Predators vs. Prey:

The Information ecology of warning signals

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This dissertation is submitted for the degree of Doctor of Philosophy

Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution. This thesis does not exceed the prescribed word limit of 60 000 words.

Summary

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Explaining the origin and maintenance of aposematism has remained a challenge for evolutionary biologists because conspicuous warning signals are predicted to have a high initial predation cost before predators learn to avoid them. Most previous work has assumed that predators need to sample prey individually (personal information) to learn about these defences, however recent research suggests that observing predation events of others (social information) may also shape selection for prey defences and help resolve this puzzle. Here I use great tits and blue tits as model predators to investigate what influences predators' decisions to use different types of information when encountering novel prey, how information use varies across predator species, and whether this can operate in a predator community in the wild.

First, I investigated if previous experience with toxins increases great tits' reliance on social information about novel aposematic prey, but found that toxin load had no effect: socially-educated birds consumed fewer aposematic prey, regardless. This indicates that social information can reduce predation pressure on novel aposematic prey even when a predator's risk of increasing their toxin load is low. Social interactions among predators might, however, also *increase* predation on aposematic prey if predators gather social information about the presence of palatable mimics. Therefore, I next investigated if educated great tits became more likely to consume mimics after observing warning signals being palatable but found that the birds were hesitant to sample palatable mimics, regardless of social information. These results suggest that while social information about models is potent in increasing predator avoidance, model-mimic dynamics are unlikely to be affected when predators have recent personal experience of the model's unpalatability.

Because predator communities are often complex and consist of multiple species, I next extended my work to blue tits that typically form mixed-species flocks with great tits. I first tested whether video playback is a suitable method for providing social information for blue tits. I then investigated conspecific and heterospecific information use in blue tits and great tits, and found that both species used social information about aposematic prey, including information from heterospecifics. Finally, I tested the ecological relevance of my results with a field experiment where blue tits and great tits were presented with novel palatable and unpalatable food. I conducted the experiment in the summer when naïve juveniles are abundant and aposematic prey suffer high predation. Consistent with my work with birds in captivity, I found that both species used social information in their food choices also in the wild. Together, my findings demonstrate that social transmission of knowledge about prey defences shapes predator-prey communities, and an information ecology approach can therefore help us to understand the evolution and maintenance of prey warning signals.

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Contents

CHAPTER 1: General introduction

Prey have evolved many different strategies to escape predation. These can be associated with prey colouration, with the most common examples being camouflage and aposematism that are both widely studied (Ruxton *et al.*, 2018). Yet, the evolution of different antipredator strategies still provides unanswered questions. Here I first describe why aposematism has interested researchers since it was first described and review previous research that has aimed to explain the evolution and maintenance of warning signals. I will then describe how predators can use multiple sources of information when learning about aposematic prey and how this can increase our understanding of predator-prey coevolution. In my thesis I am investigating this using blue tits and great tits as model predators, and at the end of the introduction I will describe this study system and the outline of my thesis.

THE PROBLEM OF APOSEMATISM

Aposematism is a common antipredator strategy where animals use warning signals to advertise their unprofitability, such as toxicity, to potential predators (Poulton, 1890; Ruxton *et al.*, 2018). The first description of aposematism dates back to Wallace who over 150 years ago suggested that conspicuous colouration of caterpillars could function as a signal to alert predators about their toxicity (Wallace, 1867). Since then, aposematism has received wide experimental and theoretical interest, becoming a classical system to study predator-prey coevolution. Explaining the origin and maintenance of aposematism, however, remains a challenge because warning signals confer advantage only after predators have learned to associate the signal with unpalatability (Mappes, Marples & Endler, 2005; Ruxton *et al.*, 2018). Typical warning signals include distinctive colours and even though conspicuous signals have been shown to facilitate predator avoidance learning (Roper & Redston, 1987; Lindström et al., 1999a), they also increase the detectability of prey and leave them vulnerable to naïve predators (Alatalo & Mappes, 1996; Mappes *et al*., 2005). The initial cost of warning colouration is therefore expected to be high if predators need to sample aposematic prey to learn about their defences. The question then remains - how can aposematism evolve and how it can be maintained when naïve juveniles and immigrants enter the predator community?

There has been a lot of empirical and theoretical work attempting to answer the question of the origin of aposematism (Ruxton *et al.*, 2018). Some of the possible explanations include receiver biases of predators (Speed, 2000, 2001), such as dietary wariness which consists of a predator's initial hesitation to attack novel prey (neophobia) and a longer refusal to add novel food to the diet (dietary conservatism; Marples & Kelly, 1999). Dietary wariness has been suggested to protect novel colour morphs and help them to increase in frequency which could facilitate the evolution of aposematism (Marples, Kelly & Thomas, 2005). This idea has got support from field studies showing that wild birds often avoid novel foods (Marples *et al.*, 1998; Thomas *et al.*, 2003; 2004). Novelty effects might, however, be short-lived (Speed, 2001), and social interactions among predators can further influence the acceptance of novel food (McMahon *et al.*, 2014). In addition, the hesitation to attack novel prey might be context-dependent and vary within and among predator species. For example, Marples & Mappes (2011) investigated great tits' foraging choices in 'novel world' that consisted of familiar cryptic prey and conspicuous novel prey, and found that novelty did not protect conspicuous prey that suffered high initial predation cost. However, great tits also showed individual variation in the degree of dietary wariness (Marples & Mappes, 2011), and evolutionary simulations predict that this variation in the predator community could be important in determining which prey types are favoured (Lee, Marples & Speed, 2010).

