

# **Context-dependent vocal communication in great tits (*Parus major*)**

## **Dissertation**

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*„Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less.“*

Marie Curie

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## Summary

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Avoiding predation risk and finding food resources are essential for the survival of all organisms. Consequently, many animals encode information about food and predators in their calls. Some species thereby use discrete call types, whereas others encode information by a variation within one call type or by altering the proportion of different call types. It is known for many passerine bird species, including great tits (*Parus major*), the study species of this thesis, that they encode information about predators in their calls. If great tits, however, are also able to decode such information from conspecific calls remains unknown. Further, if great tits use information encoding also in other, non-predatory, contexts, has so far not been investigated.

Therefore, this thesis focuses on the ways of information encoding used by great tits in various contexts and if conspecifics are able to discriminate between calls of different context. I conducted three experimental studies in the field to address these questions.

In the first chapter, I investigated how great tits call in response to taxidermy mounts of two different predators, a high-threat and a low-threat predator. The calling behaviour of tits varied greatly between the two treatments and great tits used four ways of encoding information about predator threat: call rate, D call duration, D element number and interval between D elements. Tits increased all of the four acoustic parameters when confronted with the high-threat predator. The variation in the interval between elements is so far only known from one North American passerine species, whereas the other three ways of encoding information are commonly found in passerines.

The study of the second chapter, investigated if great tits can discriminate between mobbing calls of two different contexts. I broadcasted calls recorded during the first study to great tits and measured the latency time until they approach the speaker within a radius of six meters and the minimum distance to the speaker. If tits can discriminate between mobbing calls of different contexts, one would most likely observe a difference in behaviour in response to those calls. Indeed, I found birds to have a longer latency time and to keep a greater distance to the speaker when hearing calls of the high-threat context compared to calls of the low-threat context.

This indicates that the message encoded in mobbing calls transmits information about predator threat to conspecifics that allows them to alter their behaviour. In addition, there was a difference in behaviour between the two sexes, as males approached the risky situation faster and closer than females. Consequently, mobbing behaviour seems not only to be affected by predation threat, but also by individual factors such as sex.

Lastly, in the third chapter, I compared calls of a mobbing context with calls of a food-associated context. Again, call rate was higher in the mobbing context compared to the food-associated context. Further, I found a variation in the proportion of call types between the two contexts. Great tits produced mainly D calls and a small proportion of other call types in the mobbing context. In the food-associated context, in contrast, they decreased the proportion of D calls and increased the proportion of other call types. Lastly, similar to the first chapter, the acoustic structure of D calls seems to convey contextual information as D calls in the food-associated context had longer elements and shorter intervals between elements than mobbing calls. This indicates that great tits use a set of ways to encode information about different contexts.

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## Zusammenfassung

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Die Vermeidung oder Abwehr von Prädatoren, sowie ein erfolgreiches Aufspüren von Nahrungsquellen sind für das Überleben von Tieren unerlässlich. Folglich verschlüsseln viele Tiere Informationen über Futter und Raubtiere in ihren Rufen. Einige Arten verwenden dabei unterschiedliche Ruftypen, wohingegen andere Informationen innerhalb eines Ruftyps, z.B. durch eine häufige Wiederholung eines Rufes, kodieren. Für viele Vogelarten, einschließlich der Kohlmeise (*Parus major*), die Untersuchungsart dieser Doktorarbeit, ist bekannt, dass sie eine Bedrohung durch Raubtiere in ihren Rufen kodieren. Ob Kohlmeisen jedoch auch in der Lage sind, zwischen Rufen aus verschiedenen Kontexten zu unterscheiden, ist bisher unbekannt. Des Weiteren ist bislang nicht untersucht worden, ob Kohlmeisen auch andere Informationen, wie beispielsweise das Auffinden von Futter, in ihren Rufen verschlüsseln.

Daher beschäftigte sich die vorliegende Arbeit damit, ob und wie Kohlmeisen Informationen aus verschiedenen Kontexten in ihren Rufen verschlüsseln. Darüber hinaus wurde untersucht, ob Artgenossen in der Lage sind, zwischen Rufen aus verschiedenen Kontexten zu unterscheiden und ihr Verhalten daraufhin entsprechend anpassen.

Im ersten Kapitel wurde untersucht, ob Kohlmeisen unterschiedlich reagieren, wenn sie mit Modellen von zwei verschiedenen Raubvögeln konfrontiert werden, welche sich stark in der Bedrohung, die sie für Meisen darstellen, unterscheiden. Die Ergebnisse zeigten, dass Kohlmeisen die Bedrohung durch einen Räuber auf verschiedene Weisen kodieren. Gegenüber einem gefährlicheren Prädatoren wurden sowohl mehr, als auch längere D-Rufe produziert. Des Weiteren bestanden die Rufe aus mehr Elementen und der Zeitabstand zwischen den Elementen war länger, je gefährlicher der Prädatoren war. Dass Vögel länger oder häufiger rufen, wenn sie einer größeren Bedrohung ausgesetzt sind, ist bereits von vielen anderen Vogelarten bekannt. Eine Variation im Zeitabstand zwischen den Elementen eines Rufes ist bisher allerdings nur von einer anderen nordamerikanischen Paridae Art bekannt. Somit konnte meine Studie einen neuen Mechanismus aufdecken, den Kohlmeisen nutzen um Informationen zu übermitteln.

Die Studie des zweiten Kapitels sollte aufzeigen, ob Kohlmeisen in der Lage sind, Informationen über das Prädationsrisiko, welche in den Rufen der ersten Studie kodiert sind, zu erkennen und ihr Verhalten entsprechend anpassen. Hierzu wurden die in der ersten Studie aufgenommenen Rufe abgespielt und sowohl die Latenzzeit (die Zeit, bis eine Kohlmeise in der Nähe des Lautsprechers auftaucht), als auch der Minimalabstand zum Lautsprecher gemessen. Ein Unterschied in Latenzzeit oder Minimalabstand zwischen den beiden Kontexten würde darauf hindeuten, dass Kohlmeisen erkennen können, aus welchem Kontext der konspezifische Ruf stammt. Da Kohlmeisen eine längere Latenzzeit hatten und einen größeren Abstand zum Lautsprecher einhielten, wenn sie Rufe aus dem sehr bedrohlichen Kontext hörten, ist davon auszugehen, dass sie die in Rufen verschlüsselten Informationen über eine bestehende Gefahr erkennen können und daher ihr Verhalten ändern. Darüber hinaus gab es einen Unterschied im Verhalten zwischen den beiden Geschlechtern, da sich Männchen schneller und näher annäherten als Weibchen. Dies lässt vermuten, dass das Verhalten nicht nur durch das unmittelbare Prädationsrisiko, sondern auch von individuellen Faktoren, wie zum Beispiel dem Geschlecht, beeinflusst wird.

Im letzten Kapitel sollte gezeigt werden, dass Kohlmeisen mit ihren Rufen auch Informationen über andere Umweltfaktoren übermitteln. Um dies zu überprüfen, wurden Rufe gegenüber einem Sperbermodell (gefährlicher Prädator) aufgezeichnet und mit Rufen, welche an Futterspendern aufgenommen wurden, verglichen. Ähnlich wie in der ersten Studie, riefen Meisen häufiger in der Präsenz eines Prädators, was darauf hindeutet, dass die Rufhäufigkeit den Grad einer Bedrohung anzeigt. Des Weiteren scheinen Kohlmeisen zwischen einem Futter- und Prädationskontext zu unterscheiden, indem sie das Verhältnis einzelner Ruftypen zueinander verändern. Abschließend scheinen Veränderungen in der akustischen Struktur von D- Rufen Informationen über den Kontext zu übermitteln. D-Rufe gegenüber Prädatoren hatten kürzere Elemente und längere Zeitabstände zwischen den Elementen, als Rufe, welche an Futterspendern aufgenommen wurden. Somit liefert meine Studie erste Hinweise darauf, dass Kohlmeisen ihre Rufe auch nutzen um, neben Informationen über Fressfeinde, auch Botschaften über andere Umweltfaktoren zu kommunizieren.



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## List of publications in this thesis

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### Accepted paper

- 1.) Kalb, N., F. Anger & Randler, C. (2019) **Subtle variations in mobbing calls are predator-specific in great tits (*Parus major*)**. *Scientific reports* 9(1): 6572.
- 2.) Kalb, N., & Randler, C. (2019) **Behavioral responses to conspecific mobbing calls are predator-specific in great tits (*Parus major*)**. *Ecology and Evolution*.

### Submitted papers

- 1.) Kalb, N., F. Anger & Randler, C. **Great tits encode contextual information in their food and mobbing calls.**

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## Introduction

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Animal communication is one of the biggest fields in behavioural research and there is a growing body of studies investigating how animals transmit and encode information. Animals can transmit information by visual, olfactory, tactile or acoustic cues (Bradbury and Vehrencamp 1998). Visual, tactile and olfactory signals are usually adapted to short-range communication; acoustic signals in contrast can transmit information over long distances. Hence, acoustic communication can be used to exchange information between individuals without any visual or physical contact (Bradbury and Vehrencamp 1998). Animal vocalizations are studied in many species across the animal kingdom, but most studies are conducted in mammals and birds. Vocalizations are used to attract mating partners during breeding season (Searcy and Andersson 1986), to coordinate group movements (Radford 2004, Ramanankirahina *et al.* 2016), during foraging and feeding (Clay *et al.* 2012) or predator encounters (Gill and Bierema 2013). Since acoustic communication occurs in various contexts, calls must contain some specific information about a situation, which allows receivers to adapt their behaviour accordingly. In the following, I will discuss some of the most frequent ways of how animals encode information in their calls. As the focus of this thesis is on the vocal communication of great tits in a mobbing and feeding context, I will especially emphasis how birds transmit information in these situations.

### **Mobbing**

Predation has a great effect on an individual's reproductive success, as it is one of the major causes of mortality for most organisms. Throughout the animal kingdom there is a great variety of strategies, including camouflage, fleeing, hiding in safety and deterring a predator, to prevent or decrease predation risk (Caro 2005). One commonly observed behaviour to deter predators is mobbing. It is mostly studied in birds (Altmann 1956, Curio *et al.* 1978), but also occurs in mammals (Bartecki and Heymann 1987, Graw and Manser 2007, Clara *et al.* 2008, Gill and Bierema 2013, Pitman *et al.* 2017), fish (Dominey 1983, Ishihara 1987, Lachat and Haag-Wackernagel 2016) and insects (Kastberger *et al.* 2014). Upon predator detection, many animal species show mobbing behaviours, including stereotypic movements and calls, to recruit conspecifics and heterospecifics (Kobayashi 1994, Randler and Vollmer 2013). Additionally, they often approach and sometimes directly attack the

predator during mobbing (Altmann 1956, Owings and Coss 1977). Mobbing holds the cost of an increased predation risk, because calling individuals might be easier to detect or give away the location of their nest (Smith 1969, Sordahl 1990, Krams 2001, Krams *et al.* 2007). Nevertheless, mobbing can be beneficial as it might ultimately drive the predator away, warn conspecifics of its presence or signal the predator that it has been detected and consequently decrease its hunting success (pursuit deterrent signal) (Pettifor 1990, Flasskamp 1994, Kobayashi 1994, 1996). Sometimes, mobbing can also have long-term benefits as predators such as little owls (*Athene noctua*) and tawny owls (*Strix aluco*) have been shown to avoid roosting sites where they have been recently mobbed (Flasskamp 1994). Powerful owls (*Ninox strenua*) do not only shift their roosts to habitats with less mobbing species, but also seem to prey more frequently on species that do not mob powerful owls (Pavey and Smyth 1998). Hence, even though mobbing holds costs, individuals can increase their long-term fitness by participating in mobbing. One of the best-studied mobbing behaviours are the mobbing calls of birds and mammals. These calls do not only serve the above mentioned functions, but are known to sometimes also convey information about the degree of threat a predator poses (Manser 2001, Leavesley and Magrath 2005, Dutour *et al.* 2016).

### **Why mob?**

Mobbing is a risky behaviour as it increases the immediate predation risk for participating individuals, but has the potential to increase the long-term fitness of the mobbing individual as well as of other individuals in the area. There are several hypotheses explaining mobbing that can be divided into three major categories: reciprocal altruism, part of parental care and self-interest (Ostreiher 2003). Altruistic behaviour is a form of cooperation in which one individual performs costly behaviours that benefits other individuals, which might in turn assist in risky situations in the future (West *et al.* 2007). Altruistic behaviour often occurs among individuals that share the same home range, i.e. individuals that most likely interact with each other repeatedly. In such more stable communities, individuals are able to assess if the caller is a reliable source of information and cheaters can be easily recognized and punished (Axelrod and Hamilton 1981). A study in breeding great tits (*Parus major*), for example, revealed that birds are more likely to join neighbours' nest defence, if they already shared a territory during previous years (Grabowska-Zhang *et al.* 2012). Migratory chaffinches (*Fringilla coelebs*) are more likely to initiate mobbing in multi-

species aggregations as the breeding season progresses and the community composition becomes more stable than at the beginning of the breeding season (Krams and Krama 2002). Breeding pied flycatchers (*Ficedula hypoleuca*) join conspecific neighbours during mobbing if they had received help from this pair at their own nest previously and do not join mobbing with breeding pairs that did not participate in previous mobbing events (Krams *et al.* 2008). However, if birds assist each other during mobbing can also depend on the predation risk. Breeding pied flycatchers, for example, are more likely to join mobbing neighbours in areas with increased predation risk than in low risk habitats (Krams *et al.* 2009). Hence, assisting neighbouring birds in mobbing might not only be explained by altruism, but also by the fact that it lowers predation risk in this area and hence might benefit all present individuals. Besides altruism, mobbing can be driven by self-interest, which includes direct benefits by the survival of the caller as well as indirect benefits provided by the survival of related individuals (nepotism) (Ostreiher 2003). The calling individual most likely attracts hetero- and conspecifics to the mobbing event, which decreases the likelihood of being captured (dilution effect) (Delm 1990) and increases the chance of driving the predator away (Flasckamp 1994), which might even decrease the future predation risk in this area. By producing alarm calls, the caller also warns related individuals, which can indirectly increase its own fitness by helping the receivers to detect a predator faster and applying an appropriate anti-predator response. Siberian jays (*Perisoreus infaustus*), for example, give more mobbing calls and mob longer in kin groups than in non-kin groups (Griesser and Ekman 2005). Similar, black-tailed prairie dogs (*Cynomys ludovicianus*) call more frequently in the presence of relatives (Hoogland 1983). Moreover, as part of parental care, alarm calls close to the nest might silence the offspring (Platzen and Magrath 2004), trigger an effective anti-predator response (Suzuki 2011) or teach naïve individuals about predatory threats (Griesser and Suzuki 2016) and thereby increase the fitness of the caller.

Besides warning conspecific individuals about present predators, calls of many species also transmit information about predator size (Templeton *et al.* 2005, Courter and Ritchison 2010), type (Greene and Meagher 1998, Suzuki and Ueda 2013), approaching speed and distance (Evans *et al.* 1993, Wilson and Evans 2012), threat (Furrer and Manser 2009, Dutour *et al.* 2016) and behaviour (Griesser 2008, Cunningham and Magrath 2017). According to this information, conspecifics and

heterospecifics might be able to assess the predation risk posed by a specific predator and adapt their behaviour accordingly. However, as diverse as the information is that can be transmitted, so are the possibilities of how information can be encoded in calls.

### **Referential and graded signals**

When animals vocally communicate about their environment, they can encode information either with distinct calls or with graded and combinatorial changes in call structure (Manser 2013, Suzuki 2014). Referential signals are discrete calls that are uttered in the context of a specific stimulus as, for example, predator type or food (Evans *et al.* 1993, Evans 1997, Clay *et al.* 2012). Moreover, such calls elicit an appropriate behavioural response in receivers, even without additional cues, that indicate the nature of a situation (Evans *et al.* 1993, Evans 1997). These signals are termed *functional referential* and occur in a variety of species. Vervet monkeys (*Chlorocebus pygerythrus*), for example, give different alarm calls when encountering martial eagles (*Polemaetus bellicosus*), leopards (*Panthera pardus*) or pythons (*Phyton sebae*) and show adaptive anti-predator behaviours in response to those calls. After hearing a martial eagle alarm call, vervet monkeys look up to the sky, but look down in response to python alarm calls. In response to leopard alarm calls, monkeys are more likely to flee to cover (Seyfarth *et al.* 1980). Also, marmosets (*Callithrix geoffroy*) produce acoustically distinct alarm calls in response to perched raptors and snakes and alter their behaviour by looking more frequently up or down according to the predator type (Petracca and Caine 2013). In birds, adult Japanese great tits (*Parus minor*) show different predator searching behaviours after hearing calls that encode predator type (i.e. terrestrial, aerial or snake) (Suzuki 2011, Suzuki 2014) and juveniles either flee from the nest in response to snake alarm calls or crouch in the nest when hearing aerial alarm calls (Suzuki 2011, Suzuki and Ueda 2013).

