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**Responses of Blue Tits (*Cyanistes caeruleus*) and Great  
Tits (*Parus major*) to con- and hetero-specifics alarm  
calls**

Master thesis

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Annotation:

I conducted analyses of the responses of Blue Tits and Great Tits to familiar and unfamiliar Titmice species using playbacks of alarm calls of Blue Tit, Willow Tit, Black-capped Chickadee and Varied Tit at the winter feeder in Branišovský forest, near České Budějovice.

I declare that I am the author of this qualification thesis and that in writing it I have used the sources and literature displayed in the list of used sources only.

České Budějovice, 10/04/2021.

A handwritten signature in black ink that reads "Mónica Romero". The signature is written in a cursive style with a horizontal line striking through the middle of the name.

Mónica Patricia Romero Cueva

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## INTRODUCTION

### *Alarm calls*

Animal communication systems have been studied extensively to understand how they transmit information using signals to individuals of the same or different species (Sekhar Dash, 2017). Communication is socially designed to impact receiver's behaviour, but their perspective can change fundamentally the meaning and function of the signals (Seyfarth & Cheney, 2003). The information the receiver gets from a call is stored in its memory and in combination with some acoustic features, it can respond to subsequent vocalizations (Seyfarth et al., 2010). Studies examining the evolution of calls compare two opposing points of view that have emerged regarding animal communication: that signals are used to transmit information between senders and receivers, and that they are used to control receiver behaviour (Hollén & Radford, 2009).

An ideal system for studying animal communication is vertebrate alarm calls (Evans, 1997). Alarm calling, i.e. emitting of certain vocalizations in the face of imminent danger, is an important strategy for warding off predators that has evolved in a variety of species (Caro, 2005). Alarm calls of vertebrates are often classified as "flee" alarm calls, associated with immediate escape, or "mobbing" alarm calls, associated with individuals approaching to monitor or ward off a potential predator (Leavesley & Magrath, 2005). Alarm call behaviour involves three aspects: the emission of calls with a specific set of acoustic features (call production); the use of calls in specific contexts (call use); and the response to calls produced by others (call responses) (Hollén & Radford, 2009).

There is a selfish selection pressure between the callers and the receivers, while the receivers have more probability to escape and survive responding to the alarm calls, the caller may attract predator's attention to it (Simmons et al., 2003). This relationships between the caller and the receiver divide the alarm calls in categories where both can have a mutual profit, just one profits and the other is not harmed or one profits harming the other (Caro 2005). For example, Arabian Babblers (*Turdoides squamiceps*) have one or two "sentinels" that can detect potential danger in greater distance. They are usually on the top of the trees while the other members of the flock are foraging. When the sentinels detect the predator, they display the alarm calls earlier than the foraging members and advise them about the danger. This behaviour is beneficial for the foraging members but is dangerous for the sentinels (Seyfarth & Cheney, 2003). An important

component of animal's fitness is the ability to avoid predation (Devereux et al., 2006). The communication system between caller and receiver have been helpful to be aware of the predator threat.

Predation highly contributes to animal mortality, and the persistent threat of predation has a greater impact on behaviour in many species (Digweed, 2019). The most obvious effect that predators have on prey animals is related directly with killing, but they can have non-lethal effects (Santema et al., 2019). The responses of preys to predators' risk can be morphological, or behavioural, including changes in the habitat use, vigilance, foraging, aggregation, movement patterns and sensitivity to environmental conditions (Creel & Christianson, 2008). Displaying alarm calls can be costly, it can increase the chances of predators to detect preys (Klump & Shalter, 1984) but signals can also be used to manipulate predators and possibly scare them off themselves. Prey species sometimes produce vocal signals that actually draw a predator's attention (Digweed, 2019). Signals should be sufficient to permit the receivers to respond correctly to the alarm call (Evans, 1997). There are some factors that determine the detection of a call (Brown et al., 1979): amplitude of the signal at the sound source, environmental characteristics, distance between the signal and the receiver, the ability of the receiver to discriminate the background, and auditory sensitivity of the receiver. Preys are able to generalize some predator traits and identify a novel predator that share similar "predatory features" with known predators (Carlson, Healy, et al., 2017b).

### ***Information coded in alarm calls***

Alarm calls potentially provide different information about predators (Leavesley & Magrath, 2005). Preys may emit alarm calls that encode information about the nature of the predators or the dangers they pose to the prey (Ha et al., 2020). Alarm calls can provide information about a predator's size, speed, distance, type/category and even behaviour (Slobodchikoff, 2009). But even with all the information that preys can get from the antipredator vocalizations, they often have a variety of different predators with different kinds and levels of threat. The level of threat a predator poses can also vary with predator features, seasons, or between different times of day (Carlson, Pargeter, et al., 2017).

Some bird species can indicate the presence of a higher threat predator by increases in: (1) call rate, (2) the number of elements in their calls, (3) the propensity to produce

particular call types, and (4) the proportion of one call type used (Carlson, Healy, et al., 2017a). Species vary substantially in the ways they encode information about predators, they can use multiple ways of encoding information, i.e. Meerkats (*Suricata suricatta*) increase call rate with a number of acoustic parameters to communicate an increase in the danger a predator poses (Manser, 2001). Moreover, some strategies may be driven entirely by the internal state of the caller, while others may refer to external stimuli (Gill & Bierema, 2013). The use of longer calls and higher call rate signals increased danger, the calls can indicate not only predator type (leopard, hawk, snake) but also the degree of danger through the increase in the number of elements (Carlson, Healy, et al., 2017a). Morton (1977) predicted, that harsh, low-frequency sounds indicate aggressive motivations, while tonal, high-frequency sounds indicate pacification or fear. If a signal rises in frequency it represents a decrease in hostility and an increase in pacification or fear, and if it decreases in frequency represents an increase in hostility.

Variations in alarm calls could also be random with no biological function, or it could occur in response to animal's environment. For example, an animal might vocalize more loudly to overcome the masking effects of the background “Lombard effect” (Brumm & Zollinger, 2011). Acoustic signals include modification of caller’s morphology and physiology to ensure the communication taking into account the physical and energetic limitations that allows it to transmit the information and be detected by the intended receiver (Simmons et al., 2003). Acoustic signals can be transmitted over relatively long distances which expands the area over which a signal can be detected, but also increases the probability of multiple callers producing a signal at the same time (Wilson et al., 2016).

