth audio-video) treatments, I generated linear mixed models with a Gaussian error structure. The response variable was the proportion of time each individual spent flying or on each perch. In order to control for individual differences in baseline behaviour, I subtracted the proportion of the total time each behaviour was exhibited during the initial test (before training) from the proportion of the total time each behaviour was exhibited during test one (after training) so I could test the difference in behaviour between both predator presentations. I included perch, treatment, and their interaction as the predictor variables of interest as well as the sparrowhawk exemplars used as fixed effects. I included each individual's cage, unique ID number, activity score from a personality assay (Dingemanse et al., 2002; Drent et al., 2003), and the total length of each trial as random effects. Activity scores were calculated as the number of movements an individual made during the first two minuets after entering a novel environment (Dingemanse et al., 2002; Drent et al., 2003). Although these individuals only received one novel environment test, previous experiments have shown that this test has a moderate level of repeatability ranging from 0.2 – 0.5 (Dingemanse et al., 2002). In order to test if there was an effect of the treatment (control, audio, audio-video) on the time spent flying or on each perch I ran a type III Wald chi square test on the model. All statistical tests were performed in R (R Core Team, 2014) using the lme4 package (Bates et al., 2014).

RESULTS

There was a significant interaction between the training stimuli an individual received and the difference in the amount of time they spent in proximity to the predator during their post-training compared to their initial trial (χ^2 (10) = 21.70, P = 0.017). Those juveniles in the control condition spent more time closer to the predator and decreased the time spent farther from the predator after training compared to their initial trial (Figure 5.4a). Those juveniles that only heard adults mobbing the sparrowhawk did not change their behaviour during trial 1 compared to their initial trial (Figure 5.4b). Those juveniles given a combination of video and audio of an adult great tit mobbing the sparrowhawk spent less time close to the predator and more time farther from the predator during trial 1 compared to their initial trial (Figure 5.4c).

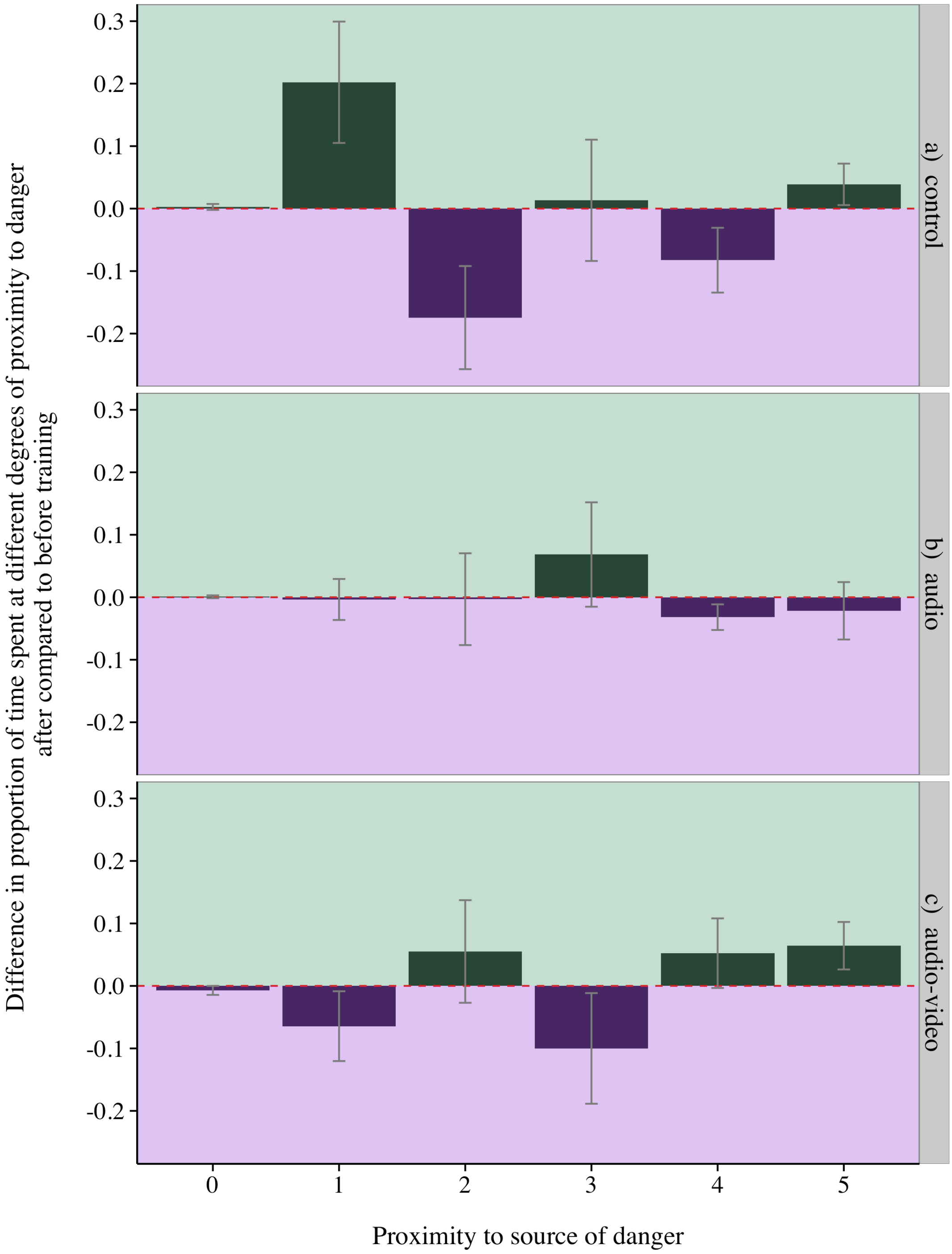


Figure 5.4 Mean (± std.error) difference in proportion of time spent at varying proximities to danger (sparrowhawk mount) before compared to after training (observing an adult mobbing the sparrowhawk) for a) control training group, b) audio only training group, and c) audio and video training group. The dashed line at zero indicates there is no difference between pre-training and post-training response to sparrowhawk, while a positive green, value represents more time spent post-training and a negative, purple, value represents less time spent post-training.

DISCUSSION

After two presentations of a sparrowhawk coupled with audio or audio-visual stimuli of an adult mobbing the sparrowhawk, juvenile great tits tended to spend more time farther from the sparrowhawk (Figure 5.4 b & c). With exposure to the sparrowhawk alone – in the absence of any conspecific mobbing – juveniles tended to spent more time close to the sparrowhawk, with three individuals even perching directly on the predator (Personal observation; Figure 5.4a). These data suggest that juvenile great tits exposed to adult mobbing stimuli can learn to be wary or frightened of a sparrowhawk whereas they would otherwise habituate to the same stimulus.

The increased avoidance of sparrowhawks in juveniles given mobbing stimuli, but not controls, supports the hypothesis that naïve young can learn about predators from watching and/or hearing adults mobbing a predator (Baker, 2004; Curio, Ernst, & Vieth, 1978a; Vieth et al., 1980). Given that shortly after fledging is the time when many species produce the most mobbing behaviour (Hinde, 1954a; Shedd, 1983), this would be an optimal time for young to make the associations between novel threats and danger. This lends further support for the idea that mobbing during the nestling and post-fledging period not only serves to protect young from predators, but to allow them to learn about novel predators without having to experience a predation event (Curio, 1978).

While the young birds in my study appeared to learn to avoid a sparrowhawk by observing adults mobbing, they did not mob the sparrowhawk themselves even though older (~ 120 days compared to my ~ 52 days) wild juveniles will mob like adults (Kullberg & Lind, 2002). It is not clear why the birds responded to the sparrowhawk but did not mob it in my study. It could be that the video was not a sufficient stimulant to induce mobbing, juvenile great tits' motor control is not sufficiently developed to mob at 52 days, or finally, the nature of testing in the lab dissuaded mobbing. Individuals in the lab frequently respond differently to those in the wild (Hinde, 1954b), and mobbing behaviour in blue and great tits especially tends to be expressed much less often and vigorously in laboratory conditions be it aviary or testing room (personal observation).

Although the effects of the treatment on the juvenile's behaviour were relatively subtle, these birds were provided with only two training sessions each lasting two minutes. This suggests that the juveniles need little experience to associate a novel stimulus with danger, congruent with other tests showing fast acquisition of anti-predator behaviour by many different species. Superb fairy-wrens, *Malurus cyaneus*, for example, learn to associate a novel sound with a predator after only two days of training (Magrath, Haff, McLachlan, & Igic, 2015), while blackbirds, *Turdus merula* (Curio, Ernst, & Vieth, 1978b), and black-capped chickadees, *Poecile atricapillus* (Baker, 2004), responded to a novel predator (blackbirds: noisy friarbird, *Philemon corniculatus*; chickadees: cinnamon teal, *Anas cyanoptera*) by mobbing it after only one 5 minute observation of a conspecific mobbing the novel predator, suggesting acquisition of anti-predator responses may require little experience.

These data show that young birds can learn to avoid predators after experiencing relatively brief mobbing events by adults. However the lack of mobbing behaviour exhibited by these individuals warrants further investigation to determine if it is a result of too few mobbing experiences, laboratory conditions, a lack of a living behavioural model, or developmental constraints inhibiting mobbing behaviour.

Chapter 6

Do wild fledgling blue tits mob?

INTRODUCTION

Mobbing behaviour increases the chance of survival of mobbing individuals by driving off the predator (Petifor, 1990), and decreases a mobbing individual's chances of being depredated in the future as predators preferentially hunt non-mobbing species and avoid roosting near mobbing species (Ekman, 1986; Pavey & Smyth, 1998). However not all species mob, and to better understand the ecological and evolutionary drivers behind mobbing behaviour across species, the focus has been directed at predator recognition and mobbing in juveniles to determine if mobbing is primarily learned or not. These studies have shown a variety of responses by juveniles to predators. For example, for many species, juveniles without experience, such as California ground squirrels, *Spermophilus beecheyi*, and black-tailed praire dogs, *Cynomys ludovicianus*, will engage in adult-like mobbing behaviour when presented with a predator (Owings & Coss, 1977; Owings & Owings, 1979). However, the juveniles of other species,such as meerkats, *Suricata suricatta* (Hollén & Manser, 2006), Verreaux's sifakas, *Propithecus verreauxi verreauxi* (Fitchel, 2008), and black-billed magpies, *Pica pica* (Buitron, 1983) do not engage in mobbing behaviour when young. While the literature shows a wide range of responses by juveniles, many of the experiments have been conducted on captive populations, which can exhibit abnormal anti-predator behaviour (Caro, 2005; de Azevedo, Young, & Rodrigues, 2012; Griffin, 2004). Therefore, to determine the effects of age (juvenile or adult) from environment (captive or wild), anti-predator response should be in the wild.

The juvenile great tits, *Parus major*, in the previous experiment (Chapter 5) did not mob a sparrowhawk (personal observation) and this lack of mobbing response could have simply been aberrant behaviour resulting from their upbringing in a lab. Animals in the lab can exhibit anti-predator behaviour that is different to that performed by animals in the wild (Hinde, 1954b). To determine whether wild juvenile tits learn to mob in response to adult mobbing calls, I conducted playback experiments to juvenile blue tits, *Cyanistes caeruleus*, in the wild across ~ 1 month during the fledging season to capture a range of post fledging ages. I chose blue tits as they are abundant and common throughout Scotland, readily mob predators, and nest in human-made nest boxes. In addition, as blue tits are more likely to mob than are great tits (personal observation), I considered that I was more likely to see an effect, should there be one. If mobbing behaviour is present in wild blue tit juveniles then in response to both blue and great tit mobbing calls juvenile blue tits should produce mobbing vocalizations as adult blue tits do in the wild.