In addition to wariness to consume novel food, predators can have innate aversions towards typical warning colours (Schuler & Hesse, 1985; Roper, 1990; Lindström, Alatalo & Mappes, 1999b). This might be particularly important when an encounter with prey could be lethal, as in the case with coral snakes whose red and yellow patterns seem to be innately avoided by avian predators (Smith, 1975; 1977). The degree of initial avoidance, however, varies among species (Exnerová *et al.*, 2007), and many studies have demonstrated that naïve juveniles are more likely to attack aposematic prey compared to more experienced individuals (Exnerová *et al.*, 2007; Svádová *et al.*, 2009). Furthermore, predation risk for aposematic prey in the wild has been shown to increase when naïve predators are abundant (Mappes *et al.*, 2014), which indicates that predators need to often sample aposematic prey to learn about their defences. Guilford (1994) suggested that even if predators attacked aposematic prey, conspicuous warning signals could provoke them to handle prey more carefully. This 'go-slow' behaviour could make warningly coloured prey more likely to survive a predator's attack and help aposematic forms to persist in the population (Guilford, 1994; Carroll & Sherratt, 2013). Indeed, it has been demonstrated that aposematic prey can often survive encounters with predators and therefore escape unharmed (Wiklund & Järvi, 1982; Sillén-Tullberg, 1985; Exnerová *et al.*, 2003; 2007; Williams, Brodie & Brodie, 2003). Aposematic prey have also been argued to benefit from aggregation which could speed up predators' avoidance learning and increase the survival of prey with novel warning signals (Mappes & Alatalo, 1997; Riipi *et al.*, 2001; Ruxton & Sherratt, 2006). However, predators often need to sample multiple prey to acquire avoidance (Riipi *et al.*, 2001) and gregarious species are relatively rare in nature (Ruxton & Sherratt, 2006). Furthermore, there is now good evidence that instead of completely avoiding aposematic prey, educated predators continue to include them in their diet when the benefits of acquiring nutrients outweigh the costs of consuming toxins (Skelhorn, Halpin & Rowe, 2016). In addition to facing predation from naïve predators (Mappes *et al.*, 2014), aposematic prey are therefore predicted to suffer attacks from educated predators when alternative prey is scarce (Halpin, Skelhorn & Rowe, 2013) or when predators are in a poor energetic state (Barnett, Bateson & Rowe, 2007; Barnett *et al.*, 2012).

The presence of deceptive mimics can further complicate selection for warning signals. In Batesian mimicry, a palatable mimic resembles a defended model species and therefore gains protection from educated predators (Bates, 1862). This can create a conflict between the model and the mimic, as predators are predicted to increase their attacks on defended models when harmless mimics are abundant (Lindström, Alatalo & Mappes, 1997). Similarly, individuals within the same species might vary in the strength of their defences (e.g. de Jong *et al.*, 1991; Eggenberger & Rowell-Rahier, 1992) and palatable individuals in a population of an aposematic species are called automimics (Brower, Brower & Corvino, 1967). If chemical defences are costly to produce, automimics are predicted to increase in the prey population (Guilford, 1994), which can reduce predator avoidance learning and increase attacks on the species, destabilising the aposematic signaling system (Gamberale-Stille & Guilford, 2004). How the presence of palatable mimics influences selection pressures on aposematic prey, however, is likely to depend also on many additional factors, such as the availability of alternative prey (Kokko, Mappes & Lindström, 2003; Lindström *et al.*, 2004), and the toxicity of the model (Lindström *et al*., 1997; Skelhorn & Rowe, 2006).

INFORMATION ECOLOGY OF PREY DEFENCES

Information ecology approach

Despite this considerable effort to explain the origin and maintenance of aposematism, we still do not have a definitive answer to this puzzle. Different hypotheses are not mutually exclusive and it is likely that many mechanisms facilitate the survival of aposematic prey. To date, most research has focused on individual learning of predators, assuming that individuals need to personally sample prey to learn about their defences (Ruxton *et al.*, 2018). However, information ecology theory predicts that individuals should use wider sources of information in their decision making (Dall *et al.*, 2005). This includes direct interactions with the environment ('personal information'), as well as gathering information by observing the behaviour of other animals ('social information'). By integrating information from a wide range of sources, predators can better assess the outcomes of attacking potential prey (Fig. 1). Prey might, for example, be undefended and palatable, be mildly defended but nutritious, or be toxic and deadly, and without prior information predators cannot differentiate among these potential outcomes. Gathering social information about prey quality by observing foraging experiences of others may help to reduce this uncertainty and help predators to make adaptive foraging decisions. In my thesis I am using this information ecology approach to explore multiple sources of information that are available to predators.