In contrast to referential calls, which are distinct call types that classify specific categories (Manser 2013), animals can also encode information by graded variation in call rate (Fasanella and Fernández 2009, Murphy *et al.* 2013), note number (Leavesley and Magrath 2005, Templeton *et al.* 2005) or call duration (Naguib *et al.* 1999, Ellis 2008). In predator-related contexts, graded signals are usually uttered according to predator threat (Manser *et al.* 2002, Templeton *et al.* 2005), size, speed

or appearance (Templeton *et al.* 2005, Slobodchikoff *et al.* 2009, Wilson and Evans 2012).

There is growing evidence, that referential and graded signals are not mutually exclusive. Some species seem to combine the two signal types to encode predator-related information. Japanese great tits utter referential alarm calls, but also alter calling rate according to predator threat (Suzuki 2014). Siberian jays give more calls when mobbing a more dangerous predator and additionally produce hawk and owl-specific calls (Griesser 2009). Tufted capuchins (*Cebus apella nigritus*) increase call rate with increasing predator proximity and additionally have specific alarm calls for aerial and terrestrial predators (Wheeler 2010). Suricats (*Sucitata suricatta*) have different calls for different predator types and gradually change call structure according to the level of urgency (Manser 2001, Manser *et al.* 2002).

As illustrated by the above-mentioned examples, vocalizations can contain various information about the environment and there are multiple ways of how information can be encoded. Up to date it remains unclear why there is such a variability in information encoding across different taxa. However, there is evidence that closely related bird species with similar vocalization repertoires, share similar ways of encoding information in a predator-related context and that these encoding mechanisms might be phylogenetic conserved (Randler 2012, Carlson *et al.* 2017, Dutour *et al.* 2017).

### **Fine- and cross scale alterations in calls**

Many avian and mammalian species vary the structure or composition of a call to encode predator threat. Species with a call system composed of multiple note or call types can change the number of calls or notes within a call to signal predation risk. A change in calling rate is one of the most observed encoding mechanisms in a predator related context. Suricates use a change in calling rate to indicate predator threat (Manser 2001). Many Paridae species including Carolina chickadees (*Poecile carolinensis*), mountain chickadees (*Poecile gambeli*), black-capped chickadees (*Poecile atricapillus*), tufted titmice (*Bealophus bicolor*), great tits, coal tits (*Periparus ater*), crested tits (*Lophophanes cristatus*) and marsh tits (*Poecile palustris*) increase calling rate with increasing predator threat (Templeton *et al.* 2005, Carlson *et al.* 2017). In addition to call rate, blue tits (*Cyanistes caeruleus*), coal tits, marsh tits, Carolina chickadees, black-capped chickadees, mountain chickadees and

tufted titmice increase the number of elements within a call with increasing predator threat (Templeton *et al.* 2005, Soard and Ritchison 2009, Bartmess-LeVasseur *et al.* 2010, Courter and Ritchison 2010, Hetrick and Sieving 2011, Carlson *et al.* 2017). A third way of information encoding is a change in the proportion of different call types or notes during mobbing. Putty-nosed monkeys (*Cercopithecus nictitans martini*) and Campbell's monkeys (*Cercopithecus campbelli*), for example, utter specific sequences of different call types depending on predator type (Arnold and Zuberbühler 2006, Ouattara *et al.* 2009). Male blue monkeys (*Cercopithecus mitis stuhlmani*) use the proportion of call types to encode predator class and distance (Murphy *et al.* 2013). Japanese great tits alter the number of 'chicka' calls and D notes according to whether they are exposed to a marten or a crow (Suzuki 2014). Similar, Carolina chickadees alter the number of 'chick' and 'dee' notes in response to different predator threats (Soard and Ritchison 2009). Similarly, blue tits, great tits, crested tits and marsh tits alter the proportion of different note types when confronted with high- and low-risk predators (Carlson *et al.* 2017). Arabian babblers (*Turdoides squamiceps*) produce "tzwicks" as the first call both in response to owls and cats, but differ in the second call type, which most likely encodes a difference in risk or urgency (Naguib *et al.* 1999). Lastly, some species change the propensity to produce certain call or note types in different situations. Great tits, for example, increase the propensity to produce rattle/jar calls during mobbing (Carlson *et al.* 2017).

There are also species that use fine-scale acoustic alterations in their calls as for example a change in frequency or note duration to encode information. Banded mongooses (*Mungos mungo*) change the frequency bandwidth of calls according to different contexts. They produce calls with small frequency bandwidth in response to predator faeces and increase the frequency bandwidth when confronted with snakes or rival banded mongooses (Furrer and Manser 2009). Campbell's monkeys change call duration, the dominant frequency at call onset and the pattern of frequency transition depending on predator type (Zuberbühler 2001). Black-capped chickadees decrease the interval between "chick" and "dee" sections, the duration of the first D note and the interval between the first and second D note when confronted with smaller, more dangerous predators (Templeton *et al.* 2005). America crows (*Corvus brachyrhynchos*) utter the same call types in response to avian and mammalian predators, but calls differ in their duration, rate and interval between calls, indicating

that these fine-scale alterations might be used to signal a difference in threat-level between predators (Yorzinski and Vehrencamp 2009).

There are various mechanisms to encode information and how species use and combine those possibilities to communicate about external events. However, to counterbalance the costs of higher immediate predation risk caused by emitting mobbing vocalizations, conspecifics should be able to decode transmitted information and adapt their behaviour accordingly to increase their chance of survival.

### **Decoding information in mobbing calls**

In order to show an appropriate adaptive behavioural response, individuals need to be able to recognize a predator and evaluate the immediate risk it poses. This evaluation can be either managed by direct visual contact with the predator or by decoding alarm calls of conspecific or heterospecific individuals. Many bird species adapt their mobbing response according to their relative prevalence in a predator's diet (Dutour *et al.* 2017, Dutour *et al.* 2019) or the type of predator (Greene and Meagher 1998, Manser *et al.* 2002, Koboroff *et al.* 2013, Suzuki 2014). Besides mobbing calls, some birds also alter the latency time to certain behaviours and distance kept to the predator according to the perceived predation risk. Great tits, for example, keep a greater minimum distance to a high-risk predator than to a low-risk predator (Curio *et al.* 1983). Further, blue tits, great tits and willow tits take longer to return to a feeder after seeing a highly dangerous predator dummy than after seeing a less-dangerous or non-threatening dummy (Hogstad 2017). In addition, some species exhibit mobbing in response to predator vocalisations: black-capped and mountain chickadees distinguish between the calls of three raptors and alter their mobbing behaviour accordingly (Billings *et al.* 2015). Similar, some European passerines, such as chaffinch, crested tit, great tit and blue tit respond more intensely to the call of a high-risk than to those of a low-risk predator (Dutour *et al.* 2016). Such behavioural differences, however, can also be observed in response to conspecific and heterospecific mobbing calls without any visual or acoustic contact to a predator (Randler and Förschler 2011, Randler 2012, Randler and Vollmer 2013, Dutour *et al.* 2017, Dutour *et al.* 2017). Black-capped chickadees produce more mobbing calls and approach a speaker closer when hearing conspecific playbacks that have been recorded in response to more dangerous predators than when hearing calls of a less-



threatening context (Templeton *et al.* 2005). Tufted titmice need longer to return to normal feeding behaviour in response to playbacks of conspecific high-threat calls than after hearing low-threat calls (Courter and Ritchison 2010). Also European passerines vary their response according to predation risk encoded in mobbing calls and even respond to playbacks of mobbing calls elicited by a predator that is absent in their area (Dutour *et al.* 2016).

As outlined above, many species encode information about predator encounters in their calls, which can be used by con- and heterospecifics to evaluate predation risk and exhibit an appropriate behavioural response. Besides surviving predator encounters, finding food resources is a key element for an animal's survival. Hence, it is not surprising that many species use vocalizations also to communicate about food availability.

### **Food-associated calls**

Even though referential calls are mainly studied in a predation context, there are also some examples of how they are used in a food-associated context (Clay *et al.* 2012). Marmosets, for example, produce food calls that elicit an increase in foraging and feeding effort in conspecifics (Kitzmann and Caine 2009) and even seem to convey information about food type (Rogers *et al.* 2018). In chimpanzees (*Pan troglodytes*) food-associated "rough grunts" result in an increased foraging effort of conspecifics (Slocombe and Zuberbühler 2005). Male domestic chicken (*Gallus gallus domesticus*) produce food calls upon discovering food, especially in the presence of hens. Hens in turn look more frequently downwards and pick at the substrate when hearing those calls, indicating that they contain referential information about food presence (Evans and Evans 1999). However, some species do not use referential, but graded variation in calls to signal the presence of food or individual food preferences: for example, cotton-top tamarins (*Saguinus oedipus*) increase calling rate in the presence of food, whereby the degree of calling correlates with an individual's food preference (Elowson *et al.* 1991). Red-bellied tamarins (*Saguinus labiatus*) respond with higher call rates to the presence of food that is in large quantities and palatable (Caine *et al.* 1995). Willow tits respond with one note type to food, but combine two call types in a non-food related context (Suzuki 2012). Carolina chickadees seem to produce more C notes and fewer D notes after finding food and conspecifics approach a feeder more frequently when hearing calls with

more C notes (Freeberg and Lucas 2002). However, Carolina chickadees of another population have been found to produce more D notes when initially finding a food source and conspecifics had a shorter latency time to arrive at a feeder after hearing such calls (Mahurin and Freeberg 2008). Results of a second study in this population, however, suggests that C notes are rather associated with flight than food, because flying birds emitted more C notes than when they were e.g. sitting on a perch (Freeberg and Mahurin 2013).

### **What is the function of food-associated calls?**

Similar to mobbing calls, there seem to be various possibilities, which could motivate an individual to produce food-associated calls. In many species such calls recruit conspecifics to a food source (Clay *et al.* 2012), which might seem counterintuitive as the caller then has to share food with others. Nonetheless, attracting others to food resources might also benefit the caller. More foragers around a feeding place might reduce the predation risk by dilution or an increase in vigilance as a greater number of individuals can detect predators faster (Delm 1990). Further, it is most likely easier to defend a feeding source when accompanied by other individuals than while being alone (Krebs *et al.* 1972, Pitcher *et al.* 1982). Food calls might also attract possible mates, which can enhance the reproductive success of the caller. Male fowl (*Gallus gallus*), for example, increase call rate in the presence of females (Evans and Marler 1994) and female Silver Sebright bantam chickens, approach calling males more frequently than silent ones (Marler *et al.* 1986). Pinyon jays (*Gymnorhinus cyanocephalus*) tend to produce food calls more frequently when being with their long-term mates compared to the presence of non-mates (Dahlin *et al.* 2005). In addition, the production of food calls can indirectly affect the fitness of the caller if they attract related individuals. For example, female rhesus macaques (*Macaca mulatta*) within large matriline groups call more than those in small matriline groups (Hauser and Marler 1993). Similar, brown capuchin monkeys (*Cebus apella*) call more frequently in groups including kin than in smaller groups or while being alone (Hauser and Marler 1993). Lastly, in some species food associated calls are related to the social status of the caller (Pollick *et al.* 2005). In summary, there is most likely no universal explanation for food-associated calls across species, as the function of such calls seems to strongly depend on the social and ecological factors that shape the behaviour of a focal species (Clay *et al.* 2012). For example, in species that live in stable groups, food-associated calls might function to establish the social status of

the caller or decrease aggression among group members. In species facing high predation risks or food competition, in contrast, food-associated calls might be selected to recruit conspecifics to the feeding site to decrease the likelihood of predation or increase the chance of defending the food source (Clay *et al.* 2012).

Using a small European passerine, the great tit (*Parus major*), the aim of this thesis was to conduct field experiments to further our understanding on the ways birds encode information about different contexts and the possible function of those calls.

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## Research goal

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The vocal system of the Paridae species has been subject to numerous studies in both, North American and European species. It is known, that these species use a change in call rate, number of elements, call proportion and propensity to communicate about predator threat (Carlson *et al.* 2017). Black-capped chickadees (*Poecile atricapilla*) are further known to use some fine-scale changes in acoustic structure to encode predation risk (Templeton *et al.* 2005). If such structural changes on a fine-scale level, however, also occur in European Parids, such as the great tit, remains yet unknown. In addition, even though it is known that tits alter their calling behaviour according to predator threat (Carlson *et al.* 2017), there are only few studies, mainly for North American species, indicating that differences in acoustic structure affect the behaviour of conspecifics (Templeton *et al.* 2005, Suzuki 2012). Hence, I designed experiments to investigate if great tits, in addition to the above-mentioned mechanisms, also use fine-scale changes in acoustic structure to encode information about predation threat (chapter 1). Further, I tested if differences in calling behaviour affect the behaviour of conspecifics (chapter 2). I conducted field experiments in which great tits were confronted with taxidermy predator mounts (chapter 1) or conspecific mobbing calls (chapter 2) to answer my research questions.

In contrast to the well-studied mobbing behaviour, if and how Parids encode information about a non-threatening context such as food, is relatively unknown. There are few studies indicating that Carolina chickadees (*Poecile carolinensis*) and willow tits (*Poecile montanus*) use call propensity and call proportion to recruit conspecifics to food (Freeberg and Lucas 2002, Mahurin and Freeberg 2008, Suzuki 2012). Therefore, I investigated if great tits also encode information about food in their calls. More specifically, I tested if food-associated calls differ from calls of a mobbing context. Such differences might enable conspecifics to gain information about the nature of a situation (i.e. predation or food) solely on the structure of conspecific calls (chapter 3).

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## Study species

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The focus of this thesis is the vocal communication in great tits (*Parus major*) in a predator-related as well as a food-associated context. Great tits belong to the Paridae family (tits, chickadees and titmice) and are widely distributed in Central Europe, but are also abundant in North Africa, Middle East and in some parts of central Asia. Tits inhabit and breed in a variety of habitats including woodlands, mixed forests and gardens (Bauer *et al.* 2012). Great tits are usually non-migratory birds living in pairs throughout the breeding season and form loose flocks during the winter time (Saitou 1978, Ekman 1989). This species exhibits a series of stereotypic behaviours during mobbing such as approaching a predator and vocalizations (Hailman 1989, Randler 2012). Further, great tits are known to respond well to taxidermy mounts of predators (Curio *et al.* 1983, Carlson *et al.* 2017) as well as playbacks of conspecific and heterospecific mobbing calls (Randler 2012, Randler and Vollmer 2013, Dutour *et al.* 2016).



Figure 1: Male great tit (*Parus major*). Photo courtesy of Randler, C.

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## Chapter 1 - Do great tits encode information about predator-threat in their calls?

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### Contributors

Author	Author position	Scientific ideas %	Data generation %	Analysis & interpretation %	Paper writing %
Nadine Kalb	1	40	50	100	70
Fabian Anger	2	0	50	0	5
Christoph Randler	3	60	0	0	25
Title of paper:		Subtle variations in mobbing calls are predator-specific in great tits ( <i>Parus major</i> )			
Status in publication process		Accepted for publication in <i>Scientific Reports</i> , 9(1), 6572. <a href="https://doi.org/10.1038/s41598-019-43087-9">https://doi.org/10.1038/s41598-019-43087-9</a>			

### Extended summary

It is known from various bird species that they encode information about predators in their calls (Evans *et al.* 1993, Soard and Ritchison 2009, Suzuki 2011, Cunningham and Magrath 2017). Usually, birds mob dangerous predators more intense than less threatening ones. For example, more species participate in mobbing when hearing pygmy owl (*Glaucidium passerinum*) calls than when hearing calls of the less dangerous boreal owl (*Aegolius funereus*) (Dutour *et al.* 2016) and smaller raptors provoke longer mobbing bouts in titmice than larger ones (Courter and Ritchison 2010). A recent study in British tits revealed that there are various ways of encoding information in mobbing calls, whereby some species use only one, whereas others use multiple ways of information encoding (Carlson *et al.* 2017). This study, however, did not perform any fine-scale measurements of calls such as, for example, peak frequency or element duration, which can also encode information about predator threat. Hence, the aim of my study was to investigate if great tits use such fine-scale alterations in their calls to transmit information about predators.