METHODS

Study Sites & Species

I conducted playbacks to juvenile and adult blue tits from the 29th of June to the 5th of August 2015 in St Andrews, Fife, Scotland (56.331247, -2.838451). To test if juveniles respond to conspecific and heterospecific mobbing calls post fledging, I conducted playback experiments to blue tits over 38 days post fledging to try and capture a range of fledgling ages. The mean (± std.error) hatch to fledging time for 38 nests in St Andrews in 2016 was 19.37 ± 0.28 days and the range of hatching dates for 41 nests in St Andrews in 2015 was from the 20th of May to the 1st of June. However, as most subjects were not ringed and therefore could not be indentified, I could nether be sure of individual's age or identity. In order to try and test juveniles of a range of ages, I returned to the same area in successive trials as this is where the same fledglings were most likely to be found (Hinde, 1952; Perrins, 1979). Adults were easily differentiated from juveniles as their plumage is of a different colour, as were very young fledglings from older fledglings by the presence and strength of their begging behaviour (only young birds, generally up until 15 days post fledging, engaged in begging behaviour frequently; Hinde, 1952).

Stimuli

I used three different call types for the playbacks: 1) conspecific calls: an adult blue tit mobbing a sparrowhawk; 2) heterospecific calls: an adult great tit mobbing a sparrowhawk; and 3) control for calls: a wood pigeon's, *Columba palumbus*, territorial call, which they produce frequently throughout the year. I made three exemplars of each treatment to mitigate pseudoreplication. I created playback sound files from series of non-overlapping calls of varying length, from recordings of each tit species mobbing a sparrowhawk mount, or from recordings of wood pigeons obtained from the Macaulay Library. Mobbing calls were separated by an average (± std.error) of 0.49 ± 0.03 sec. for blue tits and 0.88 ± 0.07 sec. for great tits across all sound files and had an average of 20.11 ± 1.88 elements/call for blue tits and 10.32 ± 0.33 element/call for great tits. Wood pigeon recordings had a natural call rate of 3.5 calls/minute with calls separated by an average of 10.00 ± 0.03 sec. and an average

13.33 ± 0.03 of elements in each call. Wood pigeon calls were simply repeated single calls, as their calls are stereotyped for each individual. Blue and great tits had five different calls repeated in the same order for each audio file with call rates of 33.5 calls/minute for blue tits and 33.5 calls/minute for great tits. All playback files were generated from .wav file recordings and were saved as .wav files with a bit depth of 24 bits per sample and a sampling rate of 48 kHz. Each sound file consisted of two minutes of playback.

Playback

During each playback presentation, I tried to present the same individual/group with all three playback stimuli. To do this, I located fledglings/juveniles by sound and chose a single focal fledgling to follow (the first I saw if there were more than one). I then placed a Wildfire FoxPro WF1 speaker (FOXPRO Inc., Lewistown, PA, USA) between 3 and 6 m away from the focal individual, retreated at least 4 m from the birds in the flock, and played one of the three stimuli. The calls were all played at natural levels (~ 80 dB at 1m SPL), and the order each individual flock received the three stimuli, as well as the exemplar used, was randomized. I recorded all behavioural and vocal responses using a Sennheiser ME 66 super-cardioid directional shotgun microphone (Sennheiser Electronics, Hanover, Germany) and a PMD 661 Marantz solid-state digital sound recorder (Marantz America, LLC., Mahwah, H.J., USA). All recordings were made with a sampling rate of 48 kHz and a bit depth of 24 bits. After a playback was finished, I followed the focal fledgling for 20 - 30 minutes and conducted the next trial. I did this for all three stimuli when possible, waiting at least 20 – 30 minutes between each playback presentation. On the few occasions that the all of the birds in the area including the focal individual did not change their behaviour in response to the control playback, I waited only 5 to 10 minutes before presenting the focal individual with the next playback (n= 8). Although this increased the chance of introducing bias, it also increased the likelihood of me testing the same individual with all three treatments before losing track of it. For those individuals I could not follow after a presentation, I returned to the same location the next day (n = 5). However as no individuals were colour ringed, it was impossible to tell individuals apart. Additionally, due to technical difficulties, there was no control playback for the first set of presentations, and three trials in later playback presentations controls were missing controls as well (n = 3).

In order to try and test fledglings' behaviour across a range of ages (so as to not bias our fledgling trials too young or old), I located blue tit fledglings in similar areas four different times throughout the summer separated anywhere from 4 to 12 days. Presentations one, three, and four were made by a field assistant, Helen Pargeter, and I did presentation two.

Behavioural analysis

I used Raven Pro v1.5 acoustical software (Bioacoustics Research Program, 2014) to analyze the recordings (details in Chapter 2). I took note of four 'agitation' behaviours which are all produced by adults during mobbing events and include: approaching the playback, wing-flicking, flip-flopping, and scanning (Table 6.1). I recorded all behaviours during and after the playback by focal juveniles and a focal adult if one was present. I defined mobbing as any of the ‘agitation’ behaviours accompanied by mobbing calls.

Table 6.1 Descriptions of juvenile blue tit agitation and relaxed behaviours.

Type	Behaviour	Description
Agitation	Approach	Moving or flying in the direction of the playback
	Wing-flick	Flicking wings open and closed rapidly while remaining on perch
	Flip-flop	Moving the whole body back and forth rapidly while remaining on perch
	Scan	Looking up or around

Statistical analysis

I generated generalized linear mixed models using the lmer function of the lme4 package in R to test whether age or playback had an effect on the proportion of trials individuals mobbed. My predictor variables were age (juvenile or adult) and playback stimulus (control, blue tit, great tit). I included individual location for each treatment as a random variable to account for multiple playbacks given at each location and included both playback exemplar and presentation order to account for variation due to experimental methodology. To test for a significant effect of these variables I ran type III Chi-squared test.

RESULTS

Blue tits (fledglings and adults combined) were significantly more likely to mob in response to blue tit playback stimuli compared with either control or great tit playbacks (proportion of trials individuals (fledglings and adults combined) mobbed: blue tit = 0.286, great tit = 0.065, control = 0.048; $\chi^2 = 12.18$, $P = 0.002$; Figure 6.1b). Fledgling blue tits, however, were significantly less likely to mob in response to playbacks than adults (proportion of all trials individuals mobbed: juveniles = 0.013, adults = 0.263; $\chi^2 = 11.11$, $P = 0.001$, Figure 6.1a). Blue tit juveniles did, however, produce 'agitation' behaviours adults exhibit during mobbing (proportion of trials individuals produced behaviour: approach = 0.563, wing-flick = 0.238, flip-flop = 0.10, scan = 0.938; Figure 6.1c).

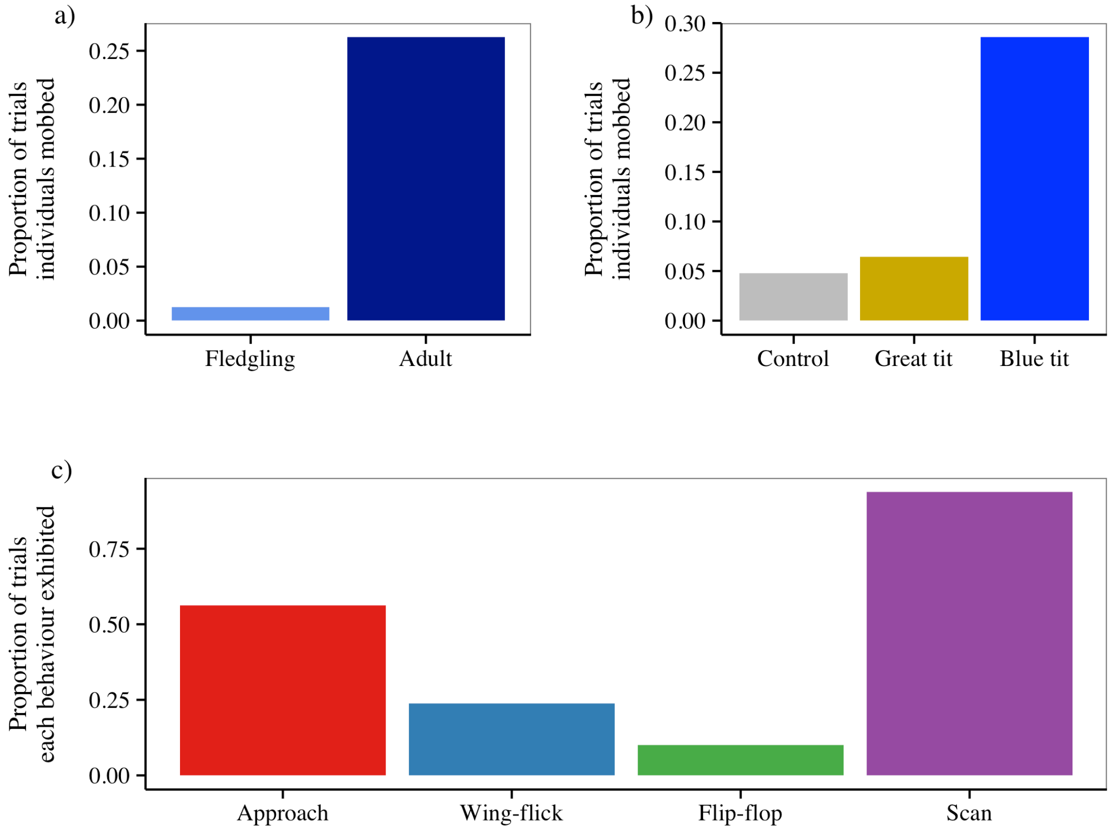


Figure 6.1 Graphs showing a) the difference of the proportion of trials juveniles (light blue) and adults (dark blue) produced mobbing behaviour defined as at least one 'agitation' behaviour accompanied by mobbing calls, b) the proportion of trials individuals produced mobbing behaviour, defined as above, in response to each different treatment (control represented by grey, great tit represented by yellow, and blue tit represented by blue), and c) the proportion of trials juveniles exhibited each 'agitation' behaviour seen in adult mobbing behaviour.

DISCUSSION

Blue tit juveniles did not mob in response to playbacks of mobbing calls whether or not those calls were produced by conspecifics. They did, however, produce all behaviours found in adult mobbing (i.e. approaching the speaker, wing-flicking, flip-flopping, and scanning). As they produced the behaviours that adults use during mobbing juvenile blue tits are at least physically capable of producing the constituent behaviours of adult mobbing, even though they did not produce them all together as would an adult.

While the lack of mobbing in juvenile blue tits could be due to underdeveloped motor control (Mateo, 1996a), it is more likely that juvenile blue tits can, but do not, engage in mobbing behaviour. This may not be entirely unexpected, as juveniles of some other species similarly do not produce adult-like anti-predator behaviour until they are older (e.g. bonnet macaques, *Macaca radiata,* Ramakrishnan & Coss, 2000, American robins, *Turdus migratorius*, Shedd, 1982, black-billed magpies, *Pica pica*, Buitron, 1983, Florida scrub jays, *Aphelocoma coerulescens*, Francis et al., 1989, and California ground squirrels, *Spermophilus beegheyi*, Hanson & Coss, 2001). Although juveniles may not exhibit adult-like mobbing behaviour, they may be developing or ‘practicing’ aspects of mobbing behaviour. However, as this experiment did not have colour ringed individuals I was unable to determine how these behaviours changed over time, or if individuals of particular ages change how they respond to conspecific or heterospecific mobbing calls.