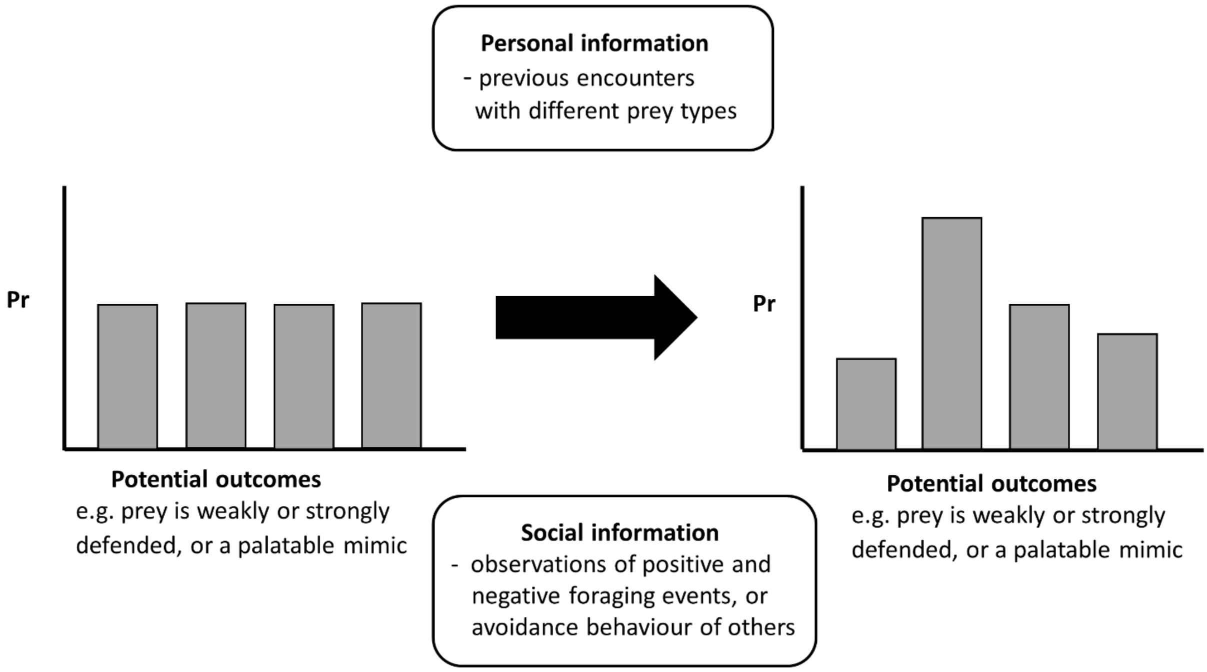


Figure 1. Information ecology theory predicts that individuals can gather both personal and social information to reduce uncertainty when making decisions. When a predator encounters a potential prey, attacking it can have multiple potential outcomes; for example, the prey might be profitable and provide a nutritious meal, or it might be chemically defended and unprofitable. To make adaptive decisions to attack prey, a predator can use its prior personal knowledge (previous encounters with the same/similar prey), as well as social information (observations of foraging events of others), and both of these information sources can change the probability distribution of potential outcomes. Modified from Dall *et al.* (2005).

Evolutionary consequences of social information

It is now well established that many animals gather information about their environment by observing others and use this social information in their decision making (Danchin *et al.*, 2004; Dall *et al.*, 2005; Galef & Laland, 2005). The number of studies investigating social learning has expanded during the past decade and social information use has been demonstrated across a wide range of taxa (Whiten, 2000; Brown & Laland, 2003; Dawson & Chittka, 2012; Kis, Huber & Wilkinson, 2015; Aplin, 2019), and in many different contexts, including foraging decisions, predator avoidance, habitat selection and mate choice (reviewed in Danchin *et al*., 2004). How social transmission of information influences selection pressures during species interactions has, however, received less attention, and only recent studies have started to address these potential evolutionary consequences (reviewed in Whitehead *et al.*, 2019). For example, Thorogood & Davies (2012) demonstrated that social transmission of information about brood parasites can influence coevolution between hosts and parasites. Reed warblers were found to learn about the presence of cuckoos by observing the mobbing of their neighbours, however, this social learning was specific to cuckoo colour morph. This suggests that social learning about brood parasites is frequency-dependent, and to avoid detection from reed warblers, selection should favour rare cuckoo colour morphs, providing an explanation for the observed cuckoo plumage polymorphism (Thorogood & Davies, 2012).

Social transmission of information about prey defences could have similar consequences for predator-prey coevolution (Mappes & Lindström, 2012). Aposematic prey are predicted to suffer high predation from naïve predators, however, this initial predation cost may be reduced if predators gather information about prey defences by observing the avoidance behaviour (Landová *et al.*, 2017) or negative foraging experiences of others (Thorogood, Kokko & Mappes, 2018). By using multiple sources of information, predators might need fewer personal encounters with aposematic prey to acquire avoidance, which could help aposematic forms to evolve and persist in the prey population. Indeed, a modelling approach by Thorogood *et al*. (2018) showed that 'social avoidance learning' of predators can increase the likelihood that aposematic phenotype reaches fixation. Furthermore, social interactions among predators have a potential to influence the frequency-dependent model-mimic dynamics in the prey population, but how this affects the survival of defended models and their mimics is still unclear. On the other hand, social transmission of avoidance could help to maintain model-mimic systems because predators could observe others consuming models and generalise this avoidance to mimics (Mason & Reidinger, 1982). However, educated predators might also gather social information by observing others consuming palatable mimics, which in turn could increase predation on both mimics and their defended models, and destabilise the model-mimic system (Alcock, 1969).

By using multiple sources of information, predators may gather both personal and social information about the unprofitability of aposematic prey, as well as about the existence of palatable mimics. This can sometimes provide individuals conflicting information, but how predators value different types of information in their foraging decisions is still poorly understood. Because sampling novel prey can be costly (Sherratt, 2003), gathering social information about prey palatability can benefit predators by lowering the costs of individual trial and error learning, such as the risk of consuming prey toxins. On the other hand, social information might provide predators less accurate information about prey defences, compared to direct contact with prey, and social learning theories predict that individuals should use social information selectively (Laland, 2004; Kendal *et al.*, 2005; 2018). Individuals might, for example, be more likely to rely on social information when personal learning is more costly or when they are more uncertain about the environment (Laland, 2004; Kendal *et al.*, 2005). Empirical evidence of social avoidance learning is, however, limited, and we do not know how predators combine these multiple information sources when encountering novel prey.

Social information use by predators: experimental evidence

The first experimental studies that investigated if animals learn to avoid objects after observing a negative experience of others included the work by Klopfer (1957; 1959). Klopfer studied this ‘empathic learning’ in Muscovy ducks that were conditioned to avoid food dishes surrounded by an electric grid (Klopfer, 1957) and in greenfinches that were trained to discriminate palatable and unpalatable food (Klopfer, 1959). Although these studies provided some evidence that social interactions might influence birds’ responses, the number of tested individuals was too small to make strong conclusions about social information use. Clearer evidence of social avoidance learning came later from the experiments with red-winged blackbirds and common grackles, which demonstrated that birds avoided consuming food from a coloured cup after observing a negative foraging experience of a demonstrator foraging from it (Mason & Reidinger, 1982; Mason, Arzt & Reidinger, 1984). Furthermore, Mason *et al.* (1984) showed that birds acquired avoidance equally well when observing heterospecifics (a common grackle demonstrator for blackbird observers and vice versa), compared to observing a demonstrator of their own species, suggesting that social transmission could occur across species boundaries. In these studies, demonstrators were intubated with a methiocarb solution that generated strong aversive responses (Mason & Reidinger, 1982; Mason *et al*., 1984). Similarly, ‘disgust responses’ of predators attacking distasteful prey can provide observers social information about prey unpalatability. Indeed, many chemically defended prey taste bitter (Glendinning, 1994) and birds often perform vigorous beak wiping and head shaking after attacking them (Clark, 1970; Skelhorn & Rowe, 2009; Rowland *et al.*, 2015). This behaviour was found to influence the foraging choices of domestic chicks that avoided unpalatable food after observing a disgust response of a conspecific consuming it (Johnston, Burne & Rose, 1998). Social information might influence predators' foraging behaviour even if they did not observe the entire predation event, as seeing only the disgust response of others can inform individuals about the presence of toxic prey (Skelhorn, 2011). This was demonstrated in domestic chicks that biased their foraging choices away from typical warning colours (red and yellow) after observing a disgust response of a conspecific (Skelhorn, 2011). In addition to providing information about specific prey type, observing a negative foraging experience of others can therefore increase predators' attention to prey warning signals and make them more hesitant to attack any conspicuous prey (Skelhorn, 2011).