I recorded the calls of wild-living great tits in response to mounts of two common predators, the sparrowhawk (*Accipiter nisus*) and the tawny owl (*Strix aluco*). These two predators differ greatly in their diet composition and hence in the threat they pose to great tits. Sparrowhawks are diurnal and their diet consists mainly of small birds (Zawadzka and Zawadzki 2001). Tawny owls in contrast are nocturnal and mainly hunt on small mammals (Galeotti *et al.* 1991, Ýmihorski and Osojca 2006). Consequently, sparrowhawks are high-threats predators for great tits, whereas tawny owls are considered to be a low-threat predator. In accordance to my expectations, I

found great tits to vocally discriminate between the two predators. They increased call rate and produced longer D calls with more elements and longer intervals between elements in response to the sparrowhawk mount than in response to the less-threatening tawny owl mount. Whereas an increase in calling rate and a variation in element number is already known from previous studies in great tits (Carlson *et al.* 2017), my results revealed an, so far unknown, additional way of encoding information, i.e. a variation in the interval between elements. The results of this studies combined with the findings of previous works indicate that great tits encode various information within one single call type. By encoding information with subtle variations within one call, information might be less prone to eavesdropping by heterospecifics. However, future studies are needed to test this hypothesis.

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## Chapter 2 - Do great tits adapt their behaviour based on subtle variations in mobbing calls?

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### Contributors

Author	Author position	Scientific ideas %	Data generation %	Analysis & interpretation %	Paper writing %
Nadine Kalb	1	50	100	100	80
Christoph Randler	2	50	0	0	20
Title of paper:		Behavioral response to conspecific mobbing calls are predator-specific in great tits ( <i>Parus major</i> )			
Status in publication process		A revised version of this manuscript was accepted for publication in Ecology and Evolution after the evaluation of this thesis. <a href="https://doi.org/10.1002/ece3.5467">https://doi.org/10.1002/ece3.5467</a>			

### Extended summary

Vocalizations are widespread throughout the animal kingdom and there is a growing body of research investigating the evolution, usage and information content of such vocalizations (Seyfarth and Cheney 2017). Sometimes vocalizations refer to external events, e.g. the presence of predators or food and are therefore termed referential signals. Further, if calls provoke an adaptive response in receivers, such as, for example, an appropriate predator avoidance behaviour, the signal is termed functional referential (Macedonia and Evans 1993, Evans 1997). The vocal behaviour of birds and mammals are often studied in the presence of food or predators to investigate the function of such calls in conspecific and heterospecific communication (Clay *et al.* 2012, Gill and Bierema 2013). Anti-predator vocalizations have several properties that make them well suited to investigate questions about information encoding and signal meaning (Macedonia and Evans 1993): the context, i.e. the presence of a predator, of alarm and mobbing vocalizations is often clearly determined. In addition, individuals usually respond with distinct behaviours to anti-predator vocalizations, whereby different predator types can elicit different sets of behaviours. Hence, playback experiments with alarm calls elicited by different predators can be used to easily determine if alarm vocalizations provoke an appropriate anti-predator response in conspecifics without any additionally cues (Macedonia and Evans 1993).

I conducted a playback experiment to assess the response of conspecifics to mobbing calls elicited by the predators used in the first study. Here, I discovered that conspecifics adapt their behaviour in response to mobbing calls of conspecifics and



that this response seems to be affected by the sex of the receiver. More specifically, great tits had shorter latency times to approach the speaker and kept shorter distances to the speaker when hearing mobbing calls elicited by a tawny owl mount than when hearing mobbing calls induced by a sparrowhawk mount. This indicates that great tits are able to recognize subtle variations in D mobbing calls and that conspecific mobbing calls might contain referential information about predators. Additionally, behaviour was affected by sex as males tended to approach the speaker faster and closer than females. Hence, male seem to take higher risk than females, which might be explained by higher male-male competition over territories and females (Regelmann and Curio 1986).

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## Chapter 3 - Do great tits alter their calling behaviour according to context?

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### Contributors

Author	Author position	Scientific ideas %	Data generation %	Analysis & interpretation %	Paper writing %
Nadine Kalb	1	30	70	100	60
Fabian Anger	2	0	30	0	5
Christoph Randler	3	70	0	0	35
Title of paper:		Great tits encode contextual information in their food and mobbing calls			
Status in publication process		Submitted			

### Extended summary

In contrast to the mobbing calls of Paridae species, the calling behaviour in other, non-predatory contexts, such as food, is less-well studied. Studies in mammals and birds showed that individuals sometimes encode information about food presence or preference in their calls, which might be used to recruit conspecifics to food resources or to reduce food competition (Clay *et al.* 2012).

The goal of this study was to determine if great tits encode information about food in their calls. Therefore, I recorded calls at a hanging feeder and compared them to mobbing calls recorded in response to a taxidermy mount of a sparrowhawk. First, great tits had a higher calling rate in the predation context, indicating that call rate signals threat-level or response urgency as already known from other studies (Templeton *et al.* 2005, Courter and Ritchison 2010, Randler 2012). Second, my results revealed that great tits use some call types in both contexts (A-E and I), but produced others (G, H and M) solely in a food-associated context. Tits reduced the proportion of D calls and produced more B, C and E calls in response to food. This indicates that the proportion of produced call types might transmits some contextual information. Third, when looking at fine-scale measurements of the D calls of both context, calls in the food-associated context had longer elements and shorter intervals between them than calls of the mobbing context. This indicates that great tits seem to not only use call type, but also fine-scale alterations in their D calls to differentiate between a mobbing and a food context. Playback studies are now necessary to determine if conspecifics are able to recognize the encoded information and adapt their behaviour accordingly.

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## General discussion

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The goal of this thesis was to determine how great tits (*Parus major*) vocally respond to different threatening and non-threatening stimuli and if calls transmit context-dependent information to conspecifics. Encoding more specific information about predators in calls is known from various passerine species (Templeton *et al.* 2005, Courter and Ritchison 2010, Carlson *et al.* 2017). The results of my thesis are in accordance with many previous results but also reveal some new aspects about how great tits encode information about different contexts. I found great tits to encode contextual information in various ways, which I will discuss in more detail in the following paragraphs.

The most obvious way of encoding information in many species is a change of call type or the proportion of uttered call types in response to different stimuli. Some species use certain call types exclusively in one context (referential signal) (Seyfarth *et al.* 1980, Greene and Meagher 1998, Evans and Evans 1999, Suzuki and Ueda 2013), whereas others alter the ratio of certain notes or call types to encode contextual information (Hailman and Ficken 1986, Soard and Ritchison 2009, Suzuki 2012). I also found great tits to alter the proportion of produced call types in response to two different contexts, i.e. mobbing and food-associated context. Overall, great tits produced nine different call types, but shifted the proportion of those calls according to context. Tits produced mostly calls consisting of D elements in the mobbing context. In the food-associated context, in contrast, great tits reduced the proportion of D calls and increased the number of other call types, especially B, C and E calls. This suggests that D calls are either used to differentiate between dangerous and non-dangerous situations or that D calls serve as a recruitment function. A higher proportion of D calls in the mobbing context is in accordance with findings in British tits where calling rate and the proportion of elements also changes with increasing threat (Carlson *et al.* 2017). Recruiting conspecifics to a dangerous mobbing situation to reduce predation risk is most likely more important than recruiting them to food resources, which might explain the difference in D call proportion between the two contexts. Moreover, by recruiting individuals to food, the individual feeding rate will most likely decrease, as the resource has to be shared with recruited individuals. Nonetheless, recruiting conspecifics might still be beneficial, as predation risk during feeding decreases and food resources might be easier to monopolize. Similar to my

results, studies in Carolina chickadees (*Poecile carolinensis*) suggest that D calls have a general recruitment function as birds produce more D notes after initially finding food (Mahurin and Freeberg 2008). In addition, Carolina chickadees produce calls with more C notes when detecting food (Freeberg and Lucas 2002), which is most likely further related to flight behaviour, i.e. flying towards and away from a feeder (Freeberg and Mahurin 2013). This explanation also seems to be likely concerning my results, as birds often flew away from and towards the feeder during the food-associated context, whereas they remained rather close to the taxidermy mount of the sparrowhawk in the mobbing context. In summary, great tits seem to gain contextual information by the ration of certain note types, which greatly differed between the contexts in my study. In addition, tits also produced three note types solely in the presence of food, which might provide additional information about food availability. Future studies are needed to investigate which information is encoded by certain note types. For example, playback studies that alter the ratio of note types could be conducted to test if and how the behaviour of conspecifics changes in response to those calls.

Another way of encoding information are changes in the acoustic structure of a call such as element number or call repetition, which is often observed in birds and mammals in response to different stimuli (Elowson *et al.* 1991, Leavesley and Magrath 2005, Courter and Ritchison 2010, Murphy *et al.* 2013, Carlson *et al.* 2017). Similar to previous studies I also found great tits to use these ways of encoding information (Carlson *et al.* 2017). Great tits increased call rate (calls/individual/minute) when confronted with the more dangerous sparrowhawk mount (*Accipiter nisus*) compared to calls produced in response to the tawny owl (*Strix aluco*). Studies in other species, including suricates (Manser 2001), chickadees (Soard and Ritchison 2009), white-throated magpie-jays (*Calocitta formosa*) (Ellis 2008) and squirrels (Warkentin *et al.* 2001) showed that call rate often encodes threat-level or response urgency. The results of my third study add evidence to this assumption, as great tits had a higher call rate in response to a stuffed sparrowhawk compared to calls of the food-associated context. This indicates that call rate functions as a graded signal that informs others about the degree of threat or the response urgency of a situation. Whereas the presence of a sparrowhawk is a highly dangerous situation that calls for immediate action, i.e. mobbing or fleeing, the

presence of food is a non-threatening situation that is only relevant to non-satiated birds. In addition, calling behaviour was affected by the number of conspecifics, which also indicates that call rate might signal response urgency or threat. In my first experiment number of conspecifics significantly affected the number of calls in three minutes, whereas calling rate was not affected by conspecific number. Hence, single individuals did not change calling rate depending on the number of conspecifics and the increased number of calls in three minutes was most likely caused by the fact that more individuals joined the mobbing flock leading to an increased number of calls. In my third experiment, in contrast, call rate decreased with increasing conspecific number, indicating that call rate might also reflect the perceived predation risk by an individual. In the first experiment, single great tits were only observed in three locations. However, a high proportion of observations of the last study, especially in the food-associated context, were conducted on single individuals. Being alone might imply a higher threat for an individual as it cannot decrease predation risk by dilution effect or benefit of the vigilance of other flock members (Delm 1990). Further, in a food-associated context, flock mates might increase the chance to monopolize or dominate a food source if interspecific competition is high. Hence, individuals might increase calling rate while being alone to recruit conspecifics fast, but decrease call rate when being accompanied by conspecifics to reduce interspecific competition. Even though recruiting conspecifics to a food source might result in a decreased feeding rate for the calling individual it might be beneficial as food keeps those conspecifics alive that later on might assist in mobbing (Ficken 1981). Lastly, the more individuals participate in mobbing, the higher is the chance of driving the predator away (Flasskamp 1994). As mobbing is not without risk for the caller, its decision to join a mobbing flock might depend on the community composition. The anti-predator behaviour of some bird species is affected by the familiarity or relationship with present individuals: Siberian jays (*Perisoreus infaustus*) produce more mobbing calls and increase mobbing duration when accompanied by kin compared to non-kin groups (Griesser and Ekman 2005) and male wintering great tits give alarm calls more often when with their mates (Krams *et al.* 2006). Further, great tit breeding pairs are more likely to assist neighbouring pairs in mobbing if they already have been neighbours in previous breeding seasons (Grabowska-Zhang *et al.* 2012). As in some of our study areas the great tit density is very high (Gottschalk and Randler 2019) it is likely that tits in those areas are, to some extent, familiar with

each other, which could affect the number of birds joining mobbing and hence might explain the increasing number of uttered mobbing calls in the first study. However, further studies are necessary to investigate if and how the mobbing behaviour of great tits outside the breeding season might be affected by familiarity and/or relationship to accompanying birds.

Besides an increase in call rate, I found tits to vary the duration of their calls according to predator threat. In general, the duration of the call can be affected by three acoustic parameters: element number, element duration and the interval between elements. In my study, tits varied the number of elements and the interval between those elements in response to both predators. The number of elements and the interval between elements increased when confronted with the high- risk predator compared to the low-risk predator. The variation in element number is in contrast to the findings by Carlson *et al.* (2017a) who did not find such a variation in relation to different predators. However, encoding predator threat by altering element number is widespread in Paridae species: tufted titmice (*Baeolophus bicolor*) and Carolina chickadees (*Poecile carolinensis*), for example, produce more D notes in response to more dangerous predators (Soard and Ritchison 2009, Courter and Ritchison 2010) and when mounts are presented closer to their feeding station (Bartmess-LeVasseur *et al.* 2010). Similar, black-capped chickadees adjust the number of D notes to predation threat, whereby the number of notes increases with increasing threat (Templeton *et al.* 2005). The fact that my results reveal such a change in element number in great tits, but Carlson *et al.* (2017a) did not find such a variation, might be due to the fact that Carlson and colleagues conducted their experiment during the winter time in proximity to feeders, whereas I recorded mobbing calls independent of feeding stations throughout all seasons. The third experiment of my thesis (chapter 3) revealed that calls of a food-associated context differ from those of a mobbing context. Therefore, it cannot be fully excluded that mobbing calls induced close to a feeding station differ from calls elicited apart from food resources. Predation close to a feeding station might be perceived as a different threat as birds during winter usually rely more on established feeders, which they can visit repeatedly. Moreover, conspecifics and heterospecifics might be distracted by feeding and hence take longer to spot a predator, which might result in a difference in perceived predation risk. To exclude this possibility, further research comparing mobbing calls from a

predation context (as in chapter 1) with calls of a “mixed” context, i.e. mobbing calls close to feeders, is necessary.

Another possibility explaining the difference between Carlson’s results and mine could be a variation in calling behaviour due to different seasons. Dutour *et al.* (2017b, 2019) showed that the mobbing intensity in passerine birds differs between seasons, as mobbing is more intense in autumn than in spring, which is most likely caused by a shift in a predator’s diet from small mammals during spring to small birds during autumn. However, if the ways of encoding information as well differ between seasons, I should have found a significant effect of season as I sampled mobbing calls throughout all seasons. However, mobbing calls were not affected by the season they were recorded in, indicating that the ways of information encoding are stable over time. Lastly, the difference in information encoding might be explained by the usage of different low-threat predators (common buzzard vs. tawny owl) or predator behaviour (head movement vs. no movement). Some studies showed that the head orientation of a predator affects the feeding and calling behaviour of birds. For example, tufted titmice increase calling and reduce foraging activities when a predator faces towards them (Freeberg *et al.* 2014, Book and Freeberg 2015). Similar, Carolina chickadees visit feeding stations less frequently and increase calling behaviour when a human observer or cat model is facing a feeding station (Freeberg *et al.* 2016). Most studies investigating mobbing behaviour in birds used stationary predator models or mounts and there is little known about how predator behaviour affects the calls of a target species. Carlson *et al.* (2017) showed that blue tits reduce feeding and increase wing-flicking, but not calling, in response to moving predator mounts compared to stationary mounts. Hence, it might be that great tits use different ways of encoding information about stationary and moving predator mounts, which could explain the difference in calling behaviour between my study and the results of Carlson *et al.* (2017a). However, further studies are needed to test this hypothesis.