### ***Bird alarm calls***

Birds have been extensively used to study and understand antipredator behaviour, they have well-developed hearing, and many species are able to recognize the vocalizations of predators, the sounds predators make moving through their environment, and the warning signals of conspecifics or heterospecifics (Templeton & Greene, 2007). The foraging behaviour in birds can affect the ability to acquire information, i.e. in mixed-species foraging flocks, species that feed high in the canopy respond less to alarm calls than species that forage on the ground (McLachlan et al., 2019). Birds reduce foraging efficiency to spend more energy reducing immediate predation risk (Creel & Christianson, 2008). However, this usually leads to foraging in areas or in ways that

reduce longer term survival or general resource levels available for reproduction. Foraging have special importance in winter, when food resources are poor (Cresswell, 2008).

### ***Heterospecific alarm calls***

To escape immediate predation risk birds can gain information individually observing a predator, or socially using other's signals and cues (Santema et al., 2019). Using other's aerial/flee alarm calls can help them, especially when they cannot detect the predator. Birds mostly use conspecific alarm calls (familiar calls produced by individuals of the same species), that are usually driven and maintained by kin selection, to detect predators, although studies have demonstrated that they can also respond to heterospecific alarm calls (unfamiliar calls produced by individuals of different species), especially in mixed bird flocks. Mixed-species flocks are considered to be an adaptation that reduce the risk of predation (Goodale & Kotagama, 2008), studies have shown that birds in these flocks listen to other species' aerial alarm calls, and these complex interactions between different species is called eavesdropping (Carlson et al., 2020).

Playback experiments have confirmed that eavesdropping on heterospecifics occurs, among both closely and distantly related species. (Magrath, Haff, Fallow, et al., 2015). For example, common ravens (*Corvus corax*) respond to a closely related species alarm calls as Eurasian Jay (*Garrulus glandarius*), and to distantly related species as the blue jay (*Cyanocitta cristata*) (Davidková et al., 2020). Response to heterospecific alarm calls can be innate because they share similar acoustic features, or learned because they share predators (Magrath et al., 2009). For example, Swamp sparrow (*Melospiza georgiana*) and Song sparrow (*Melospiza melodia*) respond strongly to each other's alarm calls which are alike in structure, but their responses are weak to White-throated sparrow (*Zonotrichia albicollis*), whose calls differ in some properties (Stefanski & Falls, 1972). Red-breasted nuthatches (*Sitta canadensis*) respond to variations of the "chick-a-dee" alarm calls produced by Black-capped Chickadees (*Poecile atricapillus*) (Templeton & Greene, 2007).

### ***Alarm calls in titmice***

Tits (family Paridae) have been widely used to study birds' behaviour and their responses to familiar and unfamiliar alarm calls (Gibb, 1954). Studies in some Paridae species suggest that they learn to recognize their own calls and generalize them to other



unfamiliar calls that are acoustically similar (Dutour et al., 2017). Their calls are structurally complex and often consist of multiple distinct elements produced in specific order. Great Tits produce “jar” calls specifically for snakes and “chicka” calls for other predators such as crows and martens (Suzuki, 2016). The alarm calls given by tits to hawks is a great example of signal design that help us to understand the significance of acoustic similarity of heterospecific calls (Marler, 1955). Studies have shown that alarm calls of many European birds, often given to hawks, are similar in structure between species and that their high pitch (approx. 6–9 kHz) and narrow band-width make these calls difficult for hawks to hear and locate (Klump, 2000).

In North America, one of the principal sentinels in mixed-species flocks are Black-capped Chickadees, they are able to transmit complex information about the predators. They produce two different alarm calls: “seet” alarm call, a high-frequency and low amplitude alarm call in response to flying raptor, and a loud, broad-band “chick-a-dee” call composed of several syllables in response to a stationary predator. Between 24 to 50 different species are known to respond to its chick-a-dee alarm calls (Templeton et al., 2005). Dutour et al. (2020) showed that Great Tits (*Parus major*) respond to Chickadee calls because their alarm calls have similar sequences, despite the fact that they have a completely different distribution and have never encounter in the wild. Great Tits calls, as most of the species in Paridae family, are composed of frequency-modulated elements, produced as alarm signals, followed by repeated loud broad-band elements produced in social context (Suzuki, 2016). Blue Tits (*Cyanistes caeruleus*) can alert others about the degree of danger that a predator poses, they produce scolding calls when a predator is closer and “seet” calls when the predator is further (Leavesley & Magrath, 2005). The common call of Willow Tits (*Poecile montanus*) (si-tää) is primary a long-distance call and is composed of 1-3 high-frequency notes. This call is similar to Chickadee calls, the notes usually descend in frequency from the first to the last one, but the last note (D-note) is a complex syllable. They can have variation of calls by changing the D-note (Haftorn, 1993).

Randler (2012) showed that Great Tit respond to heterospecific and allopatric Black-capped Chickadee mobbing calls. He played back Chickadee alarm/mobbing calls to Great Tits and compared with their own conspecific mobbing call and the heterospecific song of Chickadees as a control. Great Tits reacted most strongly towards their own mobbing calls. However, the response that Great Tits showed towards the allopatric

mobbing calls was rather similar compared to the reaction of conspecific. Great Tits were stronger attracted to Chick-a-dee calls compared to the response toward Chickadee song playback, because Black-capped Chickadee songs are usually directed to conspecifics and the mobbing calls are addressed to con- and heterospecifics. Author concludes that titmice in general may possess common features within their alarm calls resulting in successful eavesdropping even by allopatric species.