Recent studies in great tits have focused specifically on social learning about aposematic prey. Landová *et al.* (2017) found that juvenile great tits learned to avoid aposematic firebugs faster after observing an educated conspecific refusing to attack them, and Thorogood *et al.* (2018) showed that individuals learned to avoid novel aposematic prey faster after observing a negative foraging experience of a naïve conspecific. However, only a few experimental studies have investigated the role of social information in model-mimic dynamics. The first evidence comes from an early study that investigated fork-tailed flycatchers' attack rates towards distasteful *Heliconius erato* butterflies and their edible mimics *Anartia Amalthea* (Alcock, 1969). Alcock (1969) found that educated birds were more likely to handle mimics after observing a conspecific consuming them, which supports the idea that social information about mimics can decrease their protection. On the other hand, Fryday & Greig-Smith (1994) found an opposite result, showing that house sparrows did not reverse their avoidance to previously unpalatable food after receiving positive social information of its palatability. This suggests that previous personal experience about prey defences (i.e. recent encounters with defended models) might override conflicting social information, however, this requires further investigation.

Interestingly, a recent study showed that social interactions might also influence the generalisation of warning signals (Bosque *et al.*, 2018). Bosque *et al.* (2018) found that domestic chicks showed a greater hesitation to attack imperfect mimics when they were individually exposed to high model signal diversity. However, when groups of chicks were exposed to models, the results were opposite, with chicks showing a greater hesitation towards mimics when model pattern diversity was low. Although we do not know the mechanism that caused this observed difference in chicks' responses to mimics, the results of Bosque *et al.*

(2018) provide more evidence that social interactions can influence selection for prey defences in different ways to what we would predict if we only focus on personal learning. However, the role of social information in learning is likely to differ among predator communities, and this variation and its effects on prey survival remain poorly understood.

Variation in information use among predators

Although many studies have now demonstrated that animals use social information, individuals are often found to vary in their information use, and this can be influenced by many factors, such as an individual's age, sex and personality (Mesoudi *et al.*, 2016). For example, juvenile female blue tits were found to be more likely to learn a novel foraging task socially, compared to other age and sex groups (Aplin, Sheldon & Morand-Ferron, 2013), and fast exploring great tits were more likely to copy a foraging choice of a demonstrator, compared to slow exploring individuals (Marchetti & Drent, 2000). These effects might, however, be context-dependent, with a more recent experiment finding an opposite effect of personality, with slow exploring great tits relying on social information more than fast explorers (Smit & van Oers, 2019), consistent with a previous study in barnacle geese (Kurvers *et al.*, 2010). Predators might also value social information differently, depending on the circumstances, such as their previous personal experience with prey or the cost to gather personal information (Laland, 2004; Kendal *et al.*, 2005), and this could create even more heterogeneity in information use. Variation among individuals was demonstrated in the study by Thorogood et al. (2018): even though social information reduced the mean predation risk for aposematic prey, socially educated great tits still varied in their tendency to attack different prey types. This variation could be explained by individual differences in dietary wariness (Marples & Mappes, 2011; McMahon *et al.*, 2014) or personality type (Exnerová *et al.*, 2010), as well as an individual's current energetic state (Barnett *et al*., 2007; 2012; Skelhorn et al., 2016) or toxin load (Skelhorn & Rowe, 2007). How these factors influence social information use, however, remains untested, and in Chapter 2 I investigate this within-species variation in great tits by testing how previous experience of toxins influences reliance on social information about aposematic prey.

The tendency to use social information is also likely to differ among predator species. For example, in contrast to many other avian predators (Mason & Reidinger, 1982; Mason *et al*., 1984; Fryday & Greig-Smith, 1994; Landová *et al.*, 2017; Thorogood *et al*., 2018), hens were not found to develop aversion to coloured food after observing a disgust response of a demonstrator (Sherwin, Heyes & Nicol, 2002). This variation among predators could have important consequences for prey (Endler & Mappes, 2004), but so far social avoidance learning has been tested only in a handful of species (e.g. Mason & Reidinger, 1982; Mason *et al*., 1984; Fryday & Greig-Smith, 1994; Johnston *et al*., 1998; Landová *et al.*, 2017; Thorogood *et al*., 2018). Most of this experimental work has focused on birds, although there is some evidence that vervet monkeys (van de Waal, Borgeaud & Whiten, 2013) and tamarins (Snowdon & Boe, 2003) can acquire avoidance to unpalatable food by observing others (but see Visalberghi & Addessi, 2000 for contrasting results in capuchin monkeys). Experiments with avian predators might be particularly important when studying prey signals, as birds are visual foragers and potential predators for many aposematic prey. However, previous studies with bird predators (Mason *et al*., 1984; Fryday & Greig-Smith, 1994; Johnston *et al*., 1998; Sherwin *et al*., 2002; Landová *et al.*, 2017; Thorogood *et al*., 2018) differ in their experimental designs, using different foraging tasks and prey items, and providing observers with different types of social information. This makes between-species comparisons difficult, and experiments where social information and learning tasks are standardised are therefore required if we want to compare information use among different predator species. In Chapters 3 and 4, I investigate how blue tits use social information in their foraging decisions, with previous work providing only weak evidence of their social learning (Sasvári, 1979; 1985; Aplin *et al*., 2013). In Chapter 5, I then compare social information use of blue tits and great tits in the same experimental set-up. In addition, I investigate whether blue tits and great tits use heterospecific information about prey defences, which can help us to understand how social information spreads in more complex predator communities with several predator species.