My study further revealed that great tits use fine-scale alterations to encode information about predators, because they varied the interval between D elements according to predatory threat (chapter 1). D calls towards the sparrowhawk had longer intervals than calls elicited by the tawny owl. In addition, tits used differences in the acoustic structure of D elements to discriminate between a predation and a food-associated context (chapter 3). Food-associated calls were similar to mobbing

calls in duration and element number, but had longer elements and shorter intervals between elements. This suggests that great tits use a set of fine-scale acoustic measures of D calls to encode various information without changing call type. Great tits varied the interval between elements in both contexts. Hence, this variable might signal the urgency of a situation similar to call rate. Additionally, note duration seems to be used to encode additional information about the nature of a situation, i.e. mobbing or food context. This way of encoding information is, so far, only known from few other species. For example, American crows (*Corvus brachyrhynchos*) also show variation in intercall intervals while displaying different anti-predator behaviours (Yorzinski and Vehrencamp 2009). Crows had the shortest intercall intervals while swooping, i.e. flying within two meters of the predator, indicating that intercall intervals encode information about immediate predation risk. A North American Paridae species, the black capped chickadee (*Poecile atricapillus*), decreases the time between the first and second D element as well as the duration of the first D element when predator threat increases (Templeton *et al.* 2005). This is in contrast to my findings which could be explained by the fact that different species, even related ones, are known to use different ways of encoding information in their mobbing calls (Carlson *et al.* 2017).

An advantage of encoding information with fine-scale instead of gross-scale measures could be that hereby the exact contextual information of a call is only available to conspecifics. For example, great tits could be able to assess the predation threat posed by a specific predator prior to arrival at a mobbing site and hence might be more vigilant and therefore less prone to predation risk, whereas heterospecifics might be only capable to determine the actual predation risk after visual contact to the predator. Various studies tested how passerines behave in response to mobbing calls of conspecifics and heterospecifics (Freeberg and Lucas 2002, Templeton *et al.* 2005, Suzuki 2012, Randler and Vollmer 2013, Dutour *et al.* 2016, Dutour *et al.* 2017). A playback study with chaffinches (*Fringilla coelebs*) revealed that conspecifics and heterospecifics respond similar to natural and manipulated mobbing and contact calls. However, conspecifics had smaller effect sizes than heterospecifics, indicating that conspecifics might indeed be able to recognize subtle variations in calls, such as differences in frequency, whereas heterospecifics fail to do so (Randler and Förschler 2011). In my second experiment, I broadcasted the mobbing calls recorded during the first study to great tits to test if



they can recognize the subtle differences in conspecific calls and adapt their behaviour accordingly (chapter 2). Indeed, great tits showed different behavioural responses towards the two stimuli, indicating that great tits are capable of discriminating between the subtle variations in the calls of the two different contexts. Great tits kept a greater distance to the speaker when hearing mobbing calls provoked by a sparrowhawk than when hearing tawny owl mobbing calls. This is in contrast to findings by Templeton *et al.* (2005), who conducted a playback study with black-capped chickadees and showed that they approach a speaker closer in response to mobbing calls elicited by smaller, more dangerous predators than by calls provoked by less dangerous predators. Nonetheless, a study by Curio *et al.* (1983) showed that great tits feeding nestlings approach a live tawny owl closer than a sparrowhawk. Further, tits had longer latency times when hearing conspecific mobbing calls provoked by the more dangerous sparrowhawk. Similar, Hogstad (2017) found great tits to have a longer latency time until they return to a feeder after confrontation with a stuffed sparrowhawk than after seeing a Siberian jay or three-toed woodpecker (*Picoides tridactylus*). These and my results combined indicate that great tits might rather follow a “better safe than sorry” strategy, i.e. be more cautious during mobbing than other species. Such interspecific differences in mobbing are also known from a study by Nolen and Lucas (2009), who confronted nuthatches, chickadees and titmice with an Eastern screech owl (*Megascops asio*) and found that the three prey species significantly differ in mobbing duration and proximity to the predator. These differences might be explained by different predation risks, physiological or structural constraints on vocal mobbing or species composition (Nolen and Lucas 2009). A recent study on various passerine species revealed that mobbing behaviour is related to the species prevalence in a predator’s diet and the local occurrence of a predator (Dutour *et al.* 2016, Dutour *et al.* 2017). Dutour *et al.* (2017) showed that species, including great tits, which are more prevalent in a predator’s diet, participate more frequently and more intense in mobbing than less frequently eaten species. However, Dutour and colleagues did not measure risk-taking by e.g. minimum distance, but only assessed whether or not species participated in mobbing. Often eaten species could be more likely to join a mobbing flock, but still be more cautious during mobbing, which is indicated by my results.

Furthermore, mobbing behaviour might differ according to a difference in stimuli that provoke mobbing, i.e. whether focal individuals see a predator themselves or only

hear conspecific calls. A study in yellowhammers (*Emberiza citrinella*) showed that individuals, which only heard alarm calls, behaved cautiously longer than individuals that saw the predator (van der Veen 2002). Lind *et al.* (2005) found great tits to remain silent and motionless when hearing mobbing calls compared to birds seeing a stationary predator. However, there was no difference in latency time until feeding between the two groups, indicating that great tits evaluate mobbing calls as an honest signal of predation risk and the risk can be considered to be over once the calls stop (Lind *et al.* 2005). This is also supported by my observations during the second study as great tits usually resumed normal behaviour immediately after the playback stopped.

Lastly, even though great tits altered their behaviour in response to mobbing calls of different contexts, it remains unknown, which acoustic features trigger the difference in behaviour. Because great tits varied several acoustic parameters in response to the two different predators, it remains unclear which feature, or set of features, is essential to enable receivers to recognize the encoded information. Similarly, red-breasted nuthatches (*Sitta canadensis*) and black-capped chickadees adapt their behaviour, e.g. approach distance, according to predator threat encoded in chickadee mobbing calls, but it remains unclear, which acoustic parameters are used by con- and heterospecifics to assess predation risk (Templeton *et al.* 2005, Templeton and Greene 2007). A study by Wilson and Mennill (2011) suggests that the duty cycle rather than fine-scale acoustic variants are important for decoding predation risk. Hetero- and conspecifics ignored manipulations of the fine structure of black-capped chickadees 'chick-a-dee' calls, when calls were played back with constant duty cycles. Moreover, individuals responded more strongly when duty cycle was manipulated but fine-scale measures were kept constant, whereby a higher duty cycle elicited stronger responses (Wilson and Mennill 2011). Consequently, more studies that experimentally manipulate single parameters of calls are necessary to determine, which acoustic features are important for information encoding and decoding by conspecific and heterospecific individuals.

Further, my playback study revealed that males tend to approach a speaker faster and closer than females when conspecific mobbing calls were broadcasted. This indicates that mobbing behaviour in great tits might indeed be affected not only by predation threat but also by other aspects such as mating status or sex. Curio *et al.*

(1983) also found males to approach a live predator closer than females. Further, female great tits had a longer latency time to return to feeding after a startle when accompanied by a conspecific male, whereas males reduce their latency time in these situations (Van Oers *et al.* 2005). These results indicate that male great tits might be generally willing to take higher risk, which is also known from other bird species (Griesser and Ekman 2005, Hogstad 2017). Great tits often have a skewed sex ratio due to a higher annual mortality of females resulting in a good proportion of males being unmated during breeding season (Regelmann and Curio 1986, Payevsky 2006). A study by Regelmann and Curio (1986) showed that breeding male great tits have a smaller minimum distance to a predator in the presence of a female compared to situations where no female is present, indicating that males might take higher risks to protect females in their territory. Furthermore, risk taking behaviour might be a signal of male-quality to females as bolder males might be in better condition and hence be capable of escaping faster, which would allow them to approach predators closer. A study with wax moths (*Achroia grisella*) revealed that more attractive males take higher risks than less attractive ones, indicating that risk taking might indeed be a signal of male quality (Cordes *et al.* 2014). Also, in fiddler crabs (*Uca mjoebergi*) males that consistently took greater risk in a predation context have a higher mating success (Reaney and Backwell 2007).

Lastly, in various species, including great tits, differences in risk-taking behaviour are related to other personality traits, i.e. consistent inter-individual behavioural differences, such as exploration and aggression (Sih *et al.* 2004, Van Oers *et al.* 2004). Further, there is a link between personality and fitness in many species (Smith and Blumstein 2008). In great tits, personality is known to be, to some extent, heritable (Drent *et al.* 2003, Van Oers *et al.* 2004) and to affect mating behaviour and reproductive success (Both *et al.* 2005, Van Oers *et al.* 2008). In addition, studies showed that personality in great tits is related to nest defence behaviour (Hollander *et al.* 2008, Vrublevska *et al.* 2015) and latency time until feeding after a short startle, i.e. risk taking behaviour (Van Oers *et al.* 2004). However, how great tits behave after a startle is also affected by the social context and sex (Van Oers *et al.* 2005). Tits returned faster to feeding when accompanied by a conspecific compared to when being alone, but the latency time differed between sexes. Females had longer latency times when being with a male, whereas males had shorter latency times. Furthermore, the behavioural type of the male interacted with the activity of the

companion, i.e. shyer males reduced their latency time when the activity of the male companion increased, whereas female latency time, was not affected by personality or a companion's activity (Van Oers *et al.* 2005). These and mine results combined indicate that anti-predator behaviour of great tits is most likely not only determined by the immediate predation risk posed by a predator, but also by a combination of internal and external characteristics. In chapter 1, I did not assess whether the sex of accompanying conspecifics affected the mobbing behaviour of great tits, nor did I account for the presence of conspecifics or their sex in the study of chapter 2. Further, it is not possible to account for inter-individual differences with my data, as I did not test the same individuals repeatedly. Therefore, it cannot be excluded that the results of my experiments are, to some extent, influenced by the personality of individuals. Nonetheless, even if personality might influence the mobbing behaviour of individual great tits, such inter-individual difference would not alter the overall results, i.e. a difference in mobbing behaviour towards high- and low-threat predators. However, future studies might choose their experimental design to be able to account for an effect of personality, social context and sex on the mobbing behaviour of focal individuals.

The results of this thesis show that great tits are able to vocally discriminate between two common aerial predators (chapter 1) and a high-threat predator and food (chapter 3). I further revealed a new way of information encoding information in great tits as they varied the interval between elements (chapter 1 and 3) as well as the duration of the elements themselves (chapter 3). Such subtle variations in acoustic features might hold the benefit of encoding various information in one call type that can be used by conspecifics to adapt their behaviour to a given situation. I found that great tits are able to decode information about predator threat in conspecific mobbing calls as they behaved differently in response to calls of a high- and low-risk context (chapter 2). In a next step, studies should now test if great tits are also able to discriminate between D calls of a mobbing and a food context. If great tits are able to discriminate between these calls, one might observe them to show mobbing behaviour in response to D calls of the mobbing context and foraging behaviour in response to food-associated calls. Further, it remains to be tested if heterospecifics are capable to discriminate between D calls of different contexts. One benefit of encoding information by slight changes in acoustic structure might be that the signal is less prone to eavesdropping, which would be especially beneficial in a food-

associated context. Lastly, I found a difference in mobbing behaviour between sexes (chapter 2). Hence, future studies should focus on investigating the relationship between sex and mobbing behaviour in great tits. It might be that males are in general more likely to take higher risks than females, which could be linked to general differences in the hormone statuses. However, sex differences might also be linked to the reproductive season, i.e. males and females might only show differences in mobbing behaviour during breeding season, but not outside the breeding season. Hence, one might repeat the playback study of chapter 2 during different times of the year (before, during and after breeding) and compare the results with each other to reveal if sex differences in mobbing behaviour are stable over time. Finally, future studies investigating mobbing calls of birds might not only focus on changes in call type and calling rate, but also check for variations in element duration and the interval between elements to reveal if these ways of information encoding are specific for some single species or if this way of encoding information is more widespread in birds.

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## Appendix

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## **Chapter 1**

### **Do great tits encode information about predator threat in their calls?**

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# SCIENTIFIC REPORTS



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## Subtle variations in mobbing calls are predator-specific in great tits (*Parus major*)

Nadine Kalb, Fabian Anger & Christoph Randler 

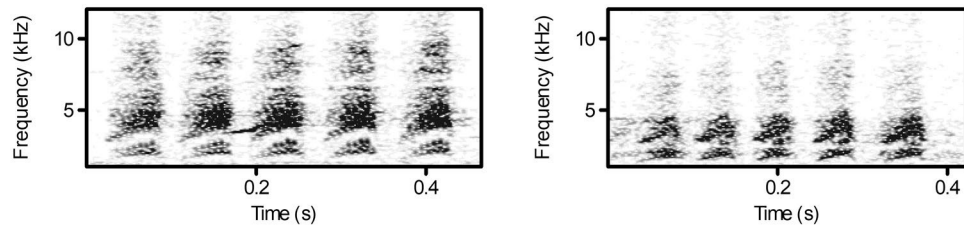
Many species are known to use vocalizations to recruit con- and heterospecifics to mobbing events. In birds, the vocalizations of the Family Paridae (titmice, tits and chickadees) are well-studied and have been shown to recruit conspecifics and encode information about predation risk. Species use the number of elements within a call, call frequency or call type to encode information. We conducted a study with great tits (*Parus major*) in the field where we presented taxidermy mounts of two predators of different threat levels (tawny owl, *Strix aluco*, and sparrowhawk, *Accipiter nisus*) and compared the mobbing calls of these two contexts. We hypothesized, based on results of studies in other paridae species, that tits vary the number or type of elements of a call according to predatory context. We found great tits to vary the number of D elements and the interval between those elements. Great tits produced significantly longer D calls with more elements and longer intervals between elements when confronted with a sparrowhawk (high-threat) compared to a tawny owl (low-threat) mount. Furthermore, birds produced more D calls towards the high-threat predator. This suggests that the basic D calls are varied depending on threat intensity.

Animals transmit information in various ways with vocal, visual and olfactory signals being the most common ones. Visual signals are normally visible over short distances due to their physical properties. Vocalizations in contrast can be transmitted over longer distances and are therefore suitable to transmit information also to individuals that are not in visual contact to the sender<sup>1</sup>. Animal vocalizations have been studied in a wide variety of taxa and some vocal signals in avian and mammalian species are even known to encode information about environmental factors such as the presence of predators and food<sup>2–5</sup>.

Many bird species produce alarm or mobbing calls after a predator has been detected<sup>6–8</sup>. Usually, alarm calls are produced to inform others about a threat that causes them to flee or hide, mobbing calls on the other hand are intended to attract hetero- and conspecifics to join a mobbing flock<sup>9–11</sup>. During mobbing, songbirds produce distinct mobbing calls, move towards the predator and display stereotype behaviors to recruit others and deter the predator<sup>12–14</sup>. Additionally, calls can transmit information about a predator's type<sup>15</sup>, size<sup>16</sup> and distance<sup>17</sup>. Although moving towards the predator while mobbing seems controversial in terms of immediate predation risk, it ultimately can hold the benefit of chasing the predator away<sup>18–20</sup>. Further, exhibiting mobbing behavior and alarm calling at or in the nest can increase the fitness of incubating females and their young<sup>21,22</sup>.

In birds, the mobbing behavior of titmice, tits and chickadees (Family Paridae) is especially well-studied. Paridae species do not only transmit information in their calls about the presence of a predator, but also about its threat level<sup>23–26</sup>. Information about a predator can be encoded by an increased call intensity, a variation in syllable number, syllable duration or call type. Some species use only one of these possibilities and others a combination of some or even all ways, whereby more dangerous predators usually elicit a stronger response<sup>23,27</sup>. Tufted titmice (*Baeolophus bicolor*) increase the total number of D notes per time unit towards more threatening predators<sup>24</sup>. Black-capped chickadees (*Poecile atricapillus*) produce calls with more D notes and decrease the duration of the first D note as well as the time between the first and the second D note, when confronted with smaller and more dangerous predators<sup>16</sup>. Similar Carolina chickadees (*Poecile carolinensis*) produce more 'chick' and fewer 'dee' notes in the presence of a larger, low-threat predator, whereas smaller and higher-threat predators elicit fewer 'chick' and more 'dee' notes<sup>28</sup>. Japanese great tit parents (*Parus minor*) produce distinct alarm calls when confronted with three of their main nest predators<sup>15,26,29</sup>. They produce jar calls solely in response to Japanese rat snakes (*Elaphe climacophora*) and vary the number of 'chicka' calls as well as the number and type of notes within

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**Figure 1.** Sonogram showing a D call with 5 elements in response to a sparrowhawk mount (left) and a tawny owl mount (right). Sparrowhawk mobbing calls have a longer duration (s) and longer intervals between elements (s) than calls in response to the tawny owl.

‘chicka’ calls to further discriminate between Japanese marten (*Martes melampus*) and jungle crow (*Corvus macrorhynchos*)<sup>29</sup>. Adults show different predator-searching<sup>30</sup> and nestlings predator-avoidance<sup>15,31</sup> responses according to the respective alarm calls. Incubating great tit females give hissing calls when an intruder enters the nest box<sup>21</sup> and breeding pairs produce churring calls (D calls) when a predator is close to the nest<sup>22</sup>. Non-breeding great tits decrease the proportion of calls containing chirp elements and increase the propensity to produce jar/rattle calls to distinguish between threatening predators and a control<sup>23</sup>. To discriminate between predators of different threat-level great tits increase their call rate in response to higher threats<sup>23,32</sup>.