### ***Aims of the study***

In this study, we conducted playback experiments to investigate the variation in response of two titmice species, Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*), exposed to the alarm calls of familiar and unfamiliar tit species. We played the alarm calls of two Eurasian Tits, Blue Tit and Willow Tit (*Poecile montanus*), since it is known that they commonly form mixed-species flocks during winter together with Great Tits (Snow, 1954). Further we presented alarm of one unfamiliar North American Tit, American Chickadee (*Poecile atricapillus*), and one Far East Tit, Varied Tit (*Sittiparus varius*). These species were shown to share some similarities in their alarm-calling system (Dutour et al., 2016), we may thus expect some responses even to the unfamiliar species. All five species used in this study are passerine birds from Paridae Family and are phylogenetically related (Johansson et al., 2013, see Supplements Figure S1)

We tested the following alternative hypotheses:

1. Blue Tits respond only conspecific alarm calls.
2. Blue Tits as well as Great Tits respond to all familiar alarm calls.
3. Blue Tits as well as Great Tits respond to all alarms of titmice species.

## METHODS

### *Tested species*

The species I focused on for the present study were Eurasian Blue Tits and Great Tits. Eurasian Blue Tits are small birds with a distinct blue and yellow plumage (see Supplements Figure S3), considered native from Europe and western Asia. They prefer niches linked to deciduous woodlands and have a narrower distribution compared to the Great Tit (Charmantier et al., 2016). The Great Tit (Figure S3) is one of the largest tits and has a wide distribution in Europe, Asia, and some habitats in Japan and Korea. They prefer woodlands but can also occupy very arid habitats (Snow, 1954; Harrap & Quinn, 1995). Great Tits and Blue Tits have overlapping foraging niches during non-breeding season in deciduous woodland. Both species normally live in the same habitat but they exhibit different feeding habits therefore they do not compete with each other for resources (Cowie & Novak, 1990). Titmice usually catch the food in the ground, fly up, and eat it near the feeder (Cowie & Novak, 1990). Studies have shown that the time that tits spend feeding is an inverse correlation with the body-weight, thus Great Tits (18g) fed less often than Blue Tits (10-11g) (Gibb, 1954).

Blue Tits and Great Tits have hierarchical flock structure, that includes some dominant individuals and other low-ranking individuals. After the appearance of a predator, high-ranking individuals are likely to wait until subordinate members of their flock resume feeding before them, they are able to be more cautious than low-ranking individuals, possibly because their ability to control food resources reduces the energetic costs of their extra caution (Hegner, 1985; Laet, 1985). Their aggressive behaviour during the non-breeding season may primarily be focused on ensuring resources rather than excluding intruders (Ekman, 1989). Observations of social behaviour have shown that Blue and Great Tits usually forage in mixed-species flocks (Székely et al., 1989). Mixed-species flocks allow them to increase the probability of finding food by spreading the search more evenly over the entire area. It also provides them increased protection against predators by detecting them earlier or confusing them (Székely et al., 1989). One of the main predators of Blue Tits and Great Tits are the Eurasian sparrowhawks (*Accipiter nisus*), their diet is mostly composed of small birds (Carlson, Pargeter, et al., 2017), but the winter feeders represent a spot with high, common occurrence of mixed flocks, where they are subjected to high predation pressure (Cresswell, 1994).

### ***Study site***

The study site was a winter feeder at the Branišovský forest, near České Budějovice, Czech Republic (48.9807870°N, 14.4178390°E). It is a mixed forest with predominating oaks (*Quercus*) and spruce (*Picea abies*, see Supplements Figure S2). The feeder was present within a young growth of spruce (5-15 meters high trees). The experiments were conducted at the end of winter (March 2021) for two weeks, when tits' flocks regularly visit the feeders. Blue Tits and Great Tits change their diet during winter to adapt to the available food supply. Their main intake during this season are seeds, particularly sunflower seeds, thus we used them to attract the birds to the feeder. Both species form mixed-species flocks in our study site, and they share the food supply.

### ***Playbacks***

We tested the responses of Blue Tits and Great Tits to alarm calls of two familiar species: Blue Tits and Willow Tits, and two unfamiliar species: Black-capped Chickadee from North America, and Varied Tit from Easter Asia. We used a Blue Tit song as a baseline control, predicting zero fear response of both species during the non-breeding season (see Supplements, Figure S3). All the stimuli were obtained from the Xeno-canto database (Planqué et al., 2021, see Table S4). All the playbacks consisted of two calls separated by a silence and lasted approximately 7 seconds. We used 5 different variants of each particular call. The playbacks were played using high performance loudspeaker (MIPRO 202-A) with volume set to correspond to natural performance of a living bird.

### ***Experiment***

We started every experiment once the birds were familiar with human presence near the feeder and visited the feeder regularly. We did not conduct the experiment after any disturbance, such as naturally occurring, or loud noises. We ran the experiments from 8:00 to 15:00 when the birds were more active, with the 5 stimuli presented in random order. Each individual playback was presented 15 times, as there were 5 playbacks for each treatment, we conducted 75 experiments in total (each type of playback presented 15 times). On average 10 Blue Tits (min = 3, max = 18) and 9 Great Tits (min = 2, max = 17) were present before the playback. The responses were recorded for one minute before the playback one minute following the playback, using one camera fixed on a tripod.