Understanding how predators use social information in their foraging decisions and how this varies among predator communities is important if we want to understand the observed diversity of prey warning signals in nature. Variation among predators in their tendency to attack aposematic prey is suggested to be an important factor influencing the evolution of warning signals, such as signal conspicuousness (Endler & Mappes, 2004). In addition to possible differences in information use, predator species might differ in their susceptibility to prey toxins (Fink *et al.*, 1983; Brodie & Brodie, 1990), as well as in their hunting strategies and visual systems (Mochida, 2011), and the ability to learn to discriminate and avoid aposematic prey (Exnerová *et al.*, 2003; 2007; Rowland, Fulford & Ruxton, 2017), which could create varying selection pressures for prey signals. For example, specialist predators might increase predation risk for aposematic prey, creating selection pressures for less conspicuous signalling (Valkonen *et al.*, 2012). Heterogeneity in a predator community can also help to maintain polymorphisms in warning signals if the selective advantage of each colour morph depends on the predator community's composition (Nokelainen *et al.*, 2014). Similar to variation in other aspects of predator behaviour, variation in social information use could have important consequences for prey. For example, if social information use is important in facilitating the evolution of aposematism (Thorogood *et al*., 2018), aposematic forms could be predicted to be more common when a predator community consists of individuals that are more likely to observe others. Social transmission of information might also be important for the maintenance of existing aposematic signals. Indeed, selection pressures for warning signals may vary temporally, depending on the number of naïve predators, as demonstrated in a field study where conspicuous prey were found to be at a disadvantage when unexperienced fledglings were abundant (Mappes *et al.*, 2014). However, this predation cost might be reduced if naïve juveniles learn about aposematic prey socially, and in Chapter 6, I investigate this by conducting an avoidance learning experiment in the field during the summer when naïve juveniles are abundant.

STUDY SYSTEM

In my thesis I use wild blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) as model predators to investigate how predators use different sources of information in their foraging decisions. Both species are visual foragers and generalist predators with a variable diet (Cowie & Hinsley, 1988; Naef-Daenzer, Naef-Daenzer & Nager, 2000), so they are potential predators for many aposematic species. Parid tits are easy to keep in temporary captivity which enables controlled laboratory experiments. Indeed, both blue tits and great tits have been used widely in captive predation experiments (e.g. Alatalo & Mappes, 1996; Exnerová *et al*., 2007; Kikuchi *et al*., 2016) and social learning studies (e.g. Sasvári, 1979; Marchetti & Drent, 2000; Aplin *et al*., 2013). There is good evidence of social information use in great tits, with birds acquiring novel foraging skills (Sasvári, 1979) and food preferences (Marchetti & Drent, 2000), as well as avoidance to aposematic prey (Landová *et al.*, 2017; Thorogood *et al*., 2018) by observing conspecifics. In blue tits, however, the evidence is less clear. Sasvári (1979; 1985) found that blue tits were less likely to use social information than great tits, with only approximately half of the individuals learning a novel foraging task socially. A more recent study found similar results, showing again that only 50 % of tested blue tits acquired the novel foraging skill after seeing a conspecific demonstrator performing it (Aplin *et al*., 2013). How blue tits use social information about defended prey, however, remains untested.

I first investigated social information use by conducting experiments with birds in captivity. I conducted part of the work at Konnevesi Research Station in Central Finland (University of Jyväskylä) and part at the Sub Department of Animal Behaviour in Madingley (University of Cambridge). Parid tits are common in both Finland and in the U.K and I captured them for my experiments using a peanut trap or mist nets. In the experiments, I provided individuals social information using video playback of a demonstrator (Fig. 2). Video playback has been used previously with great tits (Snijders, Naguib & Oers, 2017; Thorogood *et al*., 2018; Smit & van Oers, 2019) and it provides a good method to control and manipulate the information that is presented to observers. I then studied birds' foraging choices using simple multiple-choice tasks, or the 'novel world' method (Alatalo & Mappes, 1996). In novel world experiments birds are presented with prey items with artificial symbols (typically a cross and a square) that are evolutionarily novel. This is important, as birds might have initial biases towards any real prey species that they could have encountered in the wild. In the experiments one symbol is cryptic against the background and represents palatable prey, whereas the other symbol is 'aposematic', i.e. conspicuous and unpalatable. Bird are allowed to forage in the novel world environment, and we can then investigate how fast they learn to avoid novel aposematic prey, and how prior social information influences this learning process and the fitness of different prey types (Thorogood *et al*., 2018). Previous novel world experiments have been conducted in large aviaries (e.g. Lindström *et al*., 1999a; Thorogood *et al*., 2018) which increases the costs of finding prey and creates realistic foraging situations. However, this also makes the experiments time-consuming and logistically difficult. Therefore, here I developed a new 'small-scale novel world' method where birds are presented with the same symbols but in a smaller testing cage (Fig. 3). This allowed me to test multiple individuals at the same time and therefore obtain large sample sizes for my experiments.

The work at Konnevesi Research Station (Chapters 2, 4 and 5) was carried out with permission from the Central Finland Centre for Economic Development, Transport and Environment and license from the National Animal Experiment Board (ESAVI/9114/ 04.10.07/2014) and the Central Finland Regional Environmental Centre (VARELY/294/2015). The study in Madingley (Chapter 3) was conducted under existing Home Office (PPL 60/4322) and Natural England (2015-6665-SCI-SCI-3) licenses (held by Hannah Rowland). Birds in the experiments were treated following the ASAB guidelines for the treatment of animals in behavioural research and teaching.

Figure 2. Great tit watching video playback. A computer monitor is placed against the plexiglass wall of the test cage.

Figure 3. ‘Small-scale novel world’ experimental set-up. Birds are presented with backgrounds (white A1 sheets with printed crosses) that contain cryptic palatable prey (crosses) and conspicuous aposematic prey (squares). Birds are allowed to attack 4 prey items before the background is replaced with the next one.