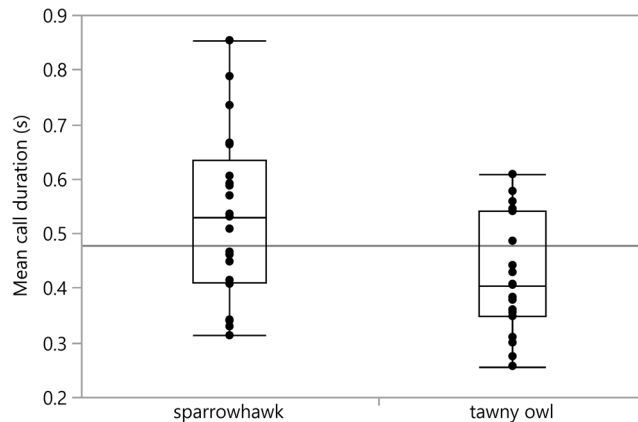
There are numerous studies that investigated how passerines encode information about predators in their calls, but most studies focused on changes in calling rate and call types in response to different predators. Hence, our goal was to investigate if wild-living great tits might use fine-scale acoustic variations in their mobbing calls as an additional way of encoding information about predatory threats. We recorded mobbing calls of great tits when confronted with taxidermy mounts of tawny owl (*Strix aluco*) and sparrowhawk (*Accipiter nisus*). Dutour, *et al.*<sup>33</sup> showed that mobbing behavior in passerines increases with the prevalence in a predator’s diet. Hence, we presented great tits two avian predator species that greatly differ in the proportion of great tits in their diet and consequently pose different predation risk to this species. Both predators are common in southwest Germany in general and in our study area in particular<sup>34,35</sup> and are known to prey on small passerine birds including great tits<sup>36–39</sup>. Sparrowhawks are high-threat predators for great tits as they are diurnal and small birds, including great tits, make up the most part of their diet<sup>39</sup>. Tawny owls on the other hand are most active at twilight and night and mainly prey on small mammals<sup>37,38</sup> and can therefore be considered as low-threat predator for great tits. Curio, *et al.*<sup>36</sup> found that great tit parents feeding fledglings respond more strongly (shorter mean minimum and average distance) during mobbing towards sparrowhawks, which have a higher “predator pressure” than towards tawny owl. We hypothesized that great tits do not only use call rate and type<sup>23</sup> but also some fine scale acoustic measures<sup>16</sup> to discriminate between the two predators.

## Results

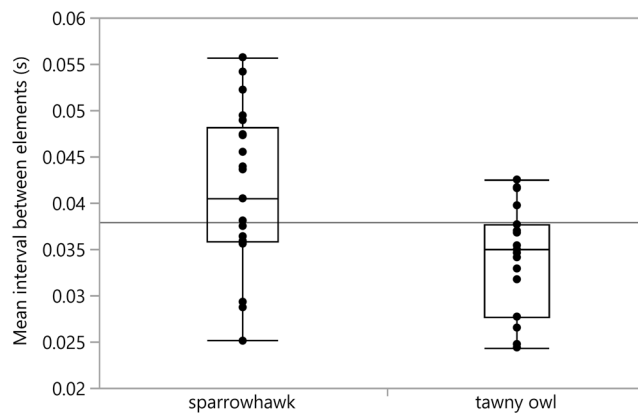
**Call types.** We compared the number and call types (D call, chirp, tonal and jar) produced towards the two predators of different threat level (sparrowhawk versus tawny owl). Season had not effect on any of the measured variables (all  $p > 0.05$ ). Great tits produced chirp, tonal, and D calls in response to both predators. Jar calls were only recorded in four locations in response to the tawny owl. Among the four call types, D calls were the most frequently given ones (tawny owl: 83.12%, sparrowhawk: 94.12%). The total number of calls, jar, chirp and tonal calls was not significantly affected by predator type or conspecifics (all  $p > 0.05$ ). However, predator type ( $F = 5.537$ ,  $df = 1,34$ ,  $p = 0.025$ ) and number of conspecifics ( $F = 6.811$ ,  $df = 1,34$ ,  $p = 0.013$ ) had an effect on the number of produced D calls in three minutes. The number of D calls was significantly higher in the sparrowhawk treatment compared to the tawny owl treatment and increased with increasing number of conspecifics. Call rate (D calls/individual/minute) was also affected by predator type ( $F = 5.402$ ,  $df = 1,1$ ,  $p = 0.026$ ), but not by the number of conspecifics ( $F = 3.176$ ,  $df = 1,1$ ,  $p = 0.084$ ). The call rate was higher in response to the sparrowhawk (mean  $\pm$  SE,  $15.03 \pm 2.75$ ) compared to the tawny owl ( $7.97 \pm 1.20$ ). We also found an effect of predator type on the mean number of elements in D calls ( $F = 5.767$ ,  $df = 1,34$ ,  $p = 0.022$ ). Here, great tits produced calls with more D elements exposed to the sparrowhawk compared to the tawny owl mount.

**D call features.** We found a significant effect of predator type on the mean duration of D calls ( $F = 6.167$ ,  $df = 1,34$ ,  $p = 0.018$ ). Great tits produced longer D calls towards the sparrowhawk ( $0.531 \pm 0.033$ ) than towards the tawny owl mount ( $0.419 \pm 0.024$ ) (Figs 1, 2). Predator type as well had an effect on the number of D elements within a call ( $F = 4.389$ ,  $df = 1,34$ ,  $p = 0.044$ ) as great tits produced calls with more elements towards the high-threat predator ( $7.095 \pm 0.391$ ) than towards the low-threat predator ( $6.063 \pm 0.371$ ). Moreover, predator type affected the mean interval between elements ( $F = 4.405$ ,  $df = 1,34$ ,  $p = 0.043$ ), whereby the interval between elements was longer when confronted with a sparrowhawk ( $0.041 \pm 0.002$ ) compared to the tawny owl ( $0.034 \pm 0.001$ ) (Figs 1, 3). The mean duration of elements was not affected by predator type ( $F = 0.796$ ,  $df = 1,34$ ,  $p = 0.379$ ). The number of conspecifics or season had no significant effect on any of our measured parameters (all  $p > 0.05$ ).

In respect of acoustic features, there was no significant effect of predator type on the mean peak frequency ( $F = 0.124$ ,  $df = 1,29$ ,  $p = 0.728$ ), maximum frequency above  $-30$  dB ( $F = 0.282$ ,  $df = 1,29$ ,  $p = 0.599$ ), number of peak above  $-10$  dB ( $F = 0.604$ ,  $df = 1,29$ ,  $p = 0.443$ ), interval between overtones ( $F = 0.075$ ,  $df = 1,29$ ,  $p = 0.786$ ),



**Figure 2.** Mean call duration (s) depending on the predator type model. Call duration is significantly longer in calls towards the sparrowhawk than towards the tawny owl.



**Figure 3.** Mean interval between D elements (s). Birds produced calls with longer intervals between elements when confronted with a sparrowhawk model compared to the tawny owl model.

bandwidth at  $-10$  dB ( $F = 0.005$ ,  $df = 1,13$ ,  $p = 0.945$ ) or bandwidth at  $-30$  dB ( $F = 0.575$ ,  $df = 1,29$ ,  $p = 0.454$ ). The number of conspecifics also had no effect on any given parameter (all  $p > 0.05$ ).

## Discussion

This study shows context-dependent variation in vocalizations in a common passerine, the great tit. Great tits responded differently towards a low-threat (tawny owl) and high-threat (sparrowhawk) predator.

Irrespective of the predator type great tits produced chirp, tonal and D calls, whereby the majority of calls were D calls. We found great tits to increase call rate and the number of D calls in three minutes when exposed to a high-threat compared to low-threat predator. This is in line with findings by Carlson, *et al.*<sup>23</sup> who found that British great tits vary calling rate to discriminate between high- and low-threat predators. Moreover, Templeton, *et al.*<sup>16</sup> showed that black-capped chickadees produce significantly more mobbing calls, particularly more D syllables, towards small high-threat predators than towards larger predators.

The number of D calls was not only affected by predator type but also by the number of conspecifics present in a radius of 50 meter. This might be explained by the fact that we did not record single individuals but all great tits participating in a mobbing event under natural conditions. Hence, an increase in the number of D calls might be explained by two factors: (i) flock size, i.e. single individuals might call more frequently when accompanied by conspecifics compared to when being alone or (ii) an additive affect, i.e. more individuals participate in mobbing leading to an increased number of calls. Since call rate (i.e. D calls/individual/minute) was not significantly affected by the number of conspecifics, the latter explanation seems to be more likely.

The more individuals join a mobbing flock and exhibit mobbing behavior the higher is the chance of successfully driving the predator away<sup>19</sup>. However, joining a mobbing flock also holds the risk of getting captured or giving away the location of the nest<sup>40–42</sup>. Therefore, if individuals assist in mobbing or stay in safety might depend on the community composition, i.e. whether it is accompanied by familiar or related individuals or not. The alarm calling and mobbing behavior of some birds, including great tits, is known to be affected by the familiarity with con- and heterospecifics<sup>43–49</sup>. The effect of number of conspecifics on D call number, irrespective of predator type, could possibly also be explained by such familiarity effects. Great tits live in monogamous pairs during breeding season and join flocks during winter<sup>50,51</sup>. In some of our study locations we observed up to 30 breeding pairs per

square-kilometer, which makes some kind of familiarity among breeding pairs likely. Great tit breeding pairs are known to be more likely to join the nest defense of familiar neighbors than of unfamiliar ones<sup>46</sup> and male wintering great tits give alarm calls more frequently when being with their mates or when being accompanied by permanent flock members in their home range<sup>48</sup>. Hence, it seems possible that the number of birds joining a mobbing flock and consequently the number of calling individuals is also affected by familiarity among great tits living in a specific area. Further, anti-predator responses in great tits can be related to the personality of the caller<sup>21,22</sup>, i.e. some individuals are repeatedly willing to take higher risks during predator defense than others. Hence, one might expect that both the number of calls and the number of mobbing individuals increases in communities with a high proportion of bold individuals. However, if and how personality and familiarity affect the composition of a mobbing flock and the mobbing behavior therein remains to be tested.

We found great tits to not only vary the number of D calls but also the duration of those calls. Great tits produced longer D calls towards the high-threat compared to the low-threat predator. Birds can alter the duration of calls by varying either one or a combination of the following variables (1) the number of elements of a call, (2) the duration of elements or (3) the intervals between elements. In our study the difference in call duration resulted from a variation in element number and the interval between elements. Calls towards the high-threat predator had more elements than calls in response to the low threat predator. Such a variation in element number according to predator threat is widespread in paridae species, including great tits<sup>16,23,24</sup>. However, to our best knowledge, we are the first to reveal that great tits also use a variation of the intervals between elements to encode information about predator threat. Great tits produced calls with longer intervals between elements in response to the sparrowhawk than in response to the tawny owl. Templeton, *et al.*<sup>16</sup> as well found such a variation in black capped-chickadees, which decrease the duration of the first D note as well as the interval between the first and second D note when confronted with smaller, more dangerous predators. Acoustic analysis of mobbing calls in American crows (*Corvus brachyrhynchos*) also suggest that calls with a longer duration, higher rate and shorter intervals between caws encode a higher predation risk<sup>52</sup>. These and our results combined indicate that subtle variations in the interval between elements of one call type might hold the potential to encode numerous information about predator threat without changing call type. Future work could investigate if great tits use variations in the interval between elements to discriminate between different predator types (e.g. terrestrial versus aerial). In addition, future research is necessary to investigate if great tits are able to recognize such subtle variation in call structure and adapt their behavior accordingly.

In our study, great tits produced jar calls only in four out of 40 locations and only in response to the tawny owl. Japanese great tits (*Parus minor*) produce jar calls as referential signal specifically in response to snakes and 'chicka' calls (including D calls) for avian and mammalian nest predators<sup>15,29,31</sup>. In *Parus major*, however, call types exclusively used only in specific predation contexts have, so far, not been found. Our finding also does not indicate such functional referential signalling as it is in contrast to findings by Carlson, *et al.*<sup>23</sup> where great tits increased the propensity to produce jar/rattle calls when confronted with an avian predator compared to the control. Such differences might be due to geographical variation or differences in the experimental design. Carlson and colleagues presented both predators (sparrowhawk, common buzzard, *Buteo buteo*) at each site. We used only one predator per site and hence cannot account for possible inter-individual differences in calling behavior. Krams, *et al.*<sup>21</sup> found that incubating great tits produce hissing calls when confronted with a nest intruder. Surprisingly, females differ in their propensity to give hissing calls, which might reflect differences in female personality. In our study, it might also be the case that birds in some locations are bolder than others and therefore differ in their propensity to produce certain call types (irrespective of predator type). Hence, future work is necessary to investigate if and how mobbing calls in great tits might be affected by personality traits. However, the difference in calling behavior could also be explained by a difference in predation risk caused by tawny owls between study sites. Dutour, *et al.*<sup>33</sup> showed that the calling behavior of great tits increases with the prevalence in a predator's diet. Even though we know that tawny owls are present in all our study locations, great tits in some locations might still be more prone to predation by this predator type and hence differ in their calling behavior. Therefore, future studies might analyze the diet composition of predators at specific study locations and relate them to the calling behavior of the prey species in those areas rather than estimating predation risk simply by the presence or absence of the predator species.

We show that great tits vocally discriminate between two common predators, sparrowhawk and tawny owl, that greatly differ in threat level. We further found that great tits use the interval between elements in addition to already known ways<sup>23</sup> to encode information about predator threat. Furthermore, the number of conspecifics affected the number of uttered calls, which indicates that some community features, such as e.g. familiarity among flock members or flock size, might affect the mobbing behavior of great tits.

## Methods

**Study location.** We studied great tits (*Parus major*) near Tübingen (48°31'N, 9°3'E), Freudenstadt (48°27'N, 8°25' E), and Rottenburg am Neckar (48°28'N, 8°56'E), Baden-Württemberg in southwest Germany. Because a minimum distance of 200 to 250 meters is often used to ensure independent measures in free-ranging parids<sup>14,53</sup>, we usually kept a minimum distance of at least 220 m between study sites (mean  $\pm$  SE, 616.4 m  $\pm$  81.5). In some of our study locations (n = 7), however, the population density of great tits is quite high (25–30 breeding pairs per square-kilometer) (personal observations). Hence, in those areas we could decrease the minimum distance to 170 m (192.7 m  $\pm$  7.8) between predator presentations while still keeping the probability of testing the same individual twice low. During all sound recordings, there was a minimum distance of 8 meters between the observer and the microphone.

**Mobbing call recordings.** Recordings were made by NK & FA and took place between 07:00 and 14:00 CET from late June 2017 to early April 2018. We used different taxidermy mounts of two different tawny owls

(*Strix aluco*;  $N = 2$ ) and sparrowhawks (*Accipiter nisus*,  $N = 2$ ) to elicit mobbing calls. Mounts were placed on tree trunks or rocks and we used only one mount per site. We recorded calls using a boundary microphone (Marantz professional, in Music GmbH, Ratingen, Germany,) placed directly beside the predator model and a digital recorder (Marantz professional PMD661MKIII, in Music GmbH, Ratingen, Germany). The observer noted the location, model number and time at the start of each recording. Recordings started immediately after setting up the equipment and were terminated 10 minutes after a great tit started to utter mobbing calls. In cases where no great tit participated in mobbing recordings were terminated after 30 minutes. The observer noted the number of conspecifics in a radius of 50 m around the taxidermy mount. In total we recorded mobbing calls at 49 different locations (tawny owl  $n = 23$ , sparrow hawk  $n = 26$ ). However, some of the recordings had poor quality ( $n = 2$ ), great tit calls strongly overlapped with other bird calls ( $n = 5$ ), observations got interrupted by pedestrians ( $n = 2$ ) and in one case a free-living sparrowhawk flew by. Hence those recordings could not be analyzed resulting in a final sample size of 40 (tawny owl  $n = 19$ , sparrow hawk  $n = 21$ ).