### ***Recorded data and analyses***

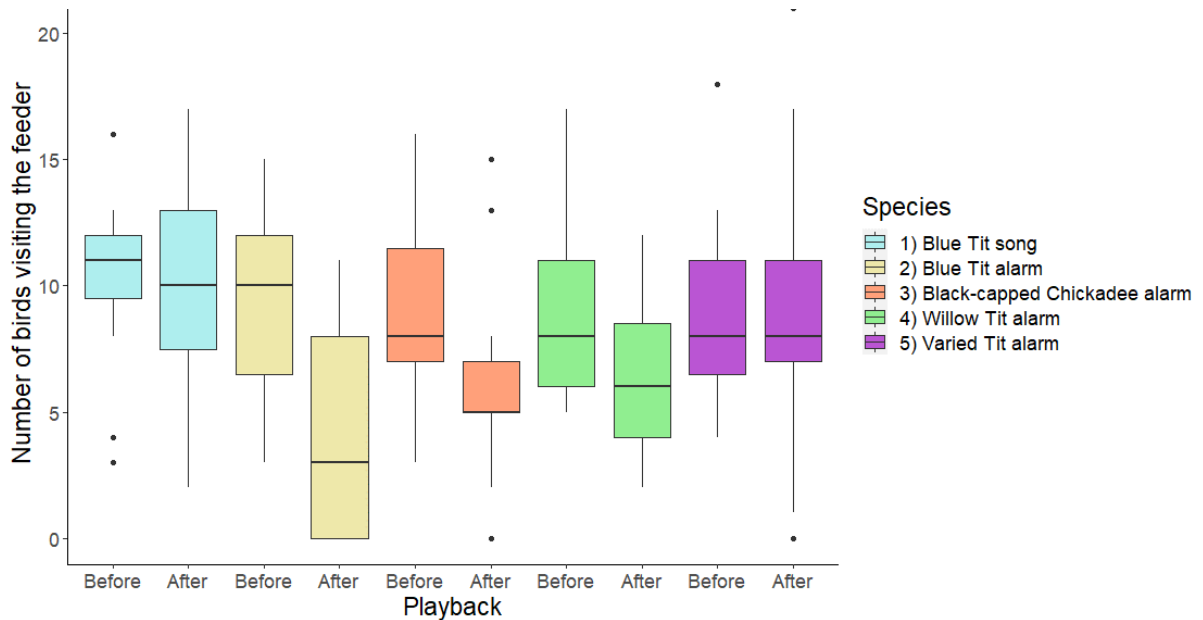
We recorded the number of Blue Tits and Great Tits successfully visiting the feeder (i.e. collecting the seeds) one minute before and one minute after the stimulus played. We did not discriminate either it was the same individual, as the birds were not individually marked.

To test for the difference in the number of visits to the feeder before and after the playback we ran a  $t$ -test with Blue Tits and Great Tits and with each treatment (playback) individually. Secondly, we checked for the effect of the treatment of the proportion of the birds visiting the feeder before and after the playback. To meet the demands of normal distribution, we used the arcsine transformation of the proportion of Blue Tits and Great Tits (separately) visiting the feeder after the playback (out of those present together before and after the playback). These data originally scored from 0 to 1. We ran two linear models (one for Blue Tits and one for Great Tits) to test the effect of the playback, with likelihood ratio test for Gaussian distribution (F test). We used a Tukey HSD post hoc test with Tukey correction to compare the actual conditions. All statistical analyses were computed using R 3.4.4 (R 92 Development Core Team 2018).

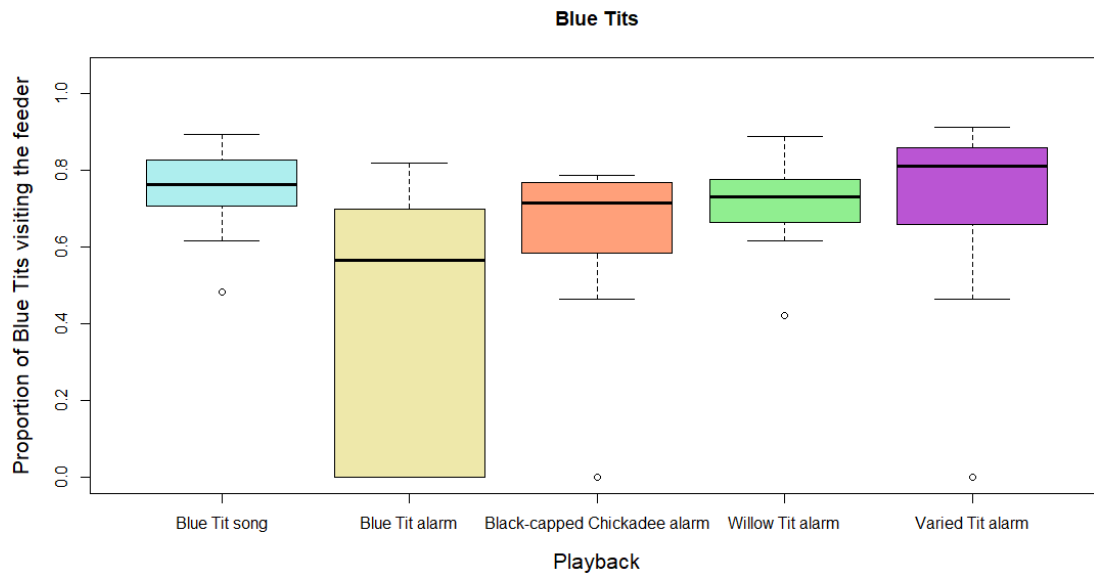
## RESULTS

### *Blue Tits*

Pairwise comparisons of the number of Blue Tits visiting the feeder before and after the playback was significantly different when the conspecific ( $t = 3.53, p = 0.001, df = 27.7$ ) and American Chickadee alarm call was presented ( $t = 2.23, p = 0.03, df = 27.9$ ) (Figure 1). The proportion of Blue Tits visiting the feeder after the stimulus out of all visiting Blue Tits was significantly affected by the playback presented ( $LM, F = 5.27, p < 0.001$ ). This proportion was significantly lower when a conspecific alarm call was present than when a conspecific song, Willow Tit alarm, or Varied Tit alarm were presented (post-hoc Tukey HSD,  $p = 0.001, p = 0.007, p = 0.005$ ; respectively) (Figure 2). Other comparisons were not significantly different.