While juvenile blue tits do not respond to mobbing calls with complete, adult-like mobbing behaviour, they do produce some of the mobbing behaviours seen during mobbing in adults. These data suggest that behaviours involved in mobbing may develop over time as individuals get feedback from observing and interacting with adults and predators. If so, then blue tit juveniles could provide a fruitful system to study the ontogeny of mobbing and anti-predator behaviour in the wild. While there are logistic issues when using wild populations by using a population in which the individuals have colour rings, and by including presentations of conspecific contact calls and acoustically dissimilar mobbing calls into the series of playbacks, we could address questions about the ontogeny of mobbing and other anti-predator behaviours in individuals across time and whether age-related behaviours like begging decrease over time through learning or other developmental processes.

Chapter 7

Aerial alarm call response: the effects of proximity & personality

INTRODUCTION

In the previous two chapters, I demonstrated that juvenile blue and great tits responded differently to mobbing calls than did adults. This result was not entirely unexpected as there is evidence in a wide range of species that many anti-predator behaviours, including the response to anti-predator vocalizations, vary across individuals based on age (Rajala et al., 2003; Rajala, Kareksela, Ratti, & Suhonen, 2011), sex (Alatalo & Helle, 1990; Cheney & Seyfarth, 1985; Maklakov, 2002), social relationships (Cheney & Seyfarth, 1985; Griesser & Ekman, 2005; Karakashian et al., 1988; Krams, Krama, & Iguaune, 2006b; Maklakov, 2002), dominance (Alatalo & Helle, 1990; Cheney & Seyfarth, 1985), and 'personality'(Cole & Quinn, 2014; Vrublevska et al., 2014). This last trait, 'personality', has received a lot of attention in recent years, especially in relation to its fitness consequences (Dingemanse & Wolf, 2010; Sih et al., 2015).

'Personality' is a term used to describe consistent individual differences in boldness, activity, exploration, etc. (Dingemanse & Wolf, 2010; Sih et al., 2015), and there is evidence that these differences in personality have been favoured through natural selection and maintained in a given population through state-behaviour feedbacks (Dingemanse & Wolf, 2010; Sih et al., 2015). Birds, then, vary, not just in how long it takes them to approach a novel object in their cage, but also in more ecologically significant behaviours such as foraging, fighting, and approaching a member of the opposite sex (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005); the repercussions of an individual's personality on their fitness may be large. Personality is often measured by observing behaviour in stressful or novel environments (novel object approach, movement scores in novel environments, etc.; Carter et al., 2012a) and repeatable behaviours that are correlated across contexts are often grouped into behavioural 'syndromes' (Carere et al., 2005; Dingemanse & Wolf, 2010; Sih et al., 2015). As boldness is often measured using movement in some way (approaching a novel object or amount of movement in a novel environment, Carter et al., 2012a), this may be a personality trait that affects the ways in which different individuals respond to predators.

Although the effects of boldness (as measured by movement) are frequently measured in stressful situations, there are other factors that vary among individuals during predator encounters that may influence an individual's anti-predator response such as an individual's distance to the signal/signaller. Given that distance to a predator (threat) is an important enough factor to be frequently encoded into alarm calls (Baker & Becker, 2002; Blumstein, 2001; Magrath, Pitcher, & Gardner, 2007; Manser, 2001; Murphy et al., 2013), and that signaller is the first to spot the predator, and then draws attention to itself by producing a signal (Krams, 2001), those individuals closer to the signal should be in more danger and respond accordingly.

As social factors can affect anti-predator behaviour (Chapter 3), closer predators pose a more immediate threat, and those individuals capable of seeing a predator are more likely to be able to be seen by said predator, I wanted to know if distance to the signaller increased perceived danger and caused a more intense behavioural response to an anti-predator signal. Further, since personality has been shown to affect behaviour during stressful situations,(Carter et al., 2012a) I wanted to know if personality (as measured by the amount of movement in a novel environment) interacted with distance to signal/signaller affect behavioural responses of individuals to anti-predator signals. Because of the challenges of investigating individual differences in mobbing behaviour in the lab and with unmarked individuals in free-living populations, I decided to use an anti-predator vocalization that is more readily produced (and responded to) in the lab: high frequency (Hz) aerial alarm calls.

Aerial alarm calls are most frequently given in high-threat situations when a predator is flying overhead and considered to be actively hunting (Marler, 1955). Individuals respond to these aerial alarm calls by freezing in place or fleeing to cover (Hinde, 1952; Owings & Virginia, 1978) in order to avoid immediate depredation (Marler, 1955; Morse, 1973). These calls, unlike many mobbing vocalizations, tend to be very high frequency and narrowband (Marler, 1955) often at the upper limits of the hearing range of many raptorial species (Klump et al., 1989), making it difficult to localize (Brown, 1982; Jones & Hill, 2001). Unlike mobbing, the behavioural responses this call induces are much more stereotyped (Hinde, 1952; Owings & Virginia, 1978), suggesting that factors such as an individual's personality or internal state due to proximity to the signaller may have a greater impact.

As identification of individuals was necessary, I used a lab population to investigate the effects of an individual's personality (measured by the amount of movement they made in a novel environment) and of their proximity to the signal on their latency to move after freezing having heard an aerial alarm call. Testing great tits in individual cages allowed me to keep track of individual identity, to run multiple tests of individuals, and to test for individual variation in movement in novel environments. To determine whether individuals varied in their response to high-threat anti-predator signals, I presented juvenile great tits with aerial alarm calls and used their latency to move after freezing as a measure of variation in individual response. If individuals differ consistently in their responses to high-threat anti-predator vocalizations then after hearing an aerial alarm call, birds 1) that are farther from the source of the aerial alarm call, and hence from the apparent danger, should move earlier than others after freezing, and that 2) this response should depend on their boldness (move more in a novel environment test): those with higher boldness scores should move sooner after freezing.

METHODS

Study site & species

I conducted these experiments at Nederlands Instituut voor Ecologie (NIOO-KNAW), Wageningen, Netherlands (latitude, longitude; 51.987718, 5.672721) from the beginning of June to mid July 2014. I used great tits, which will both produce and respond to aerial alarm calls from a young age (Rydén, 1980), and which have become a model system for studying bold and shy personality traits (Carere & van Oers, 2004; Quinn, Cole, Bates, Payne, & Cresswell, 2012; van Oers, 2008; van Oers et al., 2008; van Oers, Drent, de Goede, & van Noordwijk, 2004; van Oers, Klunder, & Drent, 2005). Due to timing and availability of subjects, individuals were still juveniles (age after fledging: mean ± std.error 40.1 ± 1.26 days). However they were old enough to be completely independent and would have already dispersed if wild (independence begins when parents stop feeding fledglings around 14 - 28 days & fledglings disperse shortly after becoming independent; Hinde, 1952). Great tit rearing and husbandry was the same as explained in Chapter 5. I tested a total of six cohorts each containing 12 individuals (although as five individuals were tested in one additional cohort the total was 67 unique individuals). Birds in each cohort were kept in individual cages (Chapter 5; Figure 5.1b) in cage banks of 12 cages (Figure 7.1). Five cohorts were positioned in cage banks of four across and three high, facing another bank of cages in the same configuration (Figure 7.1a). One cohort was arranged in two cage banks of three high and two across that were perpendicular to one another (Figure 7.1b). As the cages were the same size and cage banks were in standard fixed positions, the distances from each cage to the next was the same across all cages. This provided standard distances from each cage to all other cages in a cage bank. This allowed me to test for differences in proximity by assigning distance categories to all cages relative to the cage the stimulus was presented at (Figure 7.1c).

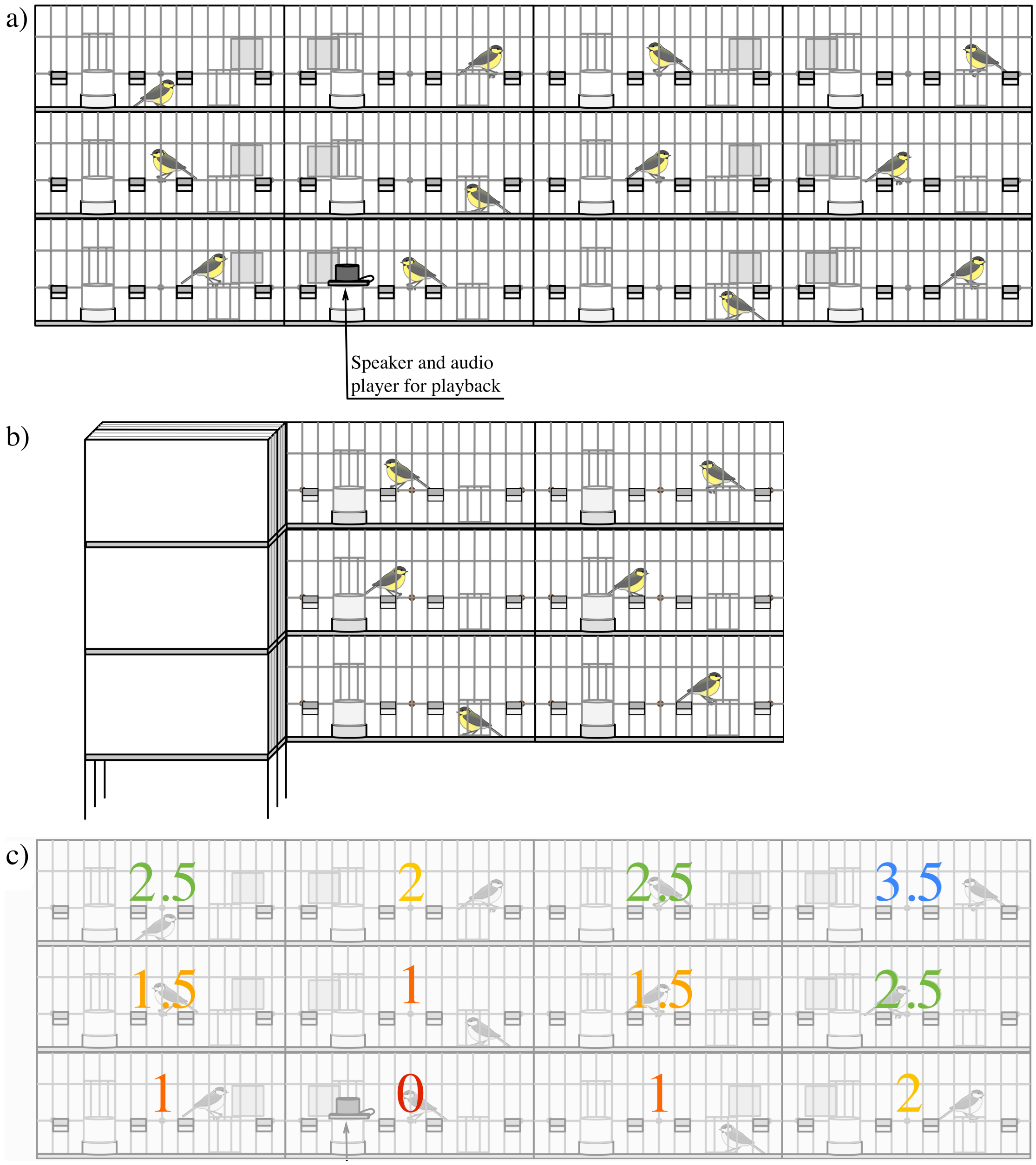


Figure 7.1 Cage bank configuration of a) cohorts one – five (including the position of the speaker and iphone during playback trials: on top of the water container), b) the sixth cohort, and c) the distance category assignment for one playback setup: 0 indicates the playback position.