**Call analysis.** Sound recordings were analysed by NK in a strictly blinded fashion. One of our colleagues (AR) copied all sound files and renamed them with numbers, so there was no reference to location or treatment (tawny owl vs. sparrowhawk). Files were analyzed using Avisoft SASLabPro with a sample rate of 44.1 kHz. We created a sonogram using the Hann window function (FFT length 1024, Frame size 25% and 98,43% overlap). First, we analysed all calls produced by great tits within three minutes of the onset of mobbing. We manually selected calls and visually categorized them into one of four call types (D, jar, chirp or tonal) following the description given by Carlson, *et al.*<sup>23</sup>. Afterwards we analyzed the first five calls of each recording and measured four acoustic parameters: the duration (s) of the call, the duration (s) of each element, the number of elements per call and the interval (s) between elements.

Furthermore, we used a power spectrum analysis (FFT = 512) to determine more detailed analyses of the acoustic features of D elements as described in Templeton, *et al.*<sup>16</sup>. Analyses were performed in the center of the first D element of each of the first five calls of a recording. We only used recordings of very high quality, i.e. the first five calls did not overlap with calls of other birds or any other background noise (tawny owl:  $n = 16$ , sparrowhawk:  $n = 16$ ). In two mobbing events with the tawny owl mount, great tits produced only two mobbing calls, which were also included in the analysis. We measured six spectral features (for details see Templeton, *et al.*<sup>16</sup>): the peak frequency (P), the maximum frequency (M), the number of peaks above  $-10$  dB, the highest (U) and lowest frequency (L) peak above  $-10$  dB relative to the peak, the first (F1) and second (F2) peak above  $-30$  dB. Further, we determined the bandwidth at  $-10$  dB and  $-30$  dB by subtracting L from U and F1 from M respectively. The interval between overtones was calculated by subtracting F1 from F2.

**Ethical note.** This study was performed in accordance with relevant guidelines and regulations for nature conservancy in Germany (§44 Abs. 1 Nr. 2 BNatSchG). Field observations and mobbing experiments were in accordance with the higher nature conservation authority in Tübingen and adhered to the Guidelines for the Use of Animals in Research of the Animal Behavior Society/Association for the Study of Animal Behaviour.

**Statistical Analysis.** We used SAS JMP 16 for data analysis. Before conducting any further analysis, we calculated the mean value of calls per location for all measured response variables.

First, we used t-tests to do a pairwise comparison of the vocal responses (i.e. number of elements, call duration, element duration and interval between elements) towards the two different mount exemplars per predator species ( $N = 2$  tawny owl,  $N = 2$  sparrowhawk) used during this study. By doing so, we tested for differences in vocal responses within treatment groups (i.e. tawny owl and sparrowhawk) that might be provoked by differences in mounts (as they slightly differed in size and color). In cases where data did not show equal variances, we used Welch-tests. None of our measured variables differed significantly between the respective two taxidermy mounts (all  $p > 0.05$ ), i.e. vocal responses did not differ according to which sparrowhawk mount or tawny owl mount was used. Hence, we pooled the data for further analysis into two categories: sparrowhawk versus tawny owl. Moreover, none of our measured variables was significantly affected by observer (all  $p > 0.05$ ), i.e. vocal responses did not differ according to who of the two observers recorded the audio file. Hence, we did not include observer as a factor in further analysis.

Secondly, we used ANOVAs to test if the number of calls and call types produced within three minutes are affected by the fixed factors predator type, season (i.e. winter (December–February), spring (March–May), summer (June–August) and autumn (September–November)) or number of conspecifics in a radius of 50 meters (henceforth number of conspecifics). We also added location as random variable to the model. Additionally, we calculated call rate (D calls/individual/minute) and conducted an ANOVA including the above-mentioned factors.

Further, we analyzed if the structure of D calls differed between predator types using ANOVAs. We defined number of elements, call duration, element duration and interval between elements as response variables and included predator type, season and number of conspecifics as fixed factors. Lastly, we added location as a random factor to the model.

To test for differences in acoustic features, i.e. peak frequency, maximum frequency above  $-30$  dB, number of peak above  $-10$  dB, interval between overtones, bandwidth at  $-10$  dB and bandwidth at  $-30$  dB, in response to the two predator types we performed ANOVAs including treatment (sparrowhawk vs. tawny owl) and number of conspecifics as a fixed and location as a random factor.

### Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.



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## Author Contributions

N.K. and C.R. designed the experiments, N.K. and F.A. collected the field data. N.K. analyzed the bioacoustics results and did the statistical analysis. All authors contributed to the writing of the paper and have approved its final stage.

## Additional Information

**Competing Interests:** The authors declare no competing interests.

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## Chapter 2

### **Do great tits adapt their behaviour based on subtle variations in mobbing calls?**

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## **Behavioral responses to conspecific mobbing calls are predator-specific in great tits (*Parus major*)**

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### **Abstract**

When facing a predator, animals need to perform an appropriate anti-predator behavior such as escaping or mobbing to prevent predation. Many bird species exhibit distinct mobbing behaviors and vocalizations once a predator has been detected. In some species, mobbing calls transmit information about predator type, size and threat, which can be assessed by conspecifics. We recently found that great tits (*Parus major*) produce calls with more elements and longer intervals between elements when confronted with a sparrowhawk, a high-threat predator, in comparison to calls produced in front of a less-threatening tawny owl. In the present study, we conducted a playback experiment to investigate if these differences in mobbing calls elicit different behavioral responses in adult great tits. We found tits to have a longer latency time and to keep a greater distance to the speaker when sparrowhawk mobbing calls were broadcast. This suggests that tits are capable of decoding information about predator threat in conspecific mobbing calls. We further found males to approach faster and closer than females, which indicates that males are willing to take higher risks in a mobbing context than females.

### **Introduction**

Predation is a main cause of mortality in animals. Therefore, animals need to be able to detect predators and exhibit an appropriate anti-predator strategy (Lima and Dill 1990) such as fleeing, hiding in safety or mobbing a predator (Caro 2005, Cooper and Blumstein 2015). Mobbing behavior is mostly studied in birds (Altmann 1956, Curio *et al.* 1978, Gill and Bierema 2013), but also occurs in mammals (Bartecki and Heymann 1987, Graw and Manser 2007, Clara *et al.* 2008, Pitman *et al.* 2017), fish (Dominey 1983, Ishihara 1987, Lachat and Haag-Wackernagel 2016) and insects

(Kastberger *et al.* 2014). Many bird species are known to deter predators by producing distinct mobbing calls and showing stereotypic behaviors (Hurd 1996, Randler and Vollmer 2013). Such mobbing calls usually encourage con- and heterospecifics to join a mobbing flock to harass and chase away a predator (Randler and Vollmer 2013, Suzuki 2016, Dutour *et al.* 2017a). Bird vocalizations can be referential and contain specific information about a predator including its type, size, speed and behavior (Evans *et al.* 1993b, Palleroni *et al.* 2005, Templeton *et al.* 2005, Griesser 2008, Suzuki 2014, Book and Freeberg 2015). Anoaer call type are urgency-based vocalizations, which signal the level of danger posed by a predator (Yorzinski and Vehrencamp 2009, Courter and Ritchison 2010, Suzuki 2015, Carlson *et al.* 2017). However, calls are often not exclusively referential or risk-based but can also contain both information categories (Courter and Ritchison 2010).

Birds have been shown to vary call intensity, syllable duration and number or call type to encode information about predators (Bartmess-LeVasseur *et al.* 2010, Carlson *et al.* 2017) and birds usually respond stronger to more threatening predators (Templeton *et al.* 2005, Soard and Ritchison 2009, Courter and Ritchison 2010). Referential calls often differ in call type or note composition and are used to encode different classes of predators (e.g. aerial and terrestrial) that require different escape strategies. Transmitting more specific information about predators might enable conspecifics to apply an adaptive escape response. Adult Japanese great tits (*Parus minor*) for example show different predator searching strategies after hearing distinct calls that encode predator type (Suzuki 2012, Suzuki 2015) and juveniles adapt their escape strategy according to parental alarm calls (Suzuki 2011, Suzuki and Ueda 2013). Also Siberian jays (*Perisoreus infaustus*) show predator specific escape responses when hearing conspecific alarm calls signaling predator behavior (i.e. searching for prey or attacking) (Griesser 2008). Risk-based calls on the other hand usually evoke a similar anti-predator response, which might differ in response time or mobbing intensity (Leavesley and Magrath 2005, Dutour *et al.* 2016, Cunha *et al.* 2017, Dutour *et al.* 2017b). Japanese great tits, for example, have a longer response latency to sparrowhawk mobbing calls than to other, less threatening, stimuli (Yu *et al.* 2017), which might reduce the risk of getting captured. Carolina chickadees (*Poecile carolinensis*) and black-capped chickadees (*Poecile atricapillus*) approach a speaker closer when hearing calls in response to smaller, more dangerous predators

than when hearing chick-a-dee calls in response to larger, less threatening predators (Templeton *et al.* 2005, Soard and Ritchison 2009).

We recently found that great tits (*Parus major*) produce D calls that slightly vary in the interval between elements as well as in element number according to context (Kalb *et al.* 2019), which is similar to findings by Templeton *et al.* (2005) in black-capped chickadees. Tits produced longer D calls with more elements and longer intervals between elements when confronted with a mount of a life-like sparrowhawk (*Accipiter nisus*) compared to a mount of a tawny owl (*Strix aluco*) (Kalb *et al.* 2019). Sparrowhawk and tawny owl differ in the proportion of great tits consumed in their diet and consequently pose different threat-levels to this species. Sparrowhawks mostly prey on small birds, including great tits (Zawadzka and Zawadzki 2001), whereas tawny owls mainly prey on small mammals, but also have passerines, including great tits, in their diet (Galeotti *et al.* 1991, Ýmihorski and Osojca 2006). Therefore, encoding the threat-level of predators in mobbing calls, which can be recognized by conspecifics and potentially alter their behavior; can be an important precondition for successful predator avoidance. Here, we conducted a playback experiment in great tits to test if mobbing calls of different predatory context (i.e. sparrowhawk and tawny owl) transmit information about predator threat to conspecifics and elicit different behavioral responses. If conspecifics are capable of decoding information about predator threat in mobbing calls, we would expect individuals to have a longer latency time until approaching the speaker in the high-threat context compared to the low-threat context. Further, we would expect great tits to keep a greater distance to the speaker in the high-threat context.

## Methods

We studied great tits within a radius of 15 km of Tübingen, Baden-Württemberg (48°31'N, 9°3'E) in southwest Germany. There was a minimum distance of 200 m (mean  $\pm$  SE: 270 m  $\pm$  25 m) between study sites. We used great tit mobbing calls in response to sparrowhawk (referred to as “sparrowhawk treatment”) and tawny owl (“tawny owl treatment”). Calls were obtained from own recordings (Kalb *et al.* 2019). We used the first five calls of ten different individuals in a mobbing event (tawny owl n=5, sparrowhawk n=5). Songs of common chiffchaff (*Phylloscopus collybita*) (n=2), chaffinch (*Fringilla coelebs*) (n=2) and Eurasian blackcap (*Sylvia atricapilla*) (n=2) were used as a control. Playback of territory song has been shown to increase

singing by conspecifics and heterospecifics suggesting that birds might use song as an indicator for predator absence (Møller 1992). Songs of two individuals per species were obtained from our own recordings in SW Germany (Randler sound archive, unpublished). Thus, great tits were assumed to be familiar with the songs of these species, because they live syntopically and are widespread throughout the study area. Lastly, we used silence as a negative-control. All calls and songs were used in their natural sequence, i.e. the time between calls was not manipulated. We selected mobbing calls with good quality and removed low-frequency noise (below 1 kHz). Calls and songs were edited using Avisoft SASLab Pro 5.12 (Avisoft Bioacoustics e.K., Glienicke/Nordbahn, Germany) and Audacity 2.2.2. Playbacks were broadcast using a portable Bluetooth loudspeaker Ultimate Ears Boom 2 (Ultimate Ears, Irvine/Newark, USA) and a mp3 player AGPTEK A26 (AGPTEK, Brooklyn, NY, USA). Playbacks were broadcasted at about 64 dB (range: 62 - 66.7) measured at one meter from the loudspeaker using a PeakTech 5035 sound level meter (PeakTech Prüf- und Messtechnik GmbH, Ahrensburg, Germany). All stimuli were standardized on ten minutes (observation time). However, we terminated the observations two minutes after the first great tit approached the speaker in a radius of six meters to minimize the stress response of focal individuals.

Before starting a playback session we checked (acoustically and visually) for the presence of great tits within a radius of 30 meters. If a focal individual was detected, we clipped the loudspeaker to a branch on the outer part of a tree approximately two meters above the ground and started the playback. During playbacks, the observer kept a distance of ten meters to the loudspeaker. We measured the latency time for each bird approaching the speaker in a radius of six meters with a stopwatch. The species, sex and age of each bird was determined using binoculars (Nikon ProStaff 7s, 10x42; Nikon GmbH, Düsseldorf, Germany). Further, we noted if birds uttered calls. After the playback the minimum distance (cm) to the speaker of each individual was determined using a folding ruler (two meter radius of the speaker) or by counting steps (2-6 meters radius of the speaker). In total, we made 48 observations (n control= 13, n tawny owl=17, n sparrowhawk =18). During one tawny owl playback, no great tit approached the speaker. During six playbacks, great tits uttered calls, but where more than ten meters away from the speaker and could not be visually detected (tawny owl n=2, sparrowhawk n=4). We excluded those individuals from the analysis as it was not clear if they reacted to the playback or some other stressor

further away. Due to technical difficulties with the loudspeaker we had to terminate two tawny owl playbacks before the observation time was over. We excluded those cases from the data analysis resulting in a final sample size of 39 (n control= 13, n tawny owl=12, n sparrowhawk =14).

### *Ethical note*

This study included no animal keeping; birds were observed in their natural habitat. The study was performed in accordance with relevant laws in Germany and guidelines and regulations for nature conservancy. Field observations were in accordance with the higher nature conservation authority in Tübingen.

### *Statistic*

We used SAS JMP 16 for data analysis and data visualization. We performed ANOVAs including minimum distance and latency time as dependent and treatment and sex as independent variables. We also added location as random factor to the analysis. We used a Likelihood ratio test to investigate if the likelihood of producing mobbing calls is affected by sex or treatment. For the comparison between treatments and sexes, the mean and standard error are given.

### **Results**

No great tit approached the speaker during any of our control playbacks (heterospecific song and silence). Treatment had a significant effect on the latency time ( $F=4.575$ ,  $df=1,23$ ,  $p=0.043$ ). Tits approached the speaker faster in the tawny owl treatment ( $135.6\pm 17.3$ ) than in the sparrowhawk treatment ( $207.4\pm 28.8$ ) (Figure 1). Latency time showed a trend to be affected by sex ( $F=3.76$ ,  $df=1,23$ ,  $p=0.065$ ). Males approached the speaker faster ( $146.4\pm 23.7$ ) than females ( $212.2\pm 26.7$ ).

Minimum distance was significantly affected by treatment ( $F=5.992$ ,  $df=1,23$ ,  $p=0.022$ ). Great tits approached the speaker closer in response to the tawny owl treatment ( $84.8\pm 25.3$ ) than in response to sparrowhawk treatment ( $224.3\pm 48.6$ ) (Figure 1). Sex had no effect on the minimum distance ( $F=1.86$ ,  $df=1,23$ ,  $p=0.186$ ), but males tended to approach the speaker closer ( $126.3\pm 41$ ) than females ( $205.8\pm 47.3$ ).

The likelihood of uttering mobbing calls did not differ between treatments (Pearson:  $X^2=1.192$ ,  $df=1$ ,  $p=0.275$ ) or sexes (Pearson:  $X^2=0.001$ ,  $df=1$ ,  $p=0.976$ ).