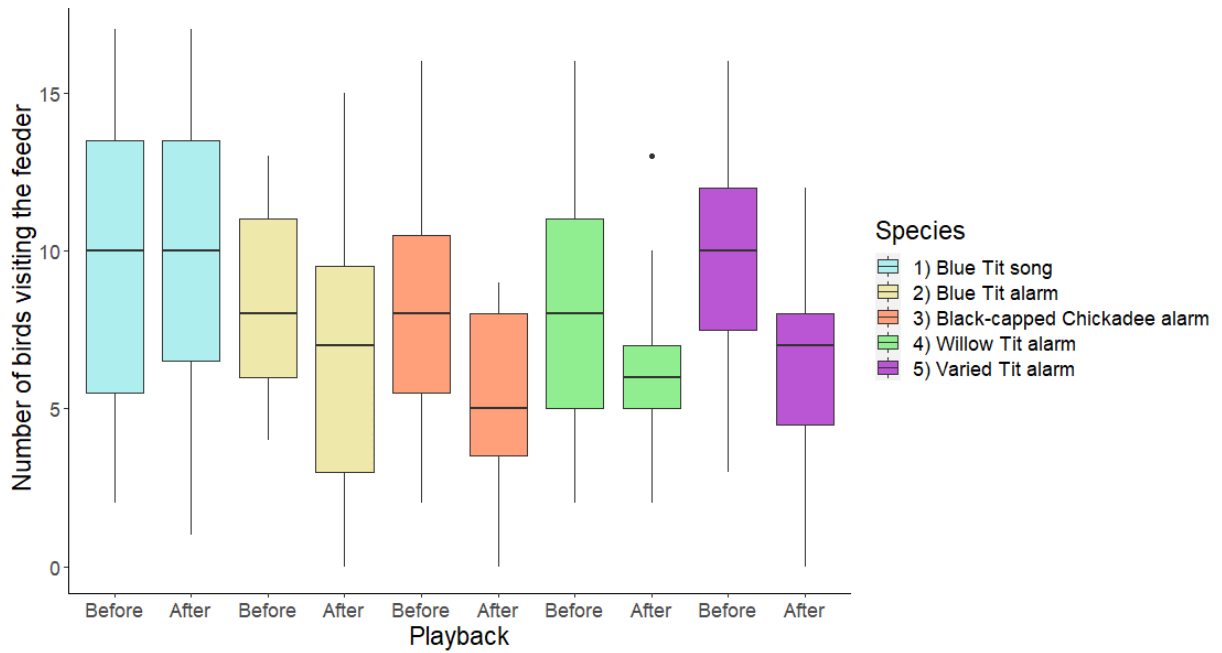
**Figure 1.** Number of Blue Tits visiting the feeder before and after each playback. The solid line refers to median value, box refers to 75 % quartile, whiskers refer to non-outlier range and dots refer to outliers.



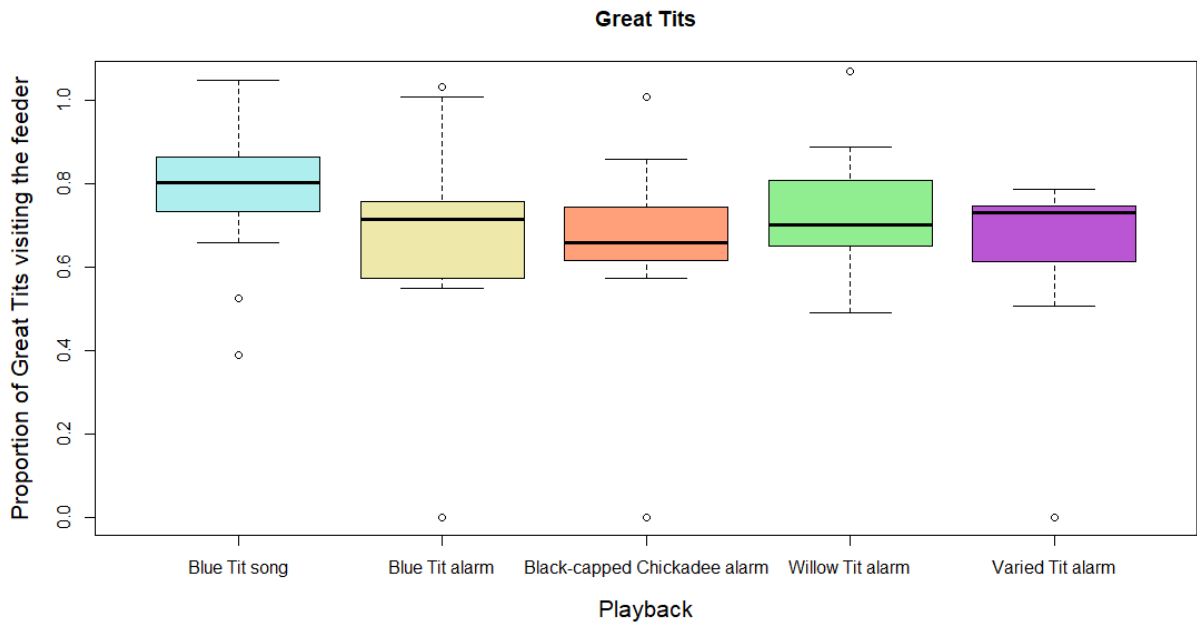
**Figure 2.** The effect of particular playbacks on the proportion of Blue Tits visiting the feeder after the playback, out of all Blue Tits visiting the feeder before and after the playback. The solid line refers to median value, box refers to 75% quartile, whiskers refer to non-outlier range and dots refer to outliers.

### *Great Tits*

The number of Great Tits visiting the feeder was significantly different when the American Chickadee ( $t = -2.38, p = 0.02, df = 24.6$ ) and Varied Tit alarm call was played back ( $t = 2.55, p = 0.01, df = 27.4$ ) (Figure 3). The proportion of the Great Tits visiting the feeder after the playback was not affected by the playback presented ( $LM, F = 1.52, p = 0.2$ ) and the post-hoc comparison between the conditions was not significant in any case ( $p > 0.05$ ) (Figure 4).



**Figure 3.** Number of Great Tits visiting the feeder before and after each playback. The solid line refers to median value, box refers to 75 % quartile, whiskers refer to non-outlier range and dots refer to outliers.



**Figure 4.** The effect of particular playbacks on the proportion of Great Tits visiting the feeder after the playback, out of all Blue Tits visiting the feeder before and after the playback. The solid line refers to median value, box refers to 75% quartile, whiskers refer to non-outlier range and dots refer to outliers.



## DISCUSSION

Playback experiments have been an important part for the development of studies focused in alarm calls responses (Hollén & Radford, 2009). The songbirds described in this study are species commonly believed to understand antipredator behaviour due to the high number of calls that they produce and their responses to familiar and unfamiliar alarm calls. Blue and Great Tits are highly representative songbird in European continent and their behaviour have been an important part in avian research. The responses of Blue Tits and Great Tits to conspecific and heterospecific alarm calls, can enlarge the knowledge of Eurasian passerines.