Stimuli

To test whether the latency to move after freezing was affected by personality and/or proximity to an aerial alarm call, I induced freezing behaviour using playbacks of aerial alarm calls. Because many individuals produced aerial alarm calls in response to movement outside the window of the room in which they were housed, I put together aerial alarm call playbacks with Raven and Audacity software using recordings of aerial alarm calls produced by other experimental birds from the lab with whom the test individuals had been previously housed while in fledgling cages. While the alarm calls were presumably induced by a variety of unknown stimuli they did not vary much acoustically (peak frequency: mean ± std.error = 8.08 ± 0.14 kHz; call length: mean ± std.error = 2.09 ±0.16 sec.) Great tit juveniles and juveniles of some other species will respond to all stimuli as being high-threat until they learn which to ignore: great tits (Gompertz, 2007), pika, *Ochotona princeps* (Ivins & Smith, 1983), California ground squirrels, *Spermophilus beecheyi* (Hanson & Coss, 1997), and vervet monkeys, *Cercopithecus aethiops* (Seyfarth & Cheney, 2009). I recorded their aerial alarm calls using a Sennheiser ME 66 super-cardioid directional shotgun microphone (Sennheiser Electronics, Hanover, Germany) and a PMD 661 Marantz solid-state digital sound recorder (Marantz America, LLC. Mahwah, H.J., USA). I generated seven call exemplars and balanced them so that each cohort was presented with all seven exemplars, with five different presentation orders evenly distributed across cohorts. Within cohorts I randomly assigned individuals one of the twelve (two unique and five repeats) aerial alarm call exemplars. The playback files had 1 minute 20 seconds of silence followed by one aerial alarm call lasting no more than one second. All playback files had a bit depth of 24 and a sampling rate of 48 kHz.

Playback

I conducted playbacks trials to six cohorts of twelve individuals (n = 72 individuals, though five birds were tested in two different cohorts for a total of 67 unique individuals), each in their own cage situated in a cage bank (Figure 7.1a and b). To test how proximity and personality may affect birds' anti-predator response to aerial alarm calls, I conducted playback trials to each cohort of twelve individuals from each individual's cage (12 trials per cohort and 12 birds per trial). This allowed me to test every individual's response at different distances to the playback: the responses of all individuals in one cage bank were recorded for all twelve playback locations within that cohort. I played each playback from an iPhone 4s © (Apple Inc., Cupertino, CA, USA) connected to a XMI X-Mini II 2nd Generation Capsule Speaker (Xmi Pte Ltd, Singapore) with a frequency response of 100 Hz – 20 kHz which was placed on top of the focal individual's water holder (Figure 7.1a). Playbacks were separated by a minimum of 20 minutes, a normal rate of aerial alarm call production (personal observation), to allow the birds to resume normal behaviour between trials. I assigned each cage (i.e. individual) a playback exemplar so each cohort received five exemplars twice and two exemplars one time (7 exemplars to 12 cages). Playback position (i.e. cage number/spatial order) was also randomized. However, as not all playbacks resulted in freezing behaviour of more than 2/3 of the cohort (n = 31 trials), not all playback exemplars were evenly represented in the final data.

Novel environment test

Shortly after they had been moved to their individual cages, I presented each bird with a novel environment test (see Methods Chapter 5). This test determined a ‘boldness’ score for each individual by measuring the amount of activity (the number of times an individual hopped between the ‘branches’ on the perches and flew between the five perches in the testing room) an individual exhibited during the first two minutes of a 10-minute trial in a novel environment (for testing specifics see: Drent et al., 2003 and Dingemanse et al., 2002; for personality score calculation see: Baugh et al., 2013). Although each individual only received one novel environment experience, previous experiments have shown a moderate level of repeatability ranging from 0.2 – 0.5 (Dingemanse et al., 2002).

Video analysis

I recorded all trials using two video cameras (Panasonic HDC-SD80 from Panasonic Corporation, Kadoma, Osaka, Japan) positioned across the room at angles allowing me to view the front of all the cage banks (each camera was able to record three cage banks). However, due to the angle of the cameras, I was not able to see into the corners of some of the cages and any birds staying in those areas. I excluded those individuals from trials in which I could not see the bird due to its position in its cage. I synchronized the time in the two recordings using a clap, given before each playback during a verbal notation of the test date, time, playback exemplar, and playback cage. This sound did not appear to affect the bird’s behaviour.

I calculated two measures of latency to movement from the time of the aerial alarm call (i.e. their freezing response). The first was latency to move, movement being any detectable movement of an individual’s head or body while both feet remained in place, henceforth ‘movement’. The second was latency to hop, hopping being any movement where both feet left the perch/ground for any amount of time, which included walking and flying, henceforth ‘hop’. For each of these measures of activity, movement and hop, I calculated both the latency (the number of seconds from the end of the aerial call to the first movement or hop) and the order in which each bird first moved and hopped relative to all other birds in the study. The cohort did not always respond to aerial alarm call playbacks by freezing (31 out of a total 101 trials). When more than 4 individuals in the cohort did not respond to the aerial playback by freezing, the trial was considered a failure (the cohort did not exhibit anti-predator behaviour) and the experiment was repeated from the same location a minimum of 2 hours later. I repeated a presentation to the cohort with the stimulus at a given location twice at most (n = 24 locations, 31 trials). Due to time constraints I could not repeat presentations at all locations (n = 11). As those trials where more than 4 individuals in the cohort did not freeze in response to aerial alarm calls, or where the latency to move for more than three birds was less than 4 seconds were not indicative of anti-predator behaviour they were not included in my models.

Statistical analysis

As measures of each individual’s response to the playback stimuli, I calculated both the latency, the number of seconds from the end of the aerial call to the first ‘movement’ or ‘hop’, as well as the order in which each bird first ‘moved’ and ‘hopped’ relative to all other birds in the study. Movement latency, movement order, hopping latency, and hopping order were the response variables in four linear, or quadratic (in the case of hopping order) mixed models. I included a quadratic term in the model for data on the order of first hop as the relationship between the order of hopping and distance from the source of the aerial call was curvilinear. As the values for movement and hopping latency were time data (seconds) and skewed right they were log transformed before being included in the model. These models included each individual's proximity to the stimulus, their boldness (movement) score, as measured through their amount of activity in a novel environment (log transformed), and the interaction of the two as fixed effects. The random effects included: the stimulus position (where in the cohort's cage bank the stimulus was placed), individual bird ID, trial order, the aerial alarm call exemplar, and cohort. All model residual were normally distributed. To test whether distance, movement score, or their interaction had an effect on an individual's latency or order of movement and/or hopping, I ran type III Chi square tests. In order to determine the effect of individual ID on the models, I compared a null model (one without the individual ID random effect term) and the full model using Δ AIC, and reported the amount of variance explained by the individual ID random effect term.

RESULTS

Neither the distance to the aerial alarm call nor the bird's 'boldness' score was correlated with the time it took great tit juveniles to move or to hop after they froze in response to hearing an experimental aerial alarm call playback (Table 7.1; Figure 7.2). The order in which different individuals moved was also not related to 'boldness' score or distance from the aerial alarm call. The birds closest to the source of the aerial alarm call, however, were more likely to hop before those individuals further from the playback speaker (Table 7.1; Figure 7.2). However, this trend was driven by the individuals in the playback cage as, if they are removed from the model, distance had no effect on hopping order (Figure 7.2 red line). Individual ID accounted for some of the residual variation in the models testing movement and hopping order, which suggests that individuals differ in some way other than proximity and personality in the order they began to move and hop after a playback of an aerial alarm call (Table 7.1).

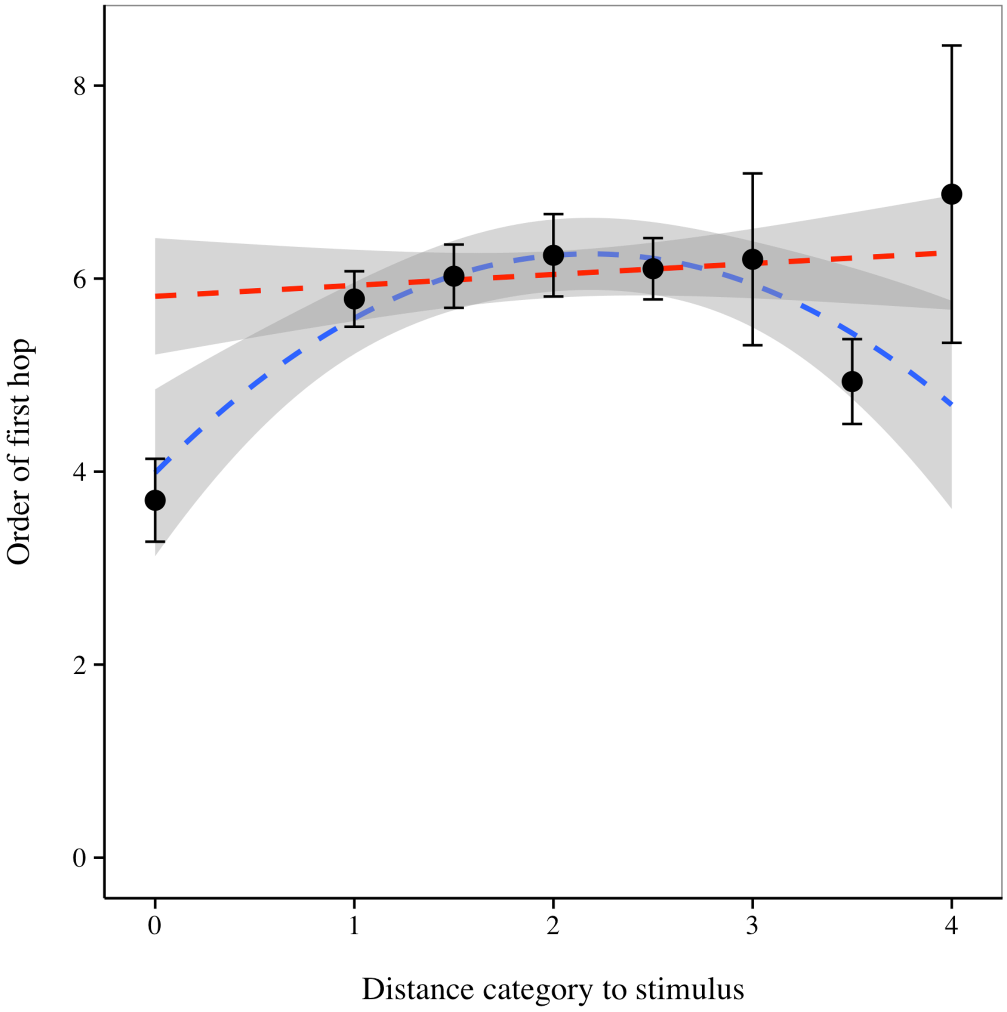


Figure 7.2 Mean (± standard error) hopping order as distance of hopping individual to the source of the aerial alarm call increases. The blue line represents the full quadratic model including the individuals who were closest to the aerial alarm call. The red line represents the model excluding the individuals who were closest to the aerial alarm call.