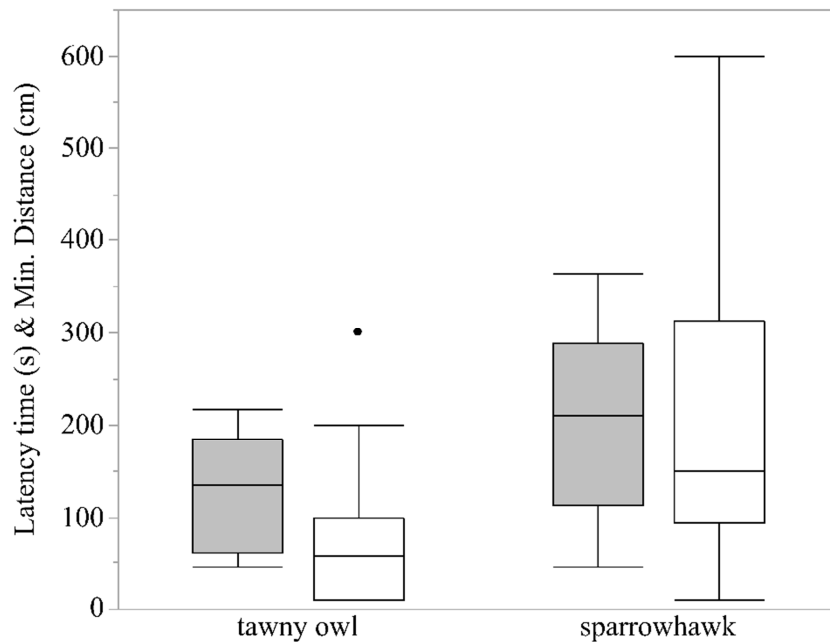


Figure 1: Latency time (s, grey) and minimum distance to loudspeaker (cm, white) dependent on the mobbing call treatment. Latency time and minimum distance were significantly shorter in the tawny owl treatment compared to the sparrowhawk treatment.

## Discussion

We tested if great tits respond differently to playbacks of mobbing calls from two different contexts, i.e. high-threat (sparrowhawk) and low-threat (tawny owl). Great tits approached the speaker faster and closer in the tawny owl treatment than in the sparrowhawk treatment.

It is known from various species that bird calls encode information about predator threat that are transmitted to conspecifics (Lind *et al.* 2005, Suzuki 2012, Suzuki and Ueda 2013, Suzuki 2014, Suzuki 2015, Yu *et al.* 2017). This predatory information in calls can be encoded with distinct call types or fine scale alterations within a call (Templeton *et al.* 2005, Suzuki 2014). Japanese great tits, for example, produce distinct alarm calls in response to different nest predators and adults show predator-searching behaviors adapted to a predator's approaching strategy (terrestrial or aerial) after hearing alarm calls for those predators (Suzuki 2015). It is known that other bird species produce different calls to warn from terrestrial and aerial predators (Evans *et al.* 1993a, Platzen and Magrath 2005). Our study species in contrast seems to use fine-scale differences within one call to discriminate between different threat levels of avian predators. We recently found great tits produce longer D mobbing calls with more elements and longer intervals between elements when confronted with a sparrowhawk mount compared to a tawny owl mount (Kalb *et al.*

2019). Because great tits in our study behaved differently in response to the two treatments, we suppose that they are able to discriminate between different threat levels based on subtle variations in mobbing calls and adapt their behavioral response accordingly. Similar, Templeton *et al.* (2005) found black-capped chickadees to alter the duration of the first D note as well as the interval between the first and second D note according to predator threat and conspecifics react differently to playbacks of calls provoked by different predators. Hence, future studies are needed to investigate if such fine-scale alterations in anti-predator vocalizations are more widespread in passerines and how they might be used during inter- and intraspecific communication.

That tits stayed farther away from the speaker in the sparrowhawk treatment is contradictory to findings in black-capped chickadees, which approach a speaker closer in response to mobbing calls towards more dangerous predators (Templeton *et al.* 2005). Nevertheless, Curio *et al.* (1983) found that great tits have a greater minimum distance when confronted with a sparrowhawk than when seeing a tawny owl. Therefore, Curio *et al.*'s (1983) results are in line with ours, which suggests that the responses may be either species-specific or predator specific, because different predators (to ours) were used in the North American context (Templeton *et al.* 2005). Hogstad (2017) showed that tits have a longer latency time to return back to a feeder after seeing a sparrowhawk dummy than after seeing a less-dangerous Siberian jay (*Perisoreus infaustu*) or a non-threatening three-toed woodpecker (*Picooides tridactylus*). These and our results combined suggest that great tits, in contrast to other species, might use a “better safe than sorry” strategy, i.e. stay farther away from high-threat predators to reduce predation risk during mobbing.

We found a trend for males to approach the speaker faster and closer than females, which is in line with findings by Curio (1983) who found males to approach predators closer than females. In addition, a study by van Oers *et al.* (2005) showed that female great tits take longer to return to feeding after being startled when being with a male, but males decrease their latency time when being accompanied by another male. Hence, similar to other species (Griesser and Ekman 2005, Hogstad 2017) great tit males might be willing to take higher risks in a predation context than females. This might be explained by males being more territorial and therefore the habitat is of higher value for the male than the female (Regelmann and Curio 1986).



Another explanation could be that males often have lower annual mortality than females leading to a skewed sex ratio and a good proportion of males being unmated (Curio and Regelmann 1982, Payevsky 2006). Hence, males might take a higher risk to protect females in their territory (Regelmann and Curio 1986) or to signal male quality to conspecifics.

We showed that great tits discriminate between conspecific mobbing calls provoked by two common predators, sparrowhawk and tawny owl, that greatly differ in predation threat. Tits kept a greater distance to the loudspeaker and had a longer latency time when hearing mobbing calls of the high-threat context. Furthermore, males tended to take higher risks than females, which indicates that, in addition to predator threat, sex might affect the mobbing behavior in this species.

### **Data accessibility statement**

The datasets generated and/or analyzed during the current study will be available on the Dryad data repository after acceptance for publication.

### **Competing interest statement**

The authors declare no competing interests.

### **Author contribution**

N.K. and C.R. designed the experiment, N.K. collected the field data and did the statistical analysis. Both authors contributed to the writing of the paper and approved its final stage.

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## **Chapter 3**

### **Do great tits alter their calling behaviour according to context?**

Kalb, N., F. Anger & Randler, C.: Great tits encode contextual information in their food and mobbing calls.

## Great tits encode contextual information in their food and mobbing calls

Running head: Great tit calls are context dependent

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### Abstract

The calling behavior of Paridae species (titmice, tits and chickadees) in a predator related context is well-studied. Parid species are known to alter call types, note composition or call duration according to predation risk. However, how these species encode information about a non-threatening context, such as food sources, has been subject to only few studies. Studies in Carolina chickadees (*Poecile carolinensis*) have shown that this species alters the ratio of C and D notes to encode information about the presence of food and/or the flight behavior of the signaler. This suggests that parids also use graded signals to encode information about non-predatory contexts. No study to date has directly compared the calls of a feeding context with those of a predation (i.e. mobbing) context. Hence, the aim of our study was to compare the calling behavior of these two situations in great tits (*Parus major*). We recorded and analyzed calls uttered at a feeder and compared them to calls uttered in front of taxidermy mounts of sparrowhawks (*Accipiter nisus*). In the food context, great tits reduced the number of D notes and increased the number of B, C and E notes compared to the mobbing context. Furthermore, tits produced calls with longer D notes and shorter intervals between D notes than in the mobbing context. This indicates that great tits use two mechanisms of graded signals (i.e. note type and acoustic structure of D calls) to inform conspecifics about the nature of a situation.

**Keywords:** social communication, *Parus major*, mobbing, food associated vocalizations

### Introduction

There is a growing body of research about if and how animals use vocalizations to encode information about their environment (reviewed in Ey and Fischer 2009). Calling behavior is especially well studied in a predation context across various taxa.

However, calling can hold costs as it can for example increase predation risks by revealing the location of the caller or nest to the predator (Denson 1979, Curio and Regelman 1986, Sordahl 1990, Krams 2001, Krams et al. 2007). Nonetheless, producing anti-predator vocalizations can also be beneficial as it might drive the predator away, warn conspecifics or signal the predator that it has been detected and consequently decrease its hunting success (pursuit deterrent signal) (Pettifor 1990, Flasskamp 1994, Kobayashi 1994). Consequently, even if calling might hold costs, transmitting information about the environment to con- and heterospecifics can increase the (long-term) fitness of the caller. Information can be encoded referentially or graded. Referential calls are discrete calls and transmit information about an event (e.g. predation) or object (e.g. food) and thereby enable the receiver to show an appropriate behavioral response without any additional cues (Macedonia and Evans 1993). Many studies have shown that animals use referential calls in various situations. In mammals, calls are used in a predation context, after food discovery and during social interaction (Townsend 2013). Vervet monkeys (*Cercopithecus aethiops*) for example produce different alarm calls for leopards (*Panthera pardus*), eagles and snakes whereby each alarm call elicits a predator-specific response (Seyfahrt et al. 1980). Red squirrels (*Tamiasciurus hudsonicus*) (Greene and Meagher 1998) and suricates (*Suricata suricatta*) (Manser 2001, Manser et al. 2001) produce distinct calls for terrestrial and aerial predators. Marmosets (*Callithrix geoffroyi*) produce distinct food calls and increase feeding and foraging rates after hearing such calls (Kitzmann and Caine 2009). In birds, Japanese great tits (*Parus minor*) produce distinct calls in response to rat snakes (*Elaphe climacophora*), jungle crows (*Corvus macrorhynchos*) and martens (*Martes melampus*) (Suzuki 2011, 2013). Further, fledglings (Suzuki 2011) and adults (Suzuki 2012a, 2015) show different antipredator behaviors after hearing such calls. Some species, such as the domestic chicken also use referential calls in a food-associated context (Evans and Evans 1999).

In contrast to referential signals, graded signals do not use different call types, but changes in calling rate or call structure to encode information. Many birds and mammals for example change calling rate in a food- or predator related context (Elowson et al. 1991, Brown et al. 1991, Hauser and Marler 1993, Blumstein 1995, Randler and Förschler, 2011, Carlson et al. 2017). Great tits (*Parus major*) increase calling rate when predation risk increases (Lind et al. 2005, Carlson et al. 2017),

whereas crested tits (*Parus cristatus*) adjust the calling rate of their calls to changes in habitat safety (Krama et al. 2008). Besides calling rate, birds have been shown to alter the duration of notes or interval between notes (Templeton et al. 2005, Kalb et al. 2019) as well as call propensity or the proportion of different call types or a combination of those parameters to encode information about predator threat (Bartmess-LeVasseur et al. 2010, Carlson et al. 2017). Tufted titmice (*Baeolophus bicolor*) and black-capped chickadees (*Poecile atricapillus*) produce calls with more D notes in front of more threatening predators (Courter and Ritchison 2010, Templeton et al. 2005), and Carolina chickadees (*Poecile carolinensis*) alter the ratio of “chick” and “dee” notes according to predation risk (Soard and Ritchison 2009). Great tits alter the number of D notes as well as the interval between them to discriminate between two common predators (Kalb et al. 2019). During playback experiments, great tits responded differently concerning different call rates and D call structure (Randler 2012, Kalb et al. 2019), suggesting that graded signals convey information about the urgency of a threat. In chaffinches (*Fringilla coelebs*), con- and heterospecifics responded with a nearer approach when confronted with the same call when play backed in a higher duty cycle (Randler and Förschler, 2011).

While the acoustic structure of predator-related calls is well-studied, studies on the acoustic structure of food-associated calls are rather scarce. Chimpanzees (*Pan troglodytes*) have been shown to alter the acoustic structure of food calls according to food preference with highly preferred foods eliciting longer calls with higher peak frequencies (Slocombe and Zuberbühler 2006). In birds, most studies focused on the proportion of different call or note types in a feeding context. Willow tits (*Poecile montanus*) for example use calls of a single note type in a food context and combine two distinct call types in a non-food context (Suzuki 2012b). Moreover, a playback study revealed that calls from a feeding-context attract con- and heterospecifics and hence most likely serve a recruitment function (Suzuki 2012c). The chick-a-dee call of the genus *Poecile* consists of up to four note types (A, B, C and D) and birds seem to encode information by altering the note composition and repetition of note types (Hailman and Ficken 1986). Black-capped chickadees for example produce chick-a-dee calls when finding a food source to attract flock members (Ficken 1981). Carolina chickadees produce calls containing a high proportion of C notes after finding food and are more likely to visit a feeding station after hearing playbacks with a large number of C notes (Freeberg and Lucas 2002). Mahurin and Freeberg (2008) in



contrast showed that Carolina chickadees in another population that initially found a food source produced calls with a higher number of D notes before a second individual arrived and birds arrived faster at a feeding site after hearing calls with a greater number of D notes.

Since both, antipredator behavior and finding food are essential for an individual's fitness, but significantly differ in their nature (i.e. dangerous vs. non-dangerous), it would be beneficial for birds to encode contextual information in their calls. However, to our best knowledge, no study to date has directly compared calls from a feeding context with calls from a predation context. Hence, the aim of this study was to examine if the calls of great tits in a mobbing context differ from those in a feeding context. Based on previous work discussed in the introduction we hypothesized that the proportion of call types uttered in a mobbing context differs from calls in a feeding context. We recently found great tits to alter the duration of D calls as well as the number of elements and the interval between them according to different predatory contexts. (Kalb et al. 2019). Therefore, we expected tits to also alter the acoustic structure of D notes between the mobbing and the feeding context. We recorded calls of wild great tits in two experimental situations (presentation of food or a predator mount) to test our hypotheses.

## **Material and methods**

### *Study species and sites*

All experiments were conducted on wild great tits (*Parus major*) in the vicinity of Tübingen, (48°31'N, 9°3'E) and Rottenburg am Neckar (48°28'N, 8°56'E), Baden-Württemberg in southwest Germany. The study was performed outside the breeding season in January – March (2017, 2018, 2019) and August – December (2017, 2018). We never visited the same location twice and stimuli presentations were always separated by a minimum distance of 214 m (mean  $\pm$ SE, 439.76 m  $\pm$  59.32 m). In this area the density of great tits is very high, e.g. at the Spitzberg between Tübingen and Rottenburg, there are about 370 to 390 pairs on 623 ha (Gottschalk and Randler 2019). Hence, even though great tits in our study were not individually ringed, the likelihood of testing an individual twice was low. Since birds could not be individually identified we further presented only one stimulus per site (food, sparrowhawk or green woodpecker (*Picus viridis*) mount) and treated each location as independent sample unit. Observations took place between 07:30 and 16:00 CET

to allow birds to recover from or prepare for the night to reduce the stress on birds. During all trials the observer kept a minimum distance of eight meters to the stimulus. Calls were recorded with a digital recorder (Marantz professional PMD661MKIII, inMusic GmbH, Ratingen, Germany) connected to either a boundary (Marantz professional, in Music GmbH, Ratingen, Germany) (food calls and mobbing calls) or a shotgun microphone (Elektret K6/ME66, Sennheiser electronic GmbH, Wedemark, Germany) (food calls in 2017 and January-March 2018).

### *Predator context*

We used two different mounts of sparrowhawks (*Accipiter nisus*) to elicit mobbing calls to reduce pseudo-replication. We always used only one sparrowhawk mount per site. We placed the mounts on tree trunks, fences or rocks approximately 150-200 cm above the ground. Sparrowhawks are common predators on small songbirds (Zawadzka and Zawadzki 2001) and breed widespread in this area, with a total of 10-20 pairs in the surrounding (personal observation). Furthermore, great tits are known to have lower body masses and reduce feeding periods when sparrowhawks are abundant in the area (Hinsley et al. 1995, Gosler et al. 1995, Krams 2000). Hence, great tits seem to perceive sparrowhawks as high-threat predators, which makes them well-suited for our study to provoke mobbing calls.

We noted the location, mount identity and time at the start of each recording. The microphone was placed next to the mount and recordings started immediately after setting up the equipment. We terminated recordings ten minutes after great tits arrived at the study location, in cases where no great tit participated in mobbing, we terminated the observation after 30 minutes. The observer noted the number of conspecifics in a radius of five m around the taxidermy mount. In total, we conducted predator presentations at 29 different locations.

### *Food calls*

Two weeks prior to sound recordings, we placed a hanging feeder in a tree two to three meters above the ground. We used ten different pvc feeders, all from the same type (dobar Art. 7948357, Germany). We stocked each feeder with black oil sunflower seeds every four to five days to get the birds accustomed to the feeders as an irregular food source.

Upon recording, the feeder was fully stocked, and the recording equipment was set up. Recordings started immediately after setting up the equipment and were terminated 30 minutes after the first great tit visited the feeder. In cases where no great tit visited the feeding station, recordings were terminated after 60 minutes. The observer noted whether a great tit visited the feeder and whether it called or not. Further, if a great tit visited the feeder we noted the number of conspecifics in a radius of five meters around the feeder. In total, we installed feeders at 35 independent locations, but only in 24 of those locations we observed great tits at the feeder taking at least one sunflower seed. At 18 locations great tits called while visiting the feeder.