Blue Tits responded to conspecific alarm call by decreasing their feeding rates. This behaviour is not surprising and confirms the function of the alarm calls at the feeder as they indicate the presence of perceived predator (Carlson, Healy, et al., 2017a). The seet calls that Blue Tits use to communicate urgency are important strategies that benefits the receiver and the signalers as are likely to be difficult for a predator to detect because of their frequency (Marler, 1955). Blue Tits can have an innate knowledge of antipredator behaviour and can also socially learn since early stage of their life. The mobbing call used in our experiments evidently also affects the bird behaviour, resulting in reduced activity of birds and hiding in the undergrowth.

On the contrary, Blue Tit alarm call did not affect significantly Great Tits feeding rates. Both species live in mixed-species flocks and share foraging niches during the non-breeding season. Despite the benefits of the life in mixed-species flocks, they compete for resources (Gorissen et al., 2006). Studies conducted with an artificial winter food supply showed that in mixed flocks of tits, Great Tits are dominant over Blue Tits and there is interspecific aggression and interference (Dhondt & Eyckerman, 1980). Great Tits are known to respond to other species' calls, such as Blue Tits and chaffinches (*Fringilla coelebs*), during predator mobbing behaviour (Dutour et al., 2021). It is therefore surprising that in our experiments, the effect of Blue Tit alarm was so weak.

There are studies showing that Great Tits can use efficient vocal strategies, like matching some Blue Tit calls to defend their nest, their territories or food sources but Great Tits do not respond to imitations of Blue Tits (Gorissen et al., 2006). Blue and Great Tits have different ways to encode the information about predators' presence and absence, Great Tits have more elaborate alarm calls (Cowie & Novak, 1990). Some studies have shown

that Great Tits responded to con- and heterospecific alarm calls more frequently when there was a bigger number of callers (Dutour & Randler, 2021), probably to reduce uncertainty of information by collecting information from several individuals (Wolf et al., 2013). In our experiment, the playback represented a single bird, which might be too weak stimulus for the Great Tits.

Doutrelant et al. (2000) demonstrated that in the places where Blue and Great Tit populations co-occur, most of the Blue Tits emit only trilled song types to avoid territorial interactions with Great Tits. The frequency of Blue Tits trilled song clearly differs from Great Tit song and calls consequently reduces their responses. Blue and Great Tits start forming mixed flocks at early autumn until late winter, when mixed species flocks begin to break up, Blue Tits and Great Tits begin forming pair bonds and selecting nest sites as early as January, consequently they may be less interested in heterospecific alarm calls, (Stokes, 1960). As we ran our experiments in March, this can be another reason that could affected our results.

Blue Tits and Great Tits differ in foraging behaviour during winter, Blue Tits forage in the ground most often in January while Great Tits forage in the ground in late March and early April, this can affect the way how they transmit the information (Gibb, 1954). Moreover, Keen et al. (2020) showed that the use of alarm calls sometimes is not enough to demonstrate the social transmission of anti-predator information between Blue and Great Tits, because social transmission in titmice species differs in how they respond to predators, i.e. Blue Tits exhibit more wing-flicking rather than producing calls in response to predators (Carlson, Pargeter, et al., 2017).

Even though Willow Tits are known to form mixed-species flocks with Blue Tits and Great Tits during non-breeding season, there was not a significant response to their alarm call in neither species. Willow Tits are less wide-spread than Blue as well as Great Tits, thus they may interact less frequently with the other species due to differing habitats (Matsuoka, 1980). Latimer (1977) showed that the alarm call of Willow Tit differs slightly from the other common species. The primary warning or alarm call consists of a series of high-pitched, short zi (zee)-notes. This call varies in length according to the number of zi's incorporate (Haftorn, 1993).

Willow Tits produce short calls when harmless birds flew overhead or when humans appeared. They produce long trill calls, in response to predators, in high-risk situations

the frequency of the trills increase, increasing the difficulty of detection (Haftorn, 1993). Maybe more importantly, in mixed-species flocks, Willow Tits are known for their common producing of false alarm calls, in the absence of a predator, to take advantage of the food in the feeders, the alarm calls are more frequently produced when the food is less dispersed (Matsuoka, 1980). Willow Tits might be thus the less reliable species within the mixed-species flocks, and this might be the reason why Blue as well as Great Tits do not respond to their alarms.

European tits and American Chickadee are allopatric species; however, the feeding rates of both Blue Tits and Great Tits were significantly affected by the alarm call of Black-capped Chickadee. Both, Blue Tits and Black-capped Chickadees, can encode the presence or absence of a predator in the alarm call and differentiate predators of different threat levels. They have shown to use all four ways to encode the information in response to predators threat (Carlson, Healy, et al., 2017a), they also use similar “seet” alarm calls to communicate the degree of danger (Leavesley & Magrath, 2005). Dutour et al. (2020) showed that Great Tits respond to Chickadee calls because their alarm calls have similar sequences, and they can extract information equivalent to their own calls.

Randler, (2012) showed that Great Tit species can perceive the encoded syllables of American Chickadee, suggesting that the heterospecific response is possibly phylogenetically conserved. Tits and American Chickadee display a sequence that involves a combination of introductory and loud notes in a fixed order (Templeton et al., 2005) therefore, they may better understand each other.

Even though we have seen that Blue and Great Tits react to unfamiliar alarm calls, Varied Tit alarm did not affect the rates of feeding in Blue Tits. On the other hand, Great Tits responded significantly to Varied Tit alarm calls. Varied Tit can be considered as allopatric and unfamiliar to both Blue and Great Tits in our experiments, despite Great Tits co-occur with Varied Tits in some temperate deciduous forest of Eastern Asia (Park et al., 2005). Varied Tits are also not closely related to any of the two tested European tit species, they are related to American Chickadees and Willow Tits (Johansson et al., 2013). Despite the familiarity and relative relatedness to Blue and Great Tits, their responses to these three tit species substantially differ. We cannot evaluate the similarity of the antipredator communication systems between Varied and Great Tits as little is known about Varied Tits antipredator behaviour and the function of their alarm calls (Hamao, 2016, Shimazaki et al., 2017). Nevertheless, generally based on previous

studies (Templeton & Greene, 2007; Magrath, et al., 2015), it seems that the main thing that secures the eavesdropping on heterospecific alarms is their similarity, presence of some specific syllables and their use. Therefore, European species in our experiments responded to American Chickadees and in the case of Great Tits also to the Far East Varied Tits.