In addition to experiments with birds in captivity, I investigated social information use in a wild bird community. Outside the breeding season parid tits form mixed species foraging flocks (Ekman, 1989) which provides opportunities for information transfer within and between species. Both blue tits and great tits are common visitors at bird feeders and new technology, such as radio frequency identification (RFID) tags, enables recording birds' visits at the feeders. Based on these records, it is possible to construct social networks of wild bird populations (Farine and Whitehead, 2015) and previous studies have found that great tits have consistent roles in these networks (Aplin *et al*., 2015a). Furthermore, information about the location of food patches (Aplin *et al.*, 2012) and novel foraging skills (Aplin *et al*., 2015b) has been shown to spread through the social network of great tits. I used similar methods to investigate how avoidance of novel food spreads through the population. I conducted a field experiment in Madingley Wood which is an established study site in Cambridge. Great tit and blue tit populations in the wood are monitored by fitting birds with British Trust of Ornithology (BTO) ID rings and small RFID tags (Fig. 4). We can investigate birds' foraging behaviour at the feeders that are fitted with RFID antennas and data loggers. These record birds' individual RFID tag codes every time they land on a feeder which enables us to collect data remotely about the social relationships among individuals, as well as record their foraging choices. In my field experiment, I presented birds with novel palatable and unpalatable food (Fig. 5), and investigated how fast they learned to discriminate the food types and whether this was influenced by social information from others.

Figure 4. Blue tit chick fitted with a RFID tag.

Figure 5. In the field experiment birds were presented with novel palatable and unpalatable food (coloured almond flakes). Bird feeders were fitted with RFID antennas and individual RFID tag codes enabled us to identify individuals that visited the feeders.

THESIS OUTLINE AND FORMAT

In my thesis I am addressing four main questions: 1) how does social information use vary within and 2) between predator species, 3) do predators use social information across species boundaries, and 4) how does social information about prey quality spread in a wild predator population? I first focused on individual variation within species by investigating how previous experience with toxic prey influences great tits' reliance on social information about aposematic prey using a small-scale novel world set-up (Chapter 2; Hämäläinen *et al*., 2019a). In Chapter 2, I also investigated the effects of social information on model-mimic dynamics in the prey population by testing whether social information about palatable mimics makes educated predators more likely to resample previously unpalatable prey.

In the following chapters, I extended my research to another species by conducting similar experiments in blue tits. Even though previous studies have shown that great tits use social information from videos of a demonstrator (Snijders *et al*., 2017; Thorogood *et al*., 2018; Smit & van Oers, 2019), this method has not been used in blue tits. Therefore, I first tested how blue tits respond to videos of a conspecific and if they then use the acquired social information in their foraging decisions (Chapter 3; Hämäläinen *et al*., 2017). Because this experiment did not provide clear evidence of social information use, I next investigated if blue tits are more likely to rely on social information from a live demonstrator, compared to video playback (Chapter 4; Hämäläinen *et al*., 2019b). In these experiments I tested social information use with simple multiple-choice tasks. To make the foraging situation more realistic and to compare information use between and across the two species, I next investigated whether blue tits and great tits use conspecific and heterospecific information about aposematic prey when prey are encountered in a novel world set-up (Chapter 5). After finding evidence that both species used social information about prey defences in a captive environment, I finally tested whether birds learned socially about prey unpalatability in the wild (Chapter 6). In Chapter 7, I discuss the broad implications of my findings and identify potential areas for further research.

Each chapter of my thesis has been written in manuscript format for publication, with Chapters 2, 3 and 4 published (Hämäläinen *et al.,* 2017; Hämäläinen *et al.,* 2019a; Hämäläinen *et al.,* 2019b), and Chapter 5 currently in review. Therefore, I have written chapters from a plural perspective ('we' instead of 'I'), and some information is repeated in each chapter. Supplementary material for different chapters is included in Appendices 1-4.

CHAPTER 2

Social information about novel aposematic prey is not influenced by a predator's previous experience with toxins

Hämäläinen, L., Mappes, J., Rowland, H.M. & Thorogood, R. (2019). *Functional Ecology.*

Data collection for this chapter was assisted by Tuuli Salmi.

Aposematism is an effective antipredator strategy. However, the initial evolution and maintenance of aposematism is paradoxical because conspicuous prey are vulnerable to attack by naïve predators. Consequently, the evolution of aposematic signal mimicry is also difficult to explain. The cost of conspicuousness can be reduced if predators learn about novel aposematic prey by observing another predator's response to that same prey. On the other hand, observing positive foraging events might also inform predators about the presence of undefended mimics, accelerating predation on both mimics and their defended models. It is currently unknown, however, how personal and social information combine to affect the fitness of aposematic prey. For example, does social information become more useful when predators have already ingested toxins and need to minimise further consumption? We investigated how toxin load influences great tits' (*Parus major*) likelihood to use social information about novel aposematic prey, and how it alters predation risk for undefended mimics. Birds were first provided with mealworms injected with bitter-tasting chloroquine (or a water-injected control), before information about a novel unpalatable prey phenotype was provided via video playback (either prey alone, or of a great tit tasting the noxious prey). An experimentally-increased toxin load made great tits warier to attack prey, but only if they lacked social information about unpalatable prey. Socially educated birds consumed fewer aposematic prey relative to a cryptic phenotype, regardless of toxin load. In contrast, after personally experiencing aposematic prey, birds ignored social information about palatable mimics and were hesitant to sample them. Our results suggest that social information use by predators could be a powerful force in facilitating the evolution of aposematism as it reduces predation pressure on aposematic prey, regardless of a predator's toxin load. Nevertheless, observing foraging events of others is unlikely to alter frequency-dependent dynamics among models and mimics, although this may depend on predators having recent personal experience of the model's unpalatability.

INTRODUCTION

Aposematism is a widespread antipredator defence where prey advertise their unprofitability with conspicuous warning signals (Poulton, 1890; Ruxton *et al*., 2018). The success of aposematic prey, however, depends on avoidance learning by predators. This makes the initial evolution of aposematism paradoxical, as novel aposematic prey are expected to suffer high initial attack risk from naïve predators (Alatalo & Mappes, 1996; Mappes, Marples & Endler, 2005). Furthermore, naïve juveniles in each predator generation increase the predation risk for aposematic prey (Mappes *et al.,* 2014), presenting a continuous problem for the maintenance of aposematism. It is now also well established that even educated predators make adaptive decisions to include aposematic prey in their diet, depending on the trade-off between consuming toxins and gaining nutrients (Skelhorn, Halpin & Rowe, 2016). How, then, are aposematic prey so widespread in nature?