Table 7.1. Type III Wald Chi-squared test results for distance from aerial alarm call and ‘boldness’ score as a significant predictor of variation in latency to move and hop in juvenile great tits. Significance of individual identity for overall model shown with Δ AIC scores (null model (full model but excluding individual ID random effect)-full model (full model including individual ID random effect): - value indicates null model is better, + value indicates individual ID model is better), individual ID variance as calculated by the model summary is shown.

Movement type		Fixed effect	χ^2	P	Δ AIC	Variance	Std. Dev.
Movement	Seconds	Distance	0.13	0.714	-2.00	0.000	0.000
		Movement	1.00	0.318			
		Interaction	1.06	0.302			
	Order	Distance	0.21	0.649	10.14	1.030	1.015
		Movement	0.41	0.522			
		Interaction	0.69	0.407			
Hopping	Seconds	Distance	0.58	0.447	-2.00	0.000	0.000
		Movement	0.99	0.320			
		Interaction	1.18	0.278			
	Order	Distance	19.93	<0.001	2.70	0.492	0.702
		Movement	0.33	0.567			
		Interaction	0.15	0.700			
		Quadratic	21.61	<0.001			

DISCUSSION

Those juvenile great tits for which an aerial alarm call had been presented in their own cage were more likely to hop before the other birds in the bank of cages. However, this effect of distance from the playback was restricted just to those particular birds as the distance from the playback had no effect on the order in which any of the other birds began hopping. There were no other consistent differences in the latency or order in which any of the young birds moved their heads or hopped after freezing in response to an aerial alarm call. Individuals did vary in the order in which they moved or hop after freezing in response to aerial alarm calls but, as this variation was not accounted for by proximity or personality, it suggests that an unknown factor(s) varies across individuals, which explains the order in which individuals first move and hop after freezing in response to an aerial alarm call.

Although it may seem counter-intuitive that those individuals in the cage in which the source call was played back were the first to hop it may be that because the call came from within their cage which meant that these birds could tell that there was little or no danger (because they could not see a predator that would have led to the production of the call). This in turn may have lead to their decreased wariness and an increased likelihood of moving again relative to those birds that could not be as sure that there was not predator associated with the aerial alarm call. Conversely, as the individual closest to the ‘caller’ these individuals may be more motivated to try and escape to cover. However, as their hopping behaviour often included non-escape behaviours such as feeding, preening, and hopping slowly across the cage floor, I do not think this was the case. The distance of the birds in the other cages seemed to have no impact on their latency or order to begin moving or hopping after freezing. ‘Boldness’ scores, as measured by the amount an individual hopped and/or flew while in a novel environment, also did not seem to explain the latency, or the order in which individuals began, to move or hop after freezing in response to an aerial alarm call.

While there may not be a biologically meaningful relationship between distance from the animal signalling the presence of a predator or ’boldness’ in aerial alarm situations, the lack of correlation could also result from the laboratory conditions or experimental design used in this experiment. First, the cages may not have been far enough apart for the distance to matter. The maximum distance between the source of the call and the furthest bird was approximately 3.8 meters, while in the wild individuals in flocks can easily range to distances up to 10 meters (Hutto, 1994). 3.8 meters, then, may have been too small a distance to affect anti-predator freezing behaviour in this species. It would be useful to include more realistic distances in future experiments. Second, while the amount of movement in novel environments is often used as a proxy for boldness, individuals may not always respond similarly in different stressful situations. Individual chacma baboons, *Papio ursinus*, for example, score very differently on ‘boldness’ measures in anti-predator contexts relative to a novel food context even though the two contexts are often both used to measure boldness and are therefore thought to be similar (Carter, Marshall, Heinsohn, & Cowlishaw, 2012b). Like baboons, juvenile great tits may respond very differently to anti-predator situations than they do in other stressful situations (i.e. novel environment), which may result in consistent individual amounts of movement in one context (novel environment) that are not correlated with individual movement behaviour in another (anti-predator response). When studying the effects of personality on anti-predatory behaviour it seems that it would be more appropriate to use a measure of boldness taken in an anti-predator context (startle test).

Finally, anti-predator behaviour in the lab may not be representative of tit behaviour in the wild (Hinde, 1954b). Although they did freeze in response to aerial alarm calls like wild birds, these captive juvenile great tits differed in the latency and order in which they moved and hopped. This individual variation in response may be due to factors such as visibility and a lack of experience. All of the playbacks took place while birds were in individual cages with relatively poor visual range, due to five opaque walls and bars on the front restricting their ability to see outside their cages, and no heavily foliated place of escape. The lack of visibility and dense vegetation in which to hide could have affected the birds’ willingness to move after hearing an aerial alarm call. Additionally, it is not clear what effect on their freezing behaviour being hand-raised in the laboratory, with no experience of observing adults responding to aerial predators or aerial alarm calls, might have had. Other species such as Belding's ground squirrels, *Spermophilus beldingi,* take longer to discriminate between alarm call types in the absence of their mother (Mateo & Holmes, 1997), suggesting they may need an adult presence to acquire correct anti-predator responses earlier in life.

Overall, then, and unexpectedly, proximity and personality appear to be poor predictors of responses to aerial alarm calls in juvenile great tits. As personality is often tested in anti-predator situations (Carere et al., 2005; Carter et al., 2012a; Dingemanse & Wolf, 2010; Sih et al., 2015), this was quite surprising and suggests that there remain some aspects of personality in anti-predator contexts we do not fully understand.

This experiment also highlighted many of the potential problems with studying anti-predator behaviour in the laboratory. While allowing individual identification and full knowledge of life experience, hand-reared animals in laboratory conditions may behave differently than those in the wild, especially in anti-predator contexts (de Azevedo et al., 2012; Griffin et al., 2000; Maloney & McLean, 1995). My data raise, then, a number of unanswered questions such as the strength of the effect of individual personality on anti-predator behaviour in different contexts (e.g. high threat aerial alarm vs. low threat mobbing), as well as whether the behavioural responses to these signals (latency to resume foraging) are relatively fixed in individuals from a young age (within a week of fledging) or if they develop over time and with the presence of adult role-models.

Chapter 8

General Discussion

SUMMARY OF RESULTS

The goal of my thesis was to determine how prey species produce, use, and respond to anti-predator information and how these behaviours may be influenced by individual, social, and phylogenetic factors that different species experience.

To determine how the tit species found in the UK encode information about predators in their mobbing calls, I conducted a series of experiments that induced mobbing in response to different threat predators. Contrary to previous research suggesting that species in the Paridae family use the same ways of encoding predator threat information in their calls, I found that the UK tit species varied considerably in how they encoded this information. While some species (marsh, *Poecile palustris*, and blue tits, *Cyanistes caeruleus*) used the same ways of encoding information as seen previously in other Paridae, the other four UK tit species used only a subset of these (coal, *Periparus ater*, great, Parus major, and crested tits, *Lophophanes cristatus*), or none at all (willow tits, *Poecile montanus*). This variation in ways of information encoding was not explained by phylogenetic relatedness, or by other ecological factors (Chapter 2). Furthermore, I discovered that, when I took flock structure into account, only blue, great, and coal tits consistently provided information regarding different levels of predator threat (Chapter 3). This consistency suggests that they produce information that is available to temporary or peripheral species found in their community, meeting one of the criteria for community informants. Of these three species, however, it was only the information that blue and great tits produced that appeared to be used by an information scrounging species, which means that they are the only species to fit the criteria to be a community informant. Because there is variation in the ways in which the tits encode information and only some of these species seem to provide reliable information to the entire community, I can conclude that the propensity to encode detailed predator threat information is not a trait shared across the entire Paridae family. Additionally, many of the ways each tit species encoded information about predator threat also varied with differences in flock structure, making the predator threat information less reliable to eavesdroppers. My data, therefore, demonstrate that the number of ways in which a species encodes information may not reliably indicate whether that species is a community informant: the number of ways a species encoded information did not predict either their reliability nor whether their calls were used by eavesdroppers.

With a better understanding of the ways these species communicate a predator's threat, I conducted a series of predator presentation and audio/video playback experiments to determine whether mobbing behaviour may be used by tit species to learn about novel predators. There were three key results from these experiments: 1) naïve adult blue and great tits did not respond to a novel predator with the correct level of danger (Chapter 4), 2) juvenile great tits learned to avoid a predator when exposed to that predator along with a simulated mobbing event (Chapter 5), and 3) wild juvenile blue tits responded to both conspecific and heterospecific mobbing calls appropriately (Chapter 6). But while these young birds appear to be able to produce all the behaviours found in mobbing events they do not yet participate in them themselves. It appears, then, that tit species do need some prior experience with a predator to recognize it as such, and one way in which they may learn to do this is through observing mobbing events of experienced individuals. Mobbing behaviour may, therefore, be one mechanism that the tits use to learn about novel predators.

One striking finding of all these experiments was that there was a lot of individual variation in anti-predator responses, so I went on to ask whether or not individual great tits varied consistently in their anti-predator behaviour based on their willingness to move in novel environments or on their proximity to an anti-predator signal (Chapter 7). I found that individuals at the source of the signal generally moved before others that were further from the source, but that distance and personality had few other effects on the latency of individuals to move or hop after freezing in response to an aerial alarm call. This suggests that distance may not play as an important role in response to aerial alarm calls and that, like in some other species, measures of movement in novel environments, may not explain movement after a high threat situation.

Together, this series of experiments has provided a number of new insights into mobbing behaviour in the Paridae. In addition, my data have also highlighted areas in the field of mobbing that require further exploration as well as raising new avenues of investigation regarding both mobbing behaviour itself and the ecology of how this behaviour functions on a community-wide scale. Below I will outline some of the questions raised by my data, focusing on those that fall into three related but distinct categories.

The first area is concerned with information encoding and its use in communities, including why species use multiple ways of encoding information. The second addresses the relationship between predators and prey, including the role that mobbing may play in the development of predator recognition and how individuals may classify predators. The third is focused on the extent to which there is individual variation in anti-predator behaviour. In each section, I will also address ways in which the scientific community could begin to answer these questions. Two approaches that would be useful across all three, however, are the use of playbacks and predator presentations. These two approaches are widely used when studying anti-predator behaviour (Gill & Bierema, 2013; Griffin, 2004; Hollén & Radford, 2009; Kelley & Magurran, 2003) for two main reasons: 1) they allow for experimental manipulation of the level of threat presented to the individual (or group) being tested; and 2) they induce naturally occurring behaviour that is a reflection of 'normal' behaviour in the wild, which allows a more useful investigation of the ecological relevance of the behaviour. However, other experimental approaches are sometimes necessary and it is on these that I will focus here. I will conclude by examining whether, in light of the experimental approaches necessary to answer these remaining questions as well as their ecology and behaviour, Paridae species remain a useful model in which to continue to test various aspects of anti-predator behaviour.

WHY DO SOME SPECIES USE MULTIPLE ENCODING METHODS WHEN OTHERS DO NOT?