For some species, it is known that sympatric heterospecifics are more attracted to playback of mobbing calls with a higher calling rate (Templeton & Greene, 2007). Varied Tits alarm calls are the most different of all alarms used in this study, and as Randler (2012) assumes, the more intense calling can lead to more attraction.

## **CONCLUSIONS**

We may conclude that Blue Tits and Great Tits do not respond to any alarm of any titmice species. Blue Tits as well as Great Tits did not respond significantly to Willow Tit alarm calls, probably due to their low reliability. Blue Tits responded to conspecifics alarm calls the strongest, while Great Tits responses toward Blue Tits alarm calls did not differ from the control song. Both species strongly responded to American Black-capped Chickadee, which seems to be a universal alarm including specific features. Great Tits also responded to alarms of Varied Tits, probably also due to some shared features within these alarms. Based on our experiments we suggest that presence of some shared specific features within the alarms is essential for successful eavesdropping. Nevertheless, further studies with multiple species and especially acoustic analyses of particular alarm calls must be conducted to get more evidence to explain these results.

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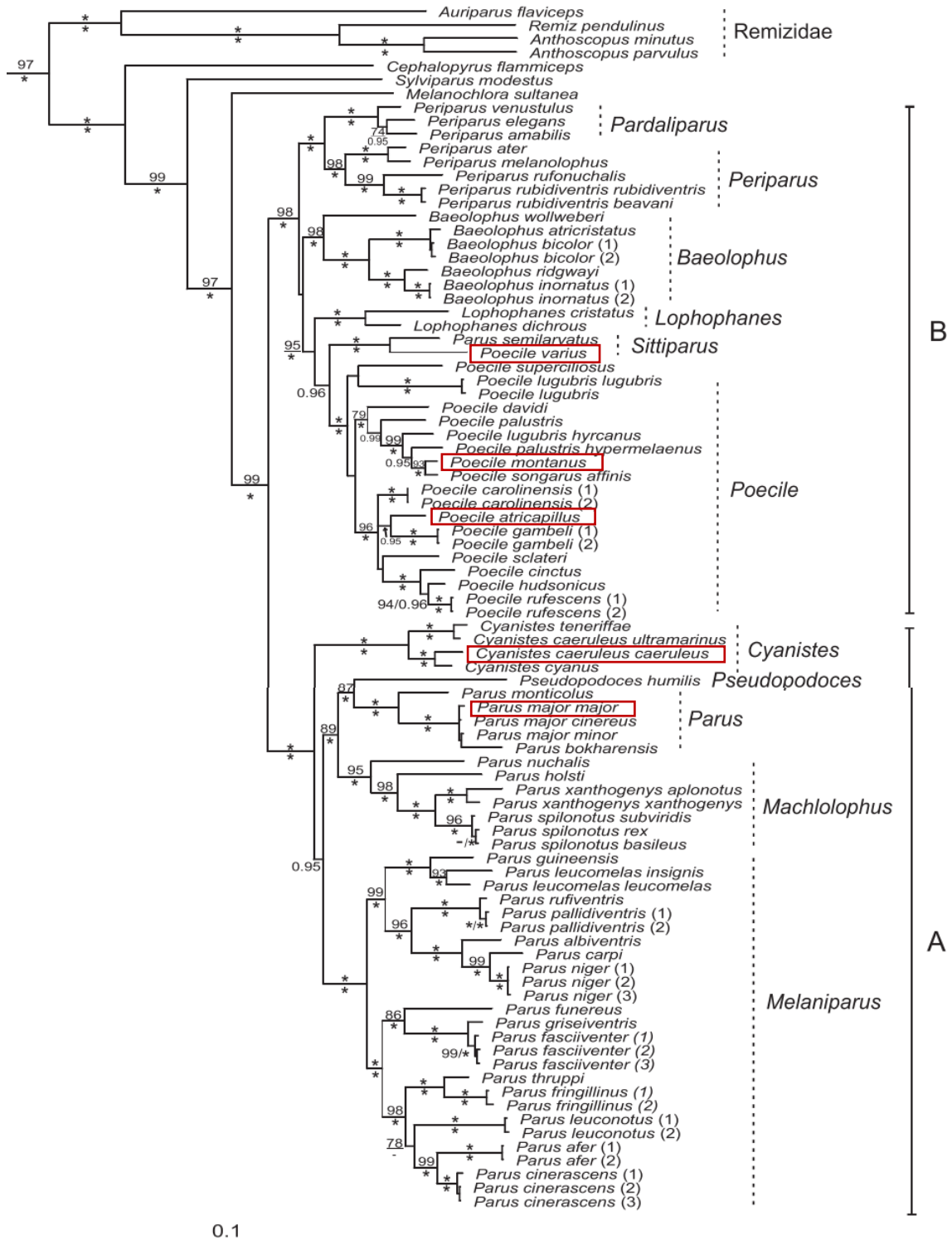
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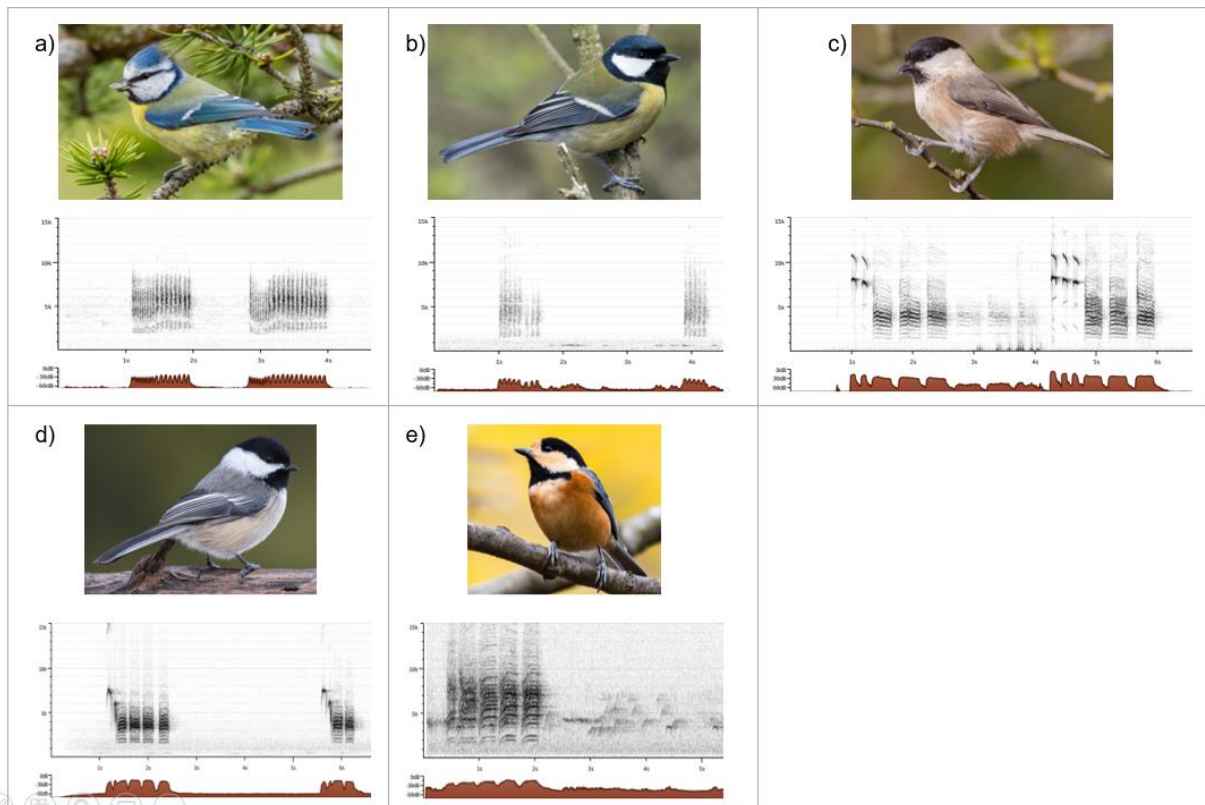
SUPPLEMENTS