One potential solution is to consider this problem from an information ecology perspective (Dall *et al*., 2005). When encountering novel prey, predators should attack them if the perceived value of a meal outweighs the potential cost of consuming toxins (Sherratt, 2011; Marples, Speed & Thomas, 2018). Predators should therefore gather as much information as possible to assess this trade-off. In addition to sampling prey themselves (Skelhorn *et al*., 2016), predators can gather social information about prey defences by observing the avoidance behaviour (Landová *et al*., 2017), or negative foraging experiences of others (Mason & Reidinger, 1982; Johnston, Burne & Rose, 1998; Thorogood, Kokko & Mappes, 2018). This reduces the predation cost for aposematic prey populations, and helps to explain how aposematism can evolve (Thorogood *et al*., 2018). However, variation in predators' physiological state (Barnett, Bateson & Rowe, 2007; Skelhorn & Rowe, 2007; Barnett *et al*., 2012), dietary wariness (Exnerová *et al.*, 2007; Marples & Mappes, 2011) or the ability to learn about prey defences (Rowland, Fulford & Ruxton, 2017) mean that predators might vary in both information use and their tendency to attack aposematic prey. Individuals are predicted to value social information more when the cost to acquire personal information is high (Laland, 2004; Kendal *et al.*, 2005), and for predators, the cost of sampling novel prey could be increased when they have already ingested toxic prey. Experience of toxins could also alert predators to the presence of other toxic prey, making them warier (Rowe & Skelhorn, 2005; Skelhorn, 2016) and more likely to pay attention to the foraging behaviour of others. This within- and between species variation in prey sampling could then create varying selection pressures for aposematic signals (Endler & Mappes, 2004) as well as create heterogeneity in social information that is available for others.

Attacks on warningly coloured prey also have potential to inform others about the presence of palatable mimics (Alcock, 1969), such as automimics (palatable individuals in the population of aposematic species; Brower, Brower & Corvino, 1967) and Batesian mimics (palatable species mimicking a defended species; Bates, 1862). These prey benefit from the warning colouration of the model without having to pay the same costs of producing chemical defences (Speed *et al*., 2012), and at the same time they degrade the protection the warning signal affords the model (Lindström, Alatalo & Mappes, 1997; Gamberale-Stille & Guilford, 2004). If predators learn about mimic palatability by observing others, then predation of palatable mimics (and the model) could escalate even faster (i.e. social information drives frequency-dependent dynamics; Mappes & Lindström, 2012; Thorogood & Davies, 2012). An early study by Alcock (1969) provided support for this idea, showing that fork-tailed flycatchers were more likely to handle an *Anartia amalthea* butterfly, a palatable mimic of aposematic *Heliconius erato,* after observing a conspecific's attacks on the mimic. More recently, Bosque *et al*. (2018) showed that predator generalisation might also be influenced by social conditions: after exposure to high model signal diversity, domestic chicks attacked imperfect mimics more if they were tested in a group, rather than alone. Social interactions among predators might therefore influence model-mimic dynamics by both enhancing avoidance learning and generalisation when individuals observe others consuming models (Mason & Reidinger, 1982), as well as increasing attack rates on both prey types when individuals observe others consuming palatable mimics (Alcock, 1969).

Previous experience with toxic prey might influence how predators use social information about defended prey and their mimics. For example, a high toxin load might make individuals less willing to sample novel prey and more likely to rely on social information obtained from observing less risk-aversive individuals. How previous consumption of toxins influences learning about novel aposematic prey, however, remains untested despite its assumed key role in post-ingestive learning. Therefore, we conducted an experiment where we tested 1) how previous experience of toxic prey influences predators' likelihood to use social information about novel aposematic prey, and 2) how social information about the presence of palatable mimics then influences educated predators' propensity to sample previously unpalatable prey. We tested this with wild-caught great tits (*Parus major*) that have been model predators in many avoidance learning studies (e.g. Alatalo & Mappes, 1996; Lindström *et al*., 1999a; Ihalainen, Lindström & Mappes, 2007; Thorogood *et al*., 2018). Similar to many other bird species (Clark, 1970; Hämäläinen *et al*., 2017), they respond to aversive food by wiping their beaks on a perch, and this can be manipulated with video playback to provide cues of food unpalatability to others (Thorogood *et al*., 2018). Responses to prey can then be investigated using a ‘novel world’ that contains cryptic and conspicuous prey of different palatability that are evolutionarily novel to predators (Alatalo & Mappes, 1996).

We first manipulated birds’ toxin load by pre-feeding individuals with two mealworms injected with either chloroquine phosphate or water (following Skelhorn & Rowe, 2007; Rowland *et al*., 2010), before providing half of the birds in each treatment with social information about the palatability of novel aposematic prey. We predicted that this higher toxin load would (i) increase the costs of sampling prey and make predators more hesitant to attack any prey, but that (ii) social information would allow predators with an increased toxin load to recover these costs and facilitate rapid learning. We then investigated whether social information of a mimic’s palatability could shift educated predators back to sampling these previously aposematic prey by testing their reversal learning. We predicted that birds receiving social information would attack the first palatable mimic faster, and consume more mimics than birds that only had opportunities to gather personal information about prey palatability.

METHODS

Predators

The experiment was conducted at Konnevesi Research Station in Central Finland during the winter of 2017. We caught wild great tits (n = 68, 15 female and 19 male juveniles, and 12 female and 22 male adults, i.e. age > 1 year) from feeding sites and housed them individually in plywood boxes (80 × 65 × 50 cm) for approximately one week before release. Sunflower seeds, tallow and peanuts were provided ad libitum, except prior and during experiments when birds where food-deprived for two hours to ensure their motivation to forage. Fresh water was always available. Birds’ sex and age were determined based on plumage, and we calculated their body condition index using weight (0.25 g) and tarsus length (0.01 cm) measures (Peig & Green, 2009). This was assumed to be related to individuals’ health and fitness by indicating their energetic reserves.