My research has shown that some species in the Paridae family use a suite of four different ways to encode information about a predator's threat, but other species use only a subset of these ways, with different species often employing different methods than others use or apparently none at all (Chapter 2). This variation in the ways in which different species encode information about predator threat in their mobbing calls raises the question as to the source of this variation. It is not possible to answer this question before two fundamental gaps in our knowledge of mobbing calls are addressed: 1) the process(es) that gives rise to variation in vocal signals in response to threat and, 2) the nature of the information contained within the different ways of encoding information. As much of the past research into mobbing has been focused on determining how different species encode predator threat information in their mobbing calls and not comparing across families (mongoose Herpestidae sp.; Manser et al., 2014, marmots *Marmota* sp., Blumstein, 1999, primates, Cäsar & Zuberbühler, 2012), or addressing possible causes of variation (mongoose, Manser et al., 2014), little attempt has yet been made to address experimentally the causes of interspecific variation in information encoding in anti-predator vocalizations.

What drives information content in signals: internal vs. external processes?

To understand variation in the information in anti-predator signals, we first need to understand the processes that give rise to the production of this information about an external threat (i.e. internal state vs. external reference). Functionally referential calls (calls that are given in reference to an external threat and induce threat-specific behaviour in receivers) are produced by a number of species (Cäsar & Zuberbühler, 2012; Gill & Bierema, 2013; Townsend & Manser, 2013). However, although for the majority of mobbing calls threat information is encoded as a gradation of one call type (Suzuki, 2016b), those species for whose vocalizations are most usually examined for functional reference, tend to be species that produce multiple call types, which are used with high production specificity (i.e. one call type produced almost exclusively to one species, while another call types is produced in response to a different species; Evans, Evans, & Marler, 1993a; Gill & Bierema, 2013; Macedonia, 1990; Naguib et al., 1999; Seyfarth et al., 1980). In contrast to referential signals, graded responses are generally thought to reflect the producer's internal state (Gill & Bierema, 2013; Suzuki, 2014). I contend that my research shows that this may not be the case. While the number of conspecifics affected the rate at which blue tits called, the number of elements in their calls was affected only by the threat of the predator and not by flock structure. This apparent lack of sensitivity to social factors in at least one way of encoding information indicates that some of the graded signals that blue tits produce are not a reflection of the bird's internal state but rather a reference to a gradation in the level of threat a predator poses during that interaction. To test whether these graded signals are, in fact, a reflection of the signaller's internal state or in reference to an external threat, it will be necessary to decouple the threat an individual experiences and the threat a predator poses. While difficult, such decoupling is feasible using techniques such as measures of physiological stress (heart rate) and manipulations of an individual's internal state (stress levels) through addition of corticosterone in the diet. Using these combined methods an experimenter could produce different levels of 'danger' both internally (heart rate and corticosterone) and externally (mounts and/or playbacks) to determine which is driving the threat level in calling birds' vocalizations.

The nature of the information encoded in mobbing vocalizations

The importance of knowing whether if the information encoded in graded signals is driven by internal state or external reference becomes clear when examining species that encode information in multiple ways. Because the information in graded signals is thought to be primarily a reflection of internal state (Blumstein, 2007;

Blumstein & Armitage, 1997; Hailman & Ficken, 1996; Marler et al., 1992; Seyfarth & Cheney, 2003; Suzuki, 2016b), multiplicity of ways of encoding information may simply be an issue of redundancy (for example, an increase in stress causes an increase in both call rate and the number of elements produced; Owings & Virginia, 1978). This redundancy could either be an artefact of increased stress, or it could be a mechanism to increase the strength or the likelihood that the signal will be received (Blumstein & Armitage, 1997; Marler et al., 1992). In either case we would expect that, for those species that encode information redundantly, species that use multiple ways of encoding information communicate the same amount of information in their calls as a species that uses only one way of encoding information. When it comes to species that encode information that is in reference to an external threat, however, different ways of encoding information could allow for different types of information (i.e. size and speed etc.; Beynon & Rasa, 1989) to be communicated. In this latter case, we may expect that species that use multiple ways of encoding information, in fact, encode more information than do those that use fewer ways (Beynon & Rasa, 1989; Griesser, 2008; Suzuki et al., 2016). For example, one species that encodes information in two ways (such as call rate and the number of elements) would encode more information (such as predator distance and size respectively) than does a species that only uses one way of encoding information (such as call rate to encode predator distance).

While there has been a lot of speculation as to whether mobbing calls are referential rather than a result of internal state, in previous experiments the focus has been on species that produce multiple call types, which may use high production specificity to differentiate between predators, rather than on species with graded calls (Townsend & Manser, 2013). Even Suzuki (2016) who found potential referentiality in graded calls still focused on two different element types within a graded call. Suzuki (2016) showed that the tonal elements of the graded Japanese great tit mobbing call (A, B, and C elements) induced scanning behaviour while the broadband elements (D elements) resulted in approach/recruitment of conspecifics. This suggests that these two different parts of the same graded mobbing call encode different types of information (Suzuki et al., 2016). Although indirect evidence, these results suggest that different parts of calls or different ways of encoding information may contain different types of information about the pertinent situation (Beynon & Rasa, 1989; Townsend et al., 2014). It would be useful to use standard predator presentation experiments followed by playbacks in the lab to determine whether these graded signals do also provide referential information (in that they refer to an external stimuli).

Once we understand whether the information contained in mobbing calls is driven by the signaller's internal state or in reference to an external threat, and if the ways in which individuals encode predator threat contain different types of information, we can begin to address why there is so much variation in information encoding across species. If the production of this information is simply a redundant artefact of high levels of stress in highly vocal species, than those species that encode information in a number of different ways, like blue tits, and those species that encode information in only one way, like coal tits, would encode the same amount of information as each other. If, however, these two types of species encode information in reference to the predator/threat external to themselves, and if they encode different types of information about said threat in the different ways they encode information, the species that encodes information in a number of different ways may produce many more times the amount of information in their mobbing calls than is produced by a species using only one way of encoding information. By understanding how these species encode information and the driving forces behind this production we can begin to understand how patterns of information encoding are distributed across different species and taxa. This in turn allows further examination of the evolution of information production and how information moves though community networks.

WHAT DOES IT TAKE TO BE A COMMUNITY INFORMANT?

One of the reasons for understanding the quantity and quality of the information a species produces is to determine which species may be key sources of information for their communities i.e. 'community informants' (Hetrick & Sieving, 2011). Given that community informants provide information about predators and the threat those predators pose, they may improve the fitness and survival of a number of other species that are more vulnerable to predation (Goodale et al., 2010; Magrath et al., 2014). However, while many species have been labelled as community informants due to the information they provide and the benefits received by at least one eavesdropping species (increased foraging due to decreased vigilance, Magrath et al., 2014), few of these 'community informant' species have been tested to see if they fit both of the criteria I laid out in Chapter 3: 1) at least one way of encoding information about predator threat that is unaffected by group structure (though this does not preclude individuals using other ways of encoding information that are sensitive to group structure) and 2) the use of this information by 'information scrounging' species.

Signal reliability across different flock structures is important in order for a species to be considered a community informant but while signal reliability is discussed thoroughly in the literature (Blumstein, Verneyre, & Daniel, 2004; Cheney & Seyfarth, 1988; Magrath et al., 2009), previous experiments have been focused on ways of encoding information averaged across flocks and receiver attention (Blumstein et al., 2004; Cheney & Seyfarth, 1988; Magrath et al., 2009). The effects of group structure on the reliability/consistency of these ways of encoding information from flock to flock, however, has been largely overlooked. The sensitivity of these signals to the flock structure (Chapter 3) raises the question of whether the information that many of the species that have already been tested produce with regard to predator threat, depends on group structure. Unlike the previous questions, testing whether the information contained in mobbing calls is sensitive to group structure, may be relatively straightforward. In many of the previous experiments quite a lot of data relevant to addressing this question will have been recorded information. For example, how individuals' calls varied in response to threat, plus the number of conspecifics, group size, and even occasionally the presence of heterospecifics (both satellite and nuclear species). In many cases, then, simply re-visiting extant data would address the role that variation in group structure plays in the reliability of predator threat signals across mobbing events. I would expect that for species that are part of incredibly stable group structures during the peak mobbing season, group structure would have a strong impact on their ways of encoding behaviour. For species that occur in much more variable groups during mobbing season, however, I would expect their ways of encoding predator threat to be relatively independent of flock structure.

Although producing signals that are reliable regardless of the flock structure is an important factor for a species to be categorized as a community informant, it is perhaps more important for the information produced by a species to be used by a wide range of species in the community. While many of the species that produce detailed predator threat information are eavesdropped on by other species, whether more than one or two species eavesdrop has rarely been tested (Fallow & Magrath, 2010; Munoz et al., 2014; Ridley et al., 2013). In even fewer experiments are there data on whether multiple peripheral or temporary species in the community eavesdrop (Anne & Rasa, 1983; Fuong et al., 2014; Templeton & Greene, 2007). In order to address the importance and impact that ‘community informants’ have on their community we need to determine which species use and/or rely on the information those informants provide. Determining the proportion of the species in the community that shares predators with a ‘community informant’ species, while time consuming, would be relatively straightforward using standard playback experiments. Such experiments, while highlighting which species appeared to ‘pay attention’ to ‘community informants’ would not, however, address 1) whether the information they produce is actually used by information scrounging species, or 2) what information encoded in those calls is used by information scrounging species.

To show that scroungers actually use information provided by community informants, one would first need to determine how these species respond to predators of different threat without the presence of community informants. My data (Chapter 3), showed that at least some of the species thought to be eavesdroppers are capable of producing predator threat information in their own calls. This suggests that they rely on the information produced by ‘community informants’ less than previously thought. Second, one would need to determine if the behaviour of ’scrounger species’ changes in the presence of community informant species. As this would only determine if a species ‘pays attention’ to a community informant, one would also need to determine what information from these calls eavesdroppers use. While community informants encode information about predator threat, some scrounger species may only use their calls as an early alarm system about predator presence (orange-billed babblers, *Turdoides rufescens,* Goodale & Kotagama, 2005a), while others may rely on the predator threat information as they are incapable of producing their own (white-bellied copper-striped skinks, *Emoia cyanura,* Fuong et al., 2014). Additionally, scrounging species may use this information only when personal information is unavailable, and once they verify the threat that a predator poses may adjust their calling behaviour accordingly. I demonstrated that European robins, *Erithacus rubecula*, only differentiate between predators when blue tits are absent suggesting that they may use the predator threat information provided by blue tits, but this may not be true of other species. As with previous suggestions, predator presentations and playbacks are the most straightforward approaches to answering these questions. Understanding which species respond to the information produced by community informants and what information they use would allow us to generate comprehensive networks of information flow through communities. We could then evaluate the importance of each species in the network as an informant and each species' reliance on the information provided.

THE ONTOGENY OF MOBBING BEHAVIOUR AND ITS ROLE IN PREDATOR RECOGNITION.