**Figure S1.** Phylogeny tree of Paridae family. Adapted from Johansson et al. (2013). In the red boxes are the species that were used in this study.



**Figure S2.** Study site.



**Figure S3.** Species of Tits and sonograms of their alarm calls used in this study. a) Eurasian Blue Tit (*Cyanistes Caeruleus*), b) Great Tit (*Parus major*), c) Willow Tit (*Poecile montanus*), d) Black-capped Chickadee (*Poecile atricapillus*), e) Varied Tit (*Sittiparus varius*). Figures adapted from eBird database (Sullivan et al., 2009) and sonograms adapted from Xeno-canto database (Planqué et al., 2021).

**Table S4.** Summary of recordings used in playback experiments downloaded from database xenocanto.com.

Species	Call type	Code	Author	Country	Number of syllables (first part)	Duration (sec)	Number of syllables (second part)	Duration (sec)
<i>Cyanistes caeruleus</i>	song	XC555029	Niels Van Doninck	Belgium	4	0.8	4	0.8
<i>Cyanistes caeruleus</i>	song	XC527591	Stephan Risch	Germany	14	12	1.2	1.2
<i>Cyanistes caeruleus</i>	song	XC330293	David M.	UK	6	0.9	7	1
<i>Cyanistes caeruleus</i>	song	XC253237	David M.	UK	7	1	11	1.8
<i>Cyanistes caeruleus</i>	song	XC243917	David M.	UK	4	0.9	4	0.8
<i>Cyanistes caeruleus</i>	alarm	XC168100	Buhl Johannes	Germany	17	1	19	1
<i>Cyanistes caeruleus</i>	alarm	XC504586	Beatrix Saadi-Varchmin	Germany	20	1.2	19	1.2
<i>Cyanistes caeruleus</i>	alarm	XC552947	Mikael Litsgård	Sweden	8	0.6	8	0.55
<i>Cyanistes caeruleus</i>	alarm	XC525916	Markus Jacobs	Germany	12	0.7	14	0.9
<i>Cyanistes caeruleus</i>	alarm	XC394169	Marco Dragonetti	Italy	20	1.4	19	1.4
<i>Poecile montanus</i>	alarm	XC610179	Thomas Bergman	Sweden	6	1.9	6	1.8
<i>Poecile montanus</i>	alarm	XC383735	Terje Kolaas	Norway	2	0.9	7	1.8
<i>Poecile montanus</i>	alarm	XC287201	Eetu Paljakka	Finland	3	1	7	1.4
<i>Poecile montanus</i>	alarm	XC406040	Jarek Matusiak	Poland	7	0.8	3	0.6
<i>Poecile montanus</i>	alarm	XC151327	Elias A. Ryberg	Norway	2	0.8	4	1.7
<i>Poecile atricapillus</i>	alarm	XC420822	Gabriel L. Leite	New York	8	1.5	7	1.25
<i>Poecile atricapillus</i>	alarm	XC544964	Thomas Magarian	Oregon	9	1.55	9	1.55
<i>Poecile atricapillus</i>	alarm	XC544962	Thomas Magarian	Oregon	7	0.8	14	1.4
<i>Poecile atricapillus</i>	alarm	XC352828	Ted Floyd	Colorado	6	1.3	4	0.7
<i>Poecile atricapillus</i>	alarm	XC348981	Ted Floyd	Pennsylvania	8	1.5	8	1.4
<i>Sittiparus varius</i>	alarm	XC566223	Anon Torimi	Japan	4	1.5	4	1.3
<i>Sittiparus varius</i>	alarm	XC332820	Jim Holmes	South Korea	5	1.5	4	1.3
<i>Sittiparus varius</i>	alarm	XC202762	Ross Gallardy	South Korea	4	0.8	7	1.5
<i>Sittiparus varius</i>	alarm	XC478589	Anon Torimi	Japan	5	1.8	3	1
<i>Sittiparus varius</i>	alarm	XC455522	Anon Torimi	Japan	7	1.5	10	1.8