Experimental set-up

Prey items were small pieces of almond (approximately 0.1 g) glued (with non-toxic UHU glue stick) inside a white paper packet (8 × 8 mm) that had black symbols printed on both sides. We used two symbols that differed in visibility and indicated palatability: cross (palatable, cryptic prey) and square (aposematic, conspicuous prey). Birds had no initial preferences towards the symbols (see Appendix 1). Aposematic prey were made bitter-tasting by soaking almonds in a chloroquine phosphate solution (2g of chloroquine dissolved in 30 ml of water) for one hour, following previously validated methods (e.g. Ihalainen *et al.*, 2007). At this chloroquine concentration, birds typically consume only small parts of the prey before rejecting it.

The experiment was conducted in a 50 × 66 × 50 cm sized plywood cage with a plexiglass front wall. In the foraging trials birds were presented with backgrounds that each contained 8 cryptic prey items (crosses) and 8 aposematic prey items (squares). Backgrounds were made of A1 sized white paper that had 140 printed crosses in random positions, similar to other 'novel world' experiments (Alatalo & Mappes, 1996; Lindström *et al*., 1999a; Ihalainen *et al*., 2007). Backgrounds contained also 20 fake cryptic prey items (piece of double-sided mounting tape with cross symbol) that made the background three-dimensional and cryptic prey more difficult to find. Prey items were randomly distributed and glued to the backgrounds. Before the experiment, we tested the visibility of the symbols with 10 individuals that did not participate in the main experiment (see Appendix 1). Similar to previous experiments in a large aviary (Lindström *et al*., 1999a; Ihalainen *et al*., 2007), we found that squares were approximately four times more visible against the background, compared to crosses.

Filming demonstrators

Birds were provided social information using video playback. All demonstrators (n = 10, 6 males and 4 females) were adults (>1 year). We always chose the observer-demonstrator pairs so that both birds were captured from the same location to control their familiarity. Each demonstrator was filmed (using an HD camcorder, Canon Legria HF R66) to consume 1) a palatable prey (to provide social information about palatable mimics) and 2) an unpalatable prey (to provide social information about aposematic prey) following previously validated methods (Thorogood *et al*., 2018). Prey items were similar to the prey used in foraging trials but larger (25 × 25 mm packets with 10 × 10 mm symbols) to ensure visibility to observers. When the prey was unpalatable (almond soaked in a solution of 2 g chloroquine and 30 ml of water), demonstrators dropped it quickly and showed a clear disgust response by performing vigorous beak wiping and head shaking. We edited these videos (with Windows Movie Maker), so that they consisted of 80 s of a demonstrator taking the prey, and either eating it (palatable prey) or dropping it and showing a disgust response (aposematic prey). Both videos also included 80 s (40 s before and 40 s after a demonstrator) of the alternative prey item (cross) in an empty cage to ensure that birds had seen both prey items before the test. We also filmed a control video that included 80 s of each prey item (cross and square) in an empty cage but provided no information of palatability.

Avoidance learning

Training

Before the experiment, birds (n = 57) were trained to open artificial prey items (brown paper packets) and forage from the training background (see Appendix 1 for details). Birds received the last training in the test cage on the same day that the experiment started. They were presented with a similar background that we used in the foraging trials, containing three brown and three cryptic (cross) prey that birds were required to eat before we started the experiment. This is similar to previous experiments (e.g. Ihalainen *et al*., 2007; Thorogood *et al*., 2018) and it ensures that birds learn to search for cryptic prey. It also means that birds gained some personal experience of the cryptic prey before the experiment, but this was the same for all individuals and therefore should not affect our results.

Toxin load

After birds had completed training, we manipulated their toxin load by offering birds two mealworms that were injected with either 0.02 ml of water or 0.02 ml of 1 % chloroquine phosphate solution (following Skelhorn & Rowe, 2007; Rowland *et al*., 2010). Birds could detect also this lower chloroquine concentration and 12 individuals that were given chloroquine-injected mealworms left a small piece of the second mealworm uneaten, while 16 individuals consumed both worms (chloroquine treatment n = 28). All birds that received palatable mealworms (n = 29) ate both worms.

Video playback

We used an LCD monitor (Dell E198FPF) placed against the plexiglass front wall of the cage to playback videos. We let the birds habituate to the monitor for 15 min before presenting a video of a demonstrator’s response to an aposematic prey (square symbol) or a control video (prey items only). We therefore had four different treatment groups that received (i) chloroquine-injected mealworms + social information (n = 14), (ii) water-injected mealworms + social information (n = 15), (iii) chloroquine-injected mealworms + control video (n = 14), and (iv) water-injected mealworms + control video (n = 14; Fig. 1).

Foraging trials

The LCD monitor was removed immediately after the video ended and the first background (containing 8 palatable and 8 aposematic prey) was placed on the cage floor. For each trial, birds were allowed to attack 16 prey items, with 4 taken from each of 4 backgrounds that were replaced sequentially. If birds did not attack all 4 prey items in 20 minutes, the background was removed and birds were given a break (at least 20 min) before continuing the experiment. To qualify as an attack, birds were required to open and taste the prey items, so only detaching them from the background was not counted. We recorded birds' prey choices, the latency to attack the first prey item (1 s precision) and the time to complete the first trial, i.e. the time to attack and handle (eat or reject) the first 16 prey items (1 min precision). We conducted two trials on the first day of the experiment (Day 1), and two trials on Day 2 to test if the effect of social information would persist. We then conducted one further foraging trial on Day 3 to ensure that birds had acquired avoidance to aposematic prey before beginning the next stage of the experiment. Altogether, birds consumed 80 prey items from five foraging trials. One individual refused to attack any prey on the second day and was therefore excluded from later tests.

Reversal learning

The reversal learning test was conducted on Day 3 after birds completed the fifth foraging trial. We allocated birds to treatment groups that (i) either received social information of previously toxic prey now being palatable (n = 29), or (ii) saw a control video of prey items only (n = 26). This was done semi-randomly, so that approximately half of the birds in each treatment had received social information about aposematic prey in the first part of the experiment but birds were now presented a different demonstrator so that previous social experience would not affect information use. We again presented birds first with video playback before conducting two foraging trials where birds were allowed to eat 16 prey (i.e. 32 prey in total). However, this time backgrounds contained only palatable prey items. Two individuals did not participate in the reversal learning test: one refused to attack any prey after Day 1 and another did not learn to avoid aposematic prey.