Both blue and great tits appear to need some degree of experience with novel predators in order to recognize them as threats (Chapter 4), suggesting that learning plays an important part of predator recognition. However, I was not able to determine the exact type of experience required (e.g., witnessing an attack, social learning, etc.)

for birds to learn the appropriate association. As mobbing is thought to provide a context for such learning (Curio, 1978), my results (Chapter 5) were surprising: although hand-raised captive juveniles appeared to learn to avoid a novel predator after witnessing a mobbing event, none of the juveniles exhibited adult-like mobbing behaviour in response to the sparrowhawk. Initially, as the change in behaviour was slight, I thought maybe the juveniles either did not actually learn about predators this young or could not exhibit mobbing behaviour. However, when I tested wild blue tit juveniles to determine if they responded to mobbing calls with a mobbing response, they too did not respond, though they did produce the component behaviours found in adult mobbing (Chapter 6). This then raised the question as to whether birds use mobbing to learn about novel predators and used later in life: how is it that individuals develop mobbing behaviour, if not by practicing or exhibiting complete mobbing behaviour during development? Do juveniles not need to practise complete adult mobbing behaviour, only the component parts, to be able to produce it when they join winter flocks, or is the lack of adult mobbing behaviour in juveniles a result of differences in the vulnerability of juveniles to these predators?

Although mobbing is a well studied behaviour across a number of species (Altmann, 1956; Caro, 2005; Crofoot, 2012; Gill & Bierema, 2013) and the development of predator recognition is of great interest (Curio, 1993; Griffin, 2004; Hollén & Radford, 2009; Kelley & Magurran, 2003; Kuhlmann, 1909), there has been little examination of the ontogeny of mobbing behaviour from an animal's first response to a predator or to mobbing calls through to adult-like mobbing behaviour. Investigating the development of mobbing behaviour and predator recognition could shed light on how different species categorize predators as well as the how flexible these responses may be over the course of an individual's life. The ontogenetic stages of this behaviour could be investigated by manipulating when individuals first experience mobbing and/or predation events. This would allow determination, for example, of whether there is a sensitive phase for mobbing behaviour. Differences in playback and predator presentation timing, combined with differences in the amount of exposure to mobbing or predator encounters, could also enable exploration of the impacts that experience has on the development of anti-predator behaviour, as it appears to do in some other species (Hollén & Radford, 2009). By understanding the way in which mobbing (and other anti-predator behaviour) is acquired and develops over time would offer a new approach to test how local predation pressure may affect population level differences in anti-predator behaviour. It would also provide information on the degree to which juveniles and adults are flexible in learning about predators and in their mobbing behaviour.

How do Paridae categorize predators?

While it appears that some Paridae do not recognize novel predators (Chapter 4; Kullberg & Lind, 2002; Saborse & Renne, 2012) and may use mobbing events to learn to identify predators (Chapter 5; Baker, 2004), it seems improbable that an individual must learn each new predator separately. Indeed, great tits do appear to be able to generalize certain ‘predatory features’ across different birds (Beránková et al., 2014), although they do not seem to generalize from sparrowhawks to little owls (Chapter 4). This raises the question of whether Paridae, or any other species, not only differentiate between predators of the same class (Aves) along a graded scale (Templeton et al., 2005), but if they group them into different discrete categories and if so, how do they do this?

Many species do appear to categorize predators into discrete groups, but this comparison is often between species from different taxonomic groups (e.g. Japanese great tits, *Parus minor*: Japanese rat snake, *Elaphe climacophora*, vs. Jungle crow, *Corvus macrorhynchos,* Suzuki, 2012; ringtailed lemurs *Lemur catta*: carnivores vs. other predators, Macedonia, 1990; vervet monkeys *Cercopithecus aethiops*: leopards, *Panthera pardus*, Martial eagles, *Polemaetus bellicosus*, and pythons, *Python sebae,* Seyfarth et al., 1980; and chickens *Gallus gallus*: racoons, *Procyon lotor*, and hawks, Evans, Evans, & Marler, 1993a). However, a few are known to differentiate between morphologically similar predators (Siberian jays *Perisoreus infaustus*: owls vs. hawks, Griesser, 2009; yellow warblers, *Dendroica petechia*: brown-headed cowbirds *Molothrus ater* vs. common grackles *Quiscalus quiscula*, and fox sparrows *Passerella iliaca,* Gill & Sealy, 2007). Although great tits are able to generalize predatory features in some contexts (Beránková et al., 2014), they do not appear to do so between little owls and sparrowhawks. It may be, then, that while some Paridae species categorize owls and hawks differently, if owls and hawks pose the same threat, and threat is what is encoded in Paridae mobbing calls, their calls may not differentiate between the two predator categories. If so, many species thought to only differentiate between predators based only on their perceived level of threat and not on morphological similarities may still categorize them, but do so differently than has been previously thought. Testing how individuals classify different types of predators would be difficult and aside from standard predator presentations would require the use of other experimental approaches. The use of eye-tracking technology could be used to determine which particular morphological features of a novel predator animals focus on when encountering them, while behavioural conditioning (often used to determine how individuals classify naturally occurring stimuli), such as habituationdishabituation experiments (Cheney & Seyfarth, 1988), could be used to test how an individual categorizes objects. By understanding how individuals group predators, we can begin to explore the ways in which prey perceive and categorize predators shapes the information content of anti-predator vocalizations. If, as may be the case with great and blue tits, for example, species categorize different avian predators into separate groups behaviourally but not vocally, this would open the way to associating the information perceived by an individual with the information they produce.

VARIATION IN MOBBING BEHAVIOUR AMONG INDIVIDUALS

Anti-predator behaviour (both calling and mobbing) varies across individuals. While there have been a number of experiments investigating the causes of individual variation in anti-predator behaviour (personality, Vrublevska et al., 2014, dominance, Alatalo & Helle, 1990; Ficken & Witkin, 1977; Gehlbach & Leverett, 1995; Griesser, 2013, sex, Curio et al., 1983; Francis et al., 1989, and age, Buitron, 1983; Fichtel, 2008; Ficken et al., 1987; Griesser, 2013; Sternalski & Bretagnolle, 2010), none of these experiments have examined whether these responses are consistent across specific individuals. There is little evidence that an individual’s behavioural response to predators is consistent over time, however, there have been almost no experiments testing individual repeatability in any anti-predator behaviour. Given that such little evidence currently exists regarding whether anti-predator behaviour, whether learned or un-learned, improves with experience and social circumstance, further investigation into this topic would be useful. Testing whether individual differences in anti-predator behaviour are repeatable would involve simply presenting predators at multiple time points to the same individuals. Knowing if anti-predator behaviour is repeatable in an individual, or if it changes over time and circumstance, would provide insight into the flexibility of anti-predator behaviour, and allow further investigation into the importance of specific individuals in instigating and maintaining mobbing events or other anti-predator behaviour.

MOBBING BEHAVIOUR: AREAS THAT REMAIN TO BE STUDIED

Mobbing vocalizations and the information in these calls has been widely studied, as have various aspects of mobbing behaviour (Altmann, 1956; Curio, 1978; Owings & Coss, 1977). While many researchers can agree on whether a given species exhibits mobbing behaviour, the description of this behaviour can vary across different species and taxa (Altmann, 1956; Dominey, 1983; Leuchtenberger, Almeida, Andriolo, & Crawshaw, 2016; Owings & Coss, 1977). Aside from early primarily descriptive studies (Altmann, 1956; Francis et al., 1989; Zimmermann & Curio, 1988), there has been no unified quantification of mobbing behaviour. This has led to a lack of consensus on how mobbing behaviour should be evaluated or how to evaluate/describe the variation in mobbing behaviour across species and individuals. To estimate mobbing responses, a variety of methods have been employed to quantify this behaviour including the amount of vocalizing (Hinde, 1954b), the closeness of approach (Curio et al., 1983; Owings & Coss, 1977), on stress-related behaviours such as freezing and short flights (Klump & Curio, 1982; Mateo, 1996b), or on a combination of different behaviours (Sandoval & Wilson, 2012; Tamura, 1989). This work has resulted in much less knowledge about mobbing behaviour than is apparent at first glance. First, there is no comprehensive list of behaviours exhibited during mobbing or their relative frequency in different species. Second, the stages of mobbing and how this behaviour unfolds across a mobbing event is almost completely un-described (Altmann, 1956; Francis et al., 1989; Zimmermann & Curio, 1988). It is not clear for example, which, if any, individuals or species instigate mobbing behaviour when a predator is first discovered; whether individuals or species have particular roles or predictable behaviours or positions (spatially or temporally) during mobbing events; how long mobbing events last (mean and range); if mobbing behaviour changes over the course of the mobbing event; if all individuals engage in mobbing during the entirety of the event; if some individuals participate and others not; or if individuals/species take turns during a mobbing event. These questions, while difficult, are not impossible to answer. But to address them will require quantification of individuals' movements and vocalizations across space and time requiring small-scale localization of both physical distance and vocalizations using technology that is still in development.

ARE PARIDAE SPECIES A USEFUL GROUP TO USE TO STUDY ANTI-PREDATOR BEHAVIOUR?

My series of experiments has highlighted the Paridae species as a potentially fruitful group of species to study the aspects of predator-prey dynamics that revolve around anti-predator vocalizations and predator recognition and classification. Paridae have a number of ecological and logistic reasons why they function as useful study subjects for anti-predator experiments. Firstly, many species in the family Paridae are known to mob predators. Each species I tested mobbed the predators present, although the intensity (length of mobbing and apparent aggressiveness towards the predators) varied across all six species. Their propensity to mob combined with the fact that many species also encode information about a predator’s threat in their mobbing calls, allows for assessment of an individual’s perception of the level of threat a predator poses while the variation in these responses allows for comparative studies. Secondly, the ways that Paridae encode predator threat varies across species, allowing for investigation into why different species use different ways and numbers of ways to encode predator threat information in their mobbing calls. These species are also incredibly common, not only in North America and the UK but across Eurasia and sub-Saharan Africa, occupying similar niches in a variety of different habitats (Cramp, 1993; Perrins, 1979) allowing for investigation into how different ecosystems, community structures, and predator populations affect mobbing behaviour and information encoding strategies. Paridae also vary in their gregariousness across different species and populations allowing for investigation into how sociality affects the propensity for a species to produce predator threat information in their mobbing calls. Finally, Paridae often feed at backyard feeders, allowing experiments to be conducted in the wild with relative ease and mitigating some of the problems arising in laboratory studies.

Although these are all good reasons for using Paridae in tests of anti-predator vocalizations and other anti-predator behaviours, there is one significant drawback to using them: many species do not mob well, if at all, in the laboratory or in aviaries. While many Paridae species are easily kept in laboratory conditions, the experiments in Chapters 5 and 7 have illustrated that some Paridae species, as may many other species, do not exhibit strong easily induced mobbing behaviour in the lab. While the effects of the lab may be partially mitigated by using enormous outdoor aviaries filled with natural cover and the use of live predators, conducting experiments investigating anti-predator behaviour in captivity with some Paridae species poses a real challenge.

The issues with laboratory testing notwithstanding, the Paridae remains a useful group with which to investigate how different species encode information about predator threat in their anti-predator vocalizations, how this information is produced and used by both conspecifics and heterospecifics in their communities, how social and ecological factors affect this information, and how individuals categorize and learn about novel predators.

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Appendix

Appendix 2.1 Type III Wald Chi-square test results for predator type (control, buzzard, sparrowhawk) as a significant predictor of variation in vocal response. § indicates a non-normal distribution. Bold type indicates p-values ≤ 0.005, italic type indicates p-values ≤ sequential Bonferroni corrected p-values. Sequential Bonferroni corrections were calculated using the total number of models run for each species respectively.

Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	$\chi2$	*P*	Sequential Bonferroni
a) Blue Tit									
Call rate	All			lmer	identity	log	43.10	***<0.001***	0.003
Number of	Total elements			lmer	Gaussian	identity	20.54	***<0.001***	0.003
	Intro elements		log	lmer	Gaussian	identity	2.38	0.305	0.008
	Mid elements			lmer	Gaussian	identity	6.76	**0.034**	0.004
	Exit elements		log	lmer	Gaussian	identity	0.18	0.912	0.050
	D elements		boxcox: 0.29	lmer	Gaussian	identity	28.84	***<0.001***	0.002
	Chirp elements			lmer	Gaussian	identity	0.92	0.630	0.025
	Tonal elements			lmer	Gaussian	identity	1.26	0.553	0.017
Proportion of	Intro calls			glmer	binomial	logit	1.68	0.432	0.010
	Mid calls	§		lmer	Gaussian	identity	3.25	0.197	0.006
	Exit calls			glmer	binomial	logit	6.27	**0.043**	0.004
	D calls			glmer	binomial	logit	4.18	0.124	0.005
	Chirp calls			glmer	binomial	logit	17.04	***<0.001***	0.002
	Tonal calls			glmer	binomial	logit	14.17	***0.001***	0.003
	Frequency-modulated calls			glmer	binomial	logit	3.16	0.206	0.006
	Short calls			glmer	binomial	logit	3.83	0.148	0.005

Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	$\chi2$	*P*	Sequential Bonferroni
a) Blue tit									
Proportion to use	Intro elements			glmer	binomial	logit	1.59	0.451	0.013
	Mid elements			lmer	Gaussian	identity	33.01	***<0.001***	0.002
	Exit elements			lmer	Gaussian	identity	14.78	***0.001***	0.003
	D elements	§		lmer	Gaussian	identity	3.06	0.217	0.007
	Chirp elements	§		glmer	binomial	logit	4.78	0.092	0.004
	Tonal elements			lmer	Gaussian	identity	14.35	***0.001***	0.003
	Frequency-modulated calls			glmer	binomial	logit	9.63	**0.008**	0.003
	Short elements			lmer	Gaussian	identity	17.27	***<0.001***	0.002
b) Great tit									
Call rate	All			lmer	identity	log	44.00	***<0.001***	0.003
Number of	Total elements		log	lmer	Gaussian	identity	0.65	0.721	0.006
	Intro elements			lmer	Gaussian	identity	0.38	0.827	0.017
	Jar/rattle elements		log	lmer	Gaussian	identity	0.05	0.975	0.050
	D elements	§	log	lmer	Gaussian	identity	3.44	0.179	0.005
	Chirp elements			lmer	Gaussian	identity	0.40	0.819	0.013
	Tonal elements			lmer	Gaussian	identity	5.11	0.078	0.004
Proportion of	Intro calls			glmer	binomial	logit	1.85	0.397	0.006
	Jar/rattle calls			glmer	binomial	logit	0.56	0.756	0.007
	D calls			glmer	binomial	logit	0.13	0.939	0.025
	Chirp calls			lmer	Gaussian	identity	7.55	**0.023**	0.003
	Tonal calls			lmer	Gaussian	identity	0.48	0.789	0.010
Proportion to use	Intro elements			glmer	binomial	logit	3.71	0.157	0.004
	Jar/rattle elements	§		lmer	Gaussian	identity	10.96	**0.004**	0.003
	D elements			lmer	Gaussian	identity	1.87	0.393	0.005
	Chirp elements	§		lmer	Gaussian	identity	0.50	0.779	0.008
	Tonal elements	§		lmer	Gaussian	identity	4.25	0.119	0.004

Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	χ2	*P*	Sequential Bonferroni
c) Coal tit									
Call rate	All			lmer	identity	log	15.46	***<0.001***	0.001
Number of	Total elements		log	lmer	Gaussian	identity	3.68	0.159	0.002
	Bowl elements		boxcox:-8.41	lmer	Gaussian	identity	0.53	0.766	0.017
	Chirp elements			lmer	Gaussian	identity	0.39	0.825	0.025
	Dot elements		boxcox:-1.70	lmer	Gaussian	identity	0.63	0.729	0.010
	Hook elements		log	lmer	Gaussian	identity	11.19	**0.004**	0.002
	Mound elements		log	lmer	Gaussian	identity	7.05	**0.029**	0.002
	Mt elements		log	lmer	Gaussian	identity	21.84	***<0.001***	0.001
	Peak elements		boxcox:-0.48	lmer	Gaussian	identity	1.78	0.412	0.004
	S elements		log	lmer	Gaussian	identity	3.18	0.204	0.002
	S-dot elements		log	lmer	Gaussian	identity	11.97	**0.003**	0.001
	Slide elements		log	lmer	Gaussian	identity	3.16	0.206	0.002
	Squeak elements		boxcox:-0.30	lmer	Gaussian	identity	7.27	**0.026**	0.002
Proportion of	Bowl elements			lmer	Gaussian	identity	0.34	0.844	0.050
	Chirp elements			lmer	Gaussian	identity	2.25	0.324	0.003
	Dot elements			glmer	binomial	cloglog	0.98	0.614	0.008
	Hook elements			lmer	Gaussian	identity	3.18	0.204	0.002
	Mound elements			lmer	Gaussian	identity	1.44	0.486	0.005
	Mt elements	§		lmer	Gaussian	identity	1.64	0.441	0.004
	Peak elements			glmer	binomial	logit	1.21	0.545	0.006
	S elements	§		lmer	Gaussian	identity	0.56	0.758	0.013
	S-dot elements			glmer	binomial	cloglog	2.95	0.229	0.003
	Slide elements			glmer	binomial	cloglog	2.70	0.260	0.003
	Squeak elements			lmer	Gaussian	identity	3.54	0.170	0.002
	Multi calls	§		glmer	binomial	logit	5.42	0.067	0.002

Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	χ2	*P*	Sequential Bonferroni
c) Coal tit									
Propensity to use	Bowl elements			lmer	Gaussian	identity	1.64	0.440	0.004
	Chirp elements			lmer	Gaussian	identity	2.41	0.300	0.003
	Dot elements			lmer	Gaussian	identity	3.06	0.216	0.002
	Hook elements			lmer	Gaussian	identity	2.22	0.329	0.003
	Mound elements			lmer	Gaussian	identity	9.75	**0.008**	0.002
	Mt elements			lmer	Gaussian	identity	1.61	0.447	0.005
	Peak elements			glmer	binomial	logit	1.44	0.488	0.006
	S elements			lmer	Gaussian	identity	5.59	0.061	0.002
	S-dot elements			lmer	Gaussian	identity	3.88	0.144	0.002
	Slide elements	§		glmer	binomial	logit	2.83	0.243	0.003
	Squeak elements			lmer	Gaussian	identity	18.58	***<0.001***	0.001
	Multi calls			lmer	Gaussian	identity	1.07	0.586	0.007
d) Crested tit									
Call rate	All			lmer	Gaussian	identity	6.21	*0.045*	0.006
Number of	Total elements		log	lmer	Gaussian	identity	2.93	0.231	0.010
	Trill elements		log	lmer	Gaussian	identity	0.55	0.760	0.017
	Tonal elements		log	lmer	Gaussian	identity	2.83	0.243	0.013
Proportion of	Trill calls	§		lmer	Gaussian	identity	0.49	0.784	0.050
	Tonal calls	§		lmer	Gaussian	identity	0.50	0.778	0.025
	Frequency-modulated calls			glmer	binomial	logit	6.32	**0.042**	0.006
Propensity to use	Trill calls			lmer	Gaussian	identity	4.72	0.094	0.008
	Frequency-modulated calls			lmer	Gaussian	identity	6.45	**0.040**	0.005
	Tonal calls			lmer	Gaussian	identity	4.72	0.094	0.007

Encoding method	Call / element type	Normality	Transform	Model Type	Family	Link	χ2	*P*	Sequential Bonferroni
e) Marsh tit									
Call rate	All			lmer	Gaussian	identity	10.39	**0.006**	0.003
Number of	Total elements		log	lmer	Gaussian	identity	1.38	0.503	0.005
	Intro elements		log	lmer	Gaussian	identity	4.03	4.031	0.050
	dä/D elements			lmer	Gaussian	identity	12.69	***0.002***	0.002
Proportion of	Intro elements	§		lmer	Gaussian	identity	0.10	0.950	0.008
	dä/D elements	§		lmer	Gaussian	identity	0.06	0.972	0.025
	All tonal elements	§		lmer	Gaussian	identity	0.06	0.972	0.017
	Full tonal elements	§		glmer	binomial	logit	6.88	**0.032**	0.003
	Peak tonal elements			lmer	Gaussian	identity	3.38	0.184	0.004
	Broken tonal elements			glmer	binomial	logit	4.06	0.131	0.003
	Whole tonal elements	§		glmer	binomial	logit	5.44	0.066	0.003
	Ptew calls	§		lmer	Gaussian	identity	0.06	0.972	0.013
	dä/D calls	§		lmer	Gaussian	identity	0.96	0.618	0.006
	Complete calls	§		lmer	Gaussian	identity	0.08	0.960	0.010
Propensity to use	Intro elements			lmer	Gaussian	identity	13.01	***0.001***	0.002
	dä/D elements			lmer	Gaussian	identity	0.54	0.764	0.006
	All tonal elements			lmer	Gaussian	identity	8.29	**0.016**	0.003
	Full tonal elements			lmer	Gaussian	identity	2.98	0.226	0.004
	Peak tonal elements			lmer	Gaussian	identity	12.37	***0.002***	0.002
	Broken tonal elements	§		lmer	Gaussian	identity	2.15	0.341	0.005
	Whole tonal elements			lmer	Gaussian	identity	2.73	0.256	0.004
	Ptew calls			lmer	Gaussian	identity	8.29	**0.016**	0.003
	dä/D calls			lmer	Gaussian	identity	0.41	0.815	0.007

	Call / element type	Normality	Transform	Model Type	Family	Link	χ2	*P*	Sequential Bonferroni
f) Willow tit									
Call rate	All			lmer	Gaussian	identity	46.36	***<0.001***	0.003
Number of	Total elements		log	lmer	Gaussian	identity	7.89	*0.019*	0.004
	Si intro elements		boxcox:-0.22	lmer	Gaussian	identity	16.46	***<0.001***	0.003
	Zi elements		boxcox:-0.48	lmer	Gaussian	identity	1.03	0.599	0.008
	Tää elements		log	lmer	Gaussian	identity	5.73	*0.057*	0.005
Proportion of	Si intro elements			glmer	binomial	logit	0.13	0.938	0.050
	Zi elements			glmer	binomial	logit	0.17	0.919	0.017
	Tää elements			glmer	binomial	logit	0.46	0.795	0.013
	Tää-tää calls			glmer	binomial	logit	0.13	0.938	0.025
	Si-tää-tää calls	§		lmer	Gaussian	identity	1.88	0.391	0.007
	Zizi calls			lmer	Gaussian	identity	0.76	0.684	0.010
Propensity to use	Si intro elements			lmer	Gaussian	identity	2.71	0.258	0.006
	Zi elements			lmer	Gaussian	identity	2.71	0.258	0.006
	Tää elements			lmer	Gaussian	identity	5.75	*0.057*	0.004
	Si-tää-tää calls			lmer	Gaussian	identity	3.65	0.162	0.005
	Zizi calls			lmer	Gaussian	identity	5.96	*0.051*	0.004