### *Control experiments*

To test if great tits respond to our specific stimuli (i.e. food or sparrowhawk) or simply utter calls in response to the presence of any stimulus, we additionally confronted them with two mounts of European green woodpeckers (*Picus viridis*) as a negative control at 16 independent locations. For woodpeckers we always used only one mount per site. We placed the mounts on tree trunks, fences or rocks approximately 150-200 cm above the ground. The population density of the green woodpecker is even higher than that of the sparrowhawk with an estimate of 50-100 pairs (see Gottschalk & Randler 2019 (Spitzberg area), Randler unpublished data (Weggental/Rottenburg)). Green woodpeckers are well known and overlap in their habitats with great tits but pose no danger nor are they competitors for food because green woodpeckers mainly feed on ants (usually *Lasius spec.*) (Glutz von Blotzheim 1971).

### *Permission to carry out fieldwork*

The study was conducted in accordance with the higher nature conservation authority in Tübingen and therefore not required to complete an additional ethical assessment prior to conducting the research.

### *Call analysis*

Files were analyzed using Avisoft SASLabPro with a sample rate of 44.1 kHz. First, we created sonograms using the Hamming window function, FFT length 512, Frame size 100 % and 75 % overlap and determined the calls produced in the respective contexts (feeding and mobbing). Because, to our best knowledge, there is no specific description of note types used during mobbing and feeding for great tits, we used the

description of note types in a closely related species, the Japanese great tit (*Parus minor*) as a guideline to classify notes (Yu et al. 2017). Furthermore, we counted the number of notes per call. We evaluated the first three minutes after great tits started to utter calls.

We created a second sonogram (Hamming window function, FFT length 1024, Frame size 25 % and 98,43 % overlap) to perform more fine scale measurements of the first five D calls, i.e. the duration (s) of calls and notes within a call as well as the interval (s) between notes. For this analysis, we evaluated only those calls that were recorded with the omnidirectional microphone to exclude any effects of the recording equipment on the measured call features.

### *Statistic*

We conducted principal component analyses (PCA) to analyze the acoustic features of calls composed of D notes. Two of the four principal components had an eigenvalue greater than one (PC1: 1.998, PC2: 1.61) and hence complied with the Kaiser' criterion (Kachigan 1991). PC1 and PC2 explained 88.8 % of the total variance. We used factor scores derived from the PCA as acoustic features of the D calls for further analysis. We conducted ANOVAs including PC1 and PC2 as response variable and context as well as number of great tits and heterospecific individuals as fixed factors. For all tests we used a significance level of  $\alpha=0.05$ . For comparison between context the mean and the standard error are given.

### **Results**

In 20 out of 29 locations, great tits participated in mobbing. However, in four locations, great tits did not produce mobbing calls. During all control experiments (n=16), great tits were present in a radius of 10 meters around the woodpecker mounts. However, tits did not approach the control within a radius of 5 meters nor did they utter calls. In the mobbing and food context, we recorded nine different note types (Figure 1). As great tits did not call during control trials but responded to food and the sparrowhawk mount, we conclude that great tits reacted to the specific stimulus (i.e. food or predator) rather than just the presence of any stimulus.

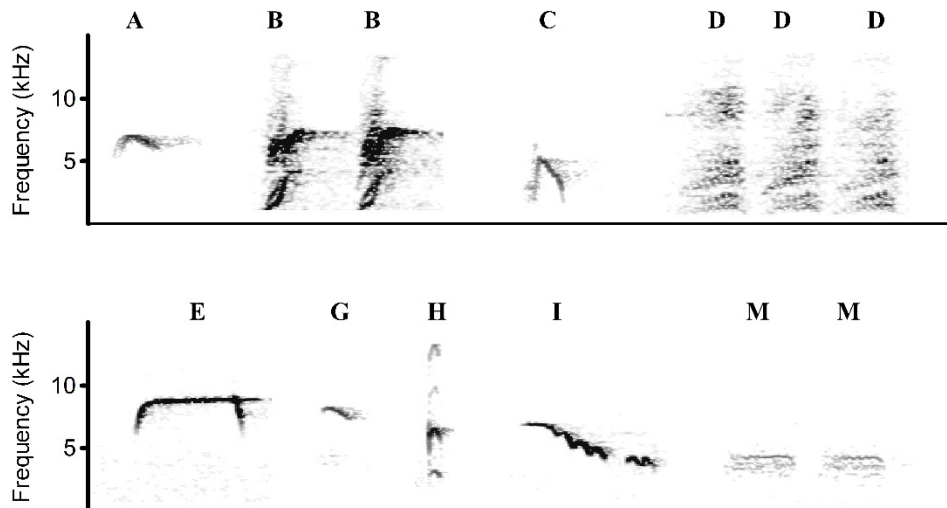


Figure 1: Spectrogram illustration of the nine different note types great tit produced during mobbing or feeding. Hamming window function FFT length 512, Frame size 100 %, 75 % overlap. Noise below 1 kHz was removed.

The proportion of note types given by great tits differed significantly between contexts (Likelihood Ratio  $X^2=287.28$ ,  $df=8$ ,  $p<0.0001$ ). Among the six note types given in both context, D notes were the most common ones (Table 1). In the mobbing context, great tits produced mainly D notes and small percentages of A, B, C, E and I notes. G, H and M notes were solely produced in the food context. Further, great tits produced a smaller percentage of D notes and an increased percentage of A, B, C and E notes compared to the mobbing context (Table 1). Call rate (calls/minute/individual) was significantly affected by context ( $F=42.544$ ,  $df=1,1$ ,  $p<0.0001$ ) and the number of conspecifics ( $F=10.027$ ,  $df=1,1$ ,  $p=0.004$ ), but not the number of heterospecific individuals ( $F=1.232$ ,  $df=1,1$ ,  $p=0.2766$ ). Great tits produced more calls per minute in the mobbing context ( $16.62\pm 2.84$ ) than in the food context ( $3.25\pm 0.73$ ).

Table 1: percentages of note types uttered by great tits in response to food and sparrowhawk.

	Food	Mobbing
A	3.83	0.44
B	15.74	9.05
C	13.19	0.38
D	41.7	85.42
E	14.47	4.02
G	0.85	0.00
H	2.13	0.00
I	5.11	0.69
M	2.98	0.00

In respect of acoustic features, we found a significant difference between contexts. PC1 explained 49.9% of the total variance and correlated strongly with the number of D notes in a calls and call duration. PC2 explained 40.3 % of the variance and correlates strongly with both, note duration and interval between notes (Table 2).

Table 2: Eigenvalues, explained variances and loading of the mean acoustic measures of D notes on the two PC factors.

	PC1	PC2
Eigenvalue	1.997	1.61
% variance	49.927	40.259
Number of D notes	<i>0.964</i>	0.17
Note duration	0.339	<i>-0.842</i>
Call duration	<i>0.972</i>	0.213
Interval between D notes	-0.094	<i>0.91</i>

Loadings in italic are larger than 0.50 or smaller than -0.50 (italic parameters have a strong relationship with the respective PC component)

According to the loading coefficients, high scores of the principal components translate into a stronger response (i.e. high number of notes, longer calls, longer notes and intervals between notes). The PC2 scores were significantly affected by context ( $F=30.52$ ,  $df=1,1$ ,  $p<0.0001$ ) whereas PC1 scores were not ( $F=0.019$ ,  $df=1,1$ ,  $p=0.9653$ ). None of the PC scores were affected by number of great tits or heterospecifics (all  $p>0.2$ ). Great tits produced calls with longer D notes and shorter intervals between notes in the food context compared to the mobbing context (Figure 2, Table 3). Mean call duration and mean number of notes did not differ between contexts (Table 3).

Table 3: Mean values  $\pm$  SD of four acoustic parameters of D calls in response to food and a sparrowhawk mount.

	Food	Mobbing
Number of D notes	6.95 $\pm$ 0.434	7.13 $\pm$ 0.467
Note duration	0.05 $\pm$ 0.002	0.039 $\pm$ 0.002
Call duration	0.507 $\pm$ 0.033	0.541 $\pm$ 0.042
Interval between D notes	0.028 $\pm$ 0.002	0.042 $\pm$ 0.008

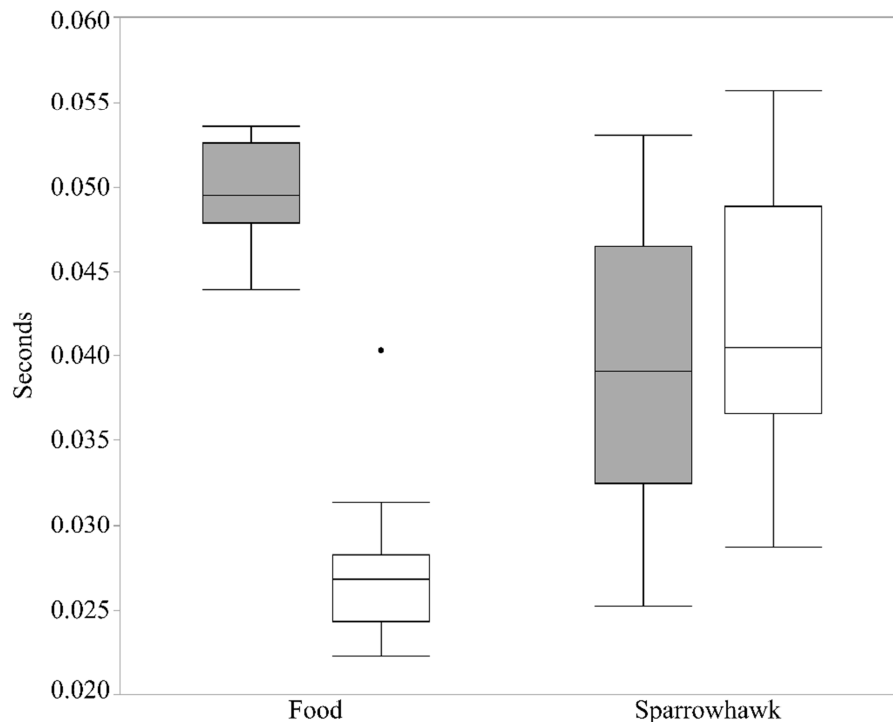


Figure 2: Mean duration of D element (grey boxplots) and interval between elements (white boxplots) in seconds. D calls in response to food have longer elements and shorter intervals between elements than D calls in response to a sparrowhawk mount.

## Discussion

Great tits are monogamous birds living in pairs during breeding season, but form flocks consisting of adults and non-related juveniles of both sexes during the non-breeding season (Saitou 1978, Ekman 1989). While being in a flock might reduce access to food due to competition, it can hold the benefit of reduced predation risk and an increased likelihood of food detection, as more eyes most likely detect both, an approaching predator and food resources faster than a single individual. Nonetheless, those possible advantages require sufficient communication between flock members about the environment. By encoding information in vocal signals, flock members are able to communicate with each other and coordinate their behavior such as mobbing (Randler and Vollmer 2013) or foraging (Elgar 1986).

In our study, we found a significant difference between calls of a food-associated and mobbing context. Great tits produced mostly D notes and a small percentage of other notes in the mobbing context. In the feeding context in contrast, great tits decreased the proportion of D notes and increased the proportion of other notes. This suggests that the ratio of D notes to other notes might be used to differentiate between mobbing and feeding situations. Great tits produced significantly more D calls in the mobbing context than in the feeding context, which is in line with previous findings in parids where calling rate and the proportion of notes changes with increasing predator threat (Carlson et al. 2017, Templeton et al. 2005). Additionally, great tits in our study produced a small proportion of G, H and M notes solely in the feeding context, indicating that note composition might convey information about food availability.

Even though in our study, G, H and M notes solely occurred in the food-associated context we would not claim them to be signals exclusively used in a food context by great tits. Japanese great tits, a closely related species, are known to produce those notes also in a predation context (Yu et al. 2017). Hence, we assume that great tits also might use those note types in a mobbing context that differs from the situation simulated in our study, e.g. when confronted with a different predator than the sparrowhawk.

Similar to our results, Freeberg and Lucas (2002) found Carolina chickadees to produce calls containing a higher proportion of C notes when detecting a food source. Moreover, birds approached a feeder more frequently after hearing C-rich playbacks than after hearing calls containing no C notes (long D-calls), indicating that C notes might convey information about the presence of food. However, a second study in a different population of Carolina chickadees found individuals to produce more D notes when first finding a food source, suggesting that D notes in this species have a general recruitment function (Mahurin and Freeberg 2008). Results of a second study in the same population suggested that C notes are associated with flight, as birds that were flying (e.g. to and from a feeder) produced more C notes than when e.g. sitting on a perch (Freeberg and Mahurin 2013). Freeberg and Mahurin suggested that these varying results might be explained by D notes being recruitment calls and C notes stimulating flight behavior in receivers, which are in turn more likely to find food as they move through the environment. This might also be an



explanation for our results, as in a feeding context, birds moved from and to the feeder, resulting in a higher proportion of C notes. In the mobbing context, in contrast, birds were more restricted to the area around the taxidermy mount and tried to recruit con- and heterospecifics, resulting in an increased D call production. Hence, we propose that great tits might be able to gain contextual information about the nature of a situation by the ratio of D to other notes. While e.g. few to no C and E notes and a high number of D notes might encode a predation context, a more balanced ratio of E and C notes and fewer D notes might encode the presence of food. Playback studies are crucial to determine if great tits alter their behavior in response to conspecific calls of a food and mobbing context. Here, future studies might alter the ratio of notes and measure the latency time until great tits arrive at a feeding station, similar to the study by Freeberg and Mahurin (2008, 2013).

In addition to variation in note types, great tits in our study might have gained additional information by subtle variations in D calls as they significantly differed between contexts. Food-associated calls had shorter intervals between notes than mobbing calls. That mobbing calls have longer intervals compared to food-associated calls is similar to findings in great tits, showing that tits have longer intervals in response to sparrowhawks than when seeing a less dangerous tawny owl mount (Kalb et al. 2019). Templeton et al. (2005) also found black-capped chickadees to alter the interval between the first and second D note, whereby the interval was shorter in response to more dangerous predators. This indicates that a variation in the interval between notes might be used by various passerine to encode information about different context and more studies are needed to investigate if and how this mechanism is used during communication. Great tits seem to be able to recognize such subtle variation in mobbing calls as they behave differently when hearing conspecific mobbing calls provoked by different predators (Kalb and Randler 2019).

Moreover, we found food-associated calls to have longer notes than D calls in response to the sparrowhawk mount. This is in contrast to findings in black-capped chickadees which decrease the duration of the first D note when confronted with smaller, more dangerous predators (Templeton et al. 2005). Nonetheless, this is most likely explained by the fact that in Templeton's study, also the number of notes and call duration increased when the note duration and interval between notes decreased. In our study, however, call duration and number of notes did not differ. Further, a previous study in great tits comparing mobbing calls in response to two

predators did not find a variation in note duration (Kalb et al. 2019). This suggest that great tits might use D note duration to discriminate between a predation and a non-predatory context (e.g. feeding) and note number, interval between notes as well as calling rate is used to encode information about threat-level (Carlson et al. 2017, Templeton et al. 2005, Kalb et al. 2019). However, a playback study which experimentally manipulates those parameters is necessary to test this assumption.

We showed that great tits alter the fine-scale acoustic structure of D calls according to different context. Moreover, the proportion of notes differed between a food associated and a mobbing context, which indicates that tits, similar to other species, might use the ratio of notes to discriminate between different contexts. Future studies are needed to determine if also other parids use these mechanisms of encoding information and further, if con- and heterospecifics alter their behavior in response to such calls.

### **Ethics**

The study was not required to complete an ethical assessment prior to conducting the observations. It was performed in accordance with relevant guidelines and regulations for nature conservancy in Germany (§44 Abs. 1 Nr. 2 BNatSchG) and adhered to the Guidelines for the Use of Animals in Research of the Animal Behavior Society/Association for the Study of Animal Behaviour.

### **Data accessibility statement**

The datasets generated and analyzed during the study is available on the Dryad data repository after acceptance for publication (doi:10.5061/dryad.h7k7551).

### **Competing interest**

All authors declare no conflict of interest.

### **Author contribution**

NK and CR designed the experiments, NK and FA collected the field data. NK analyzed the bioacoustics results and did the statistical analysis. All authors contributed to the writing of the paper and have approved its final stage.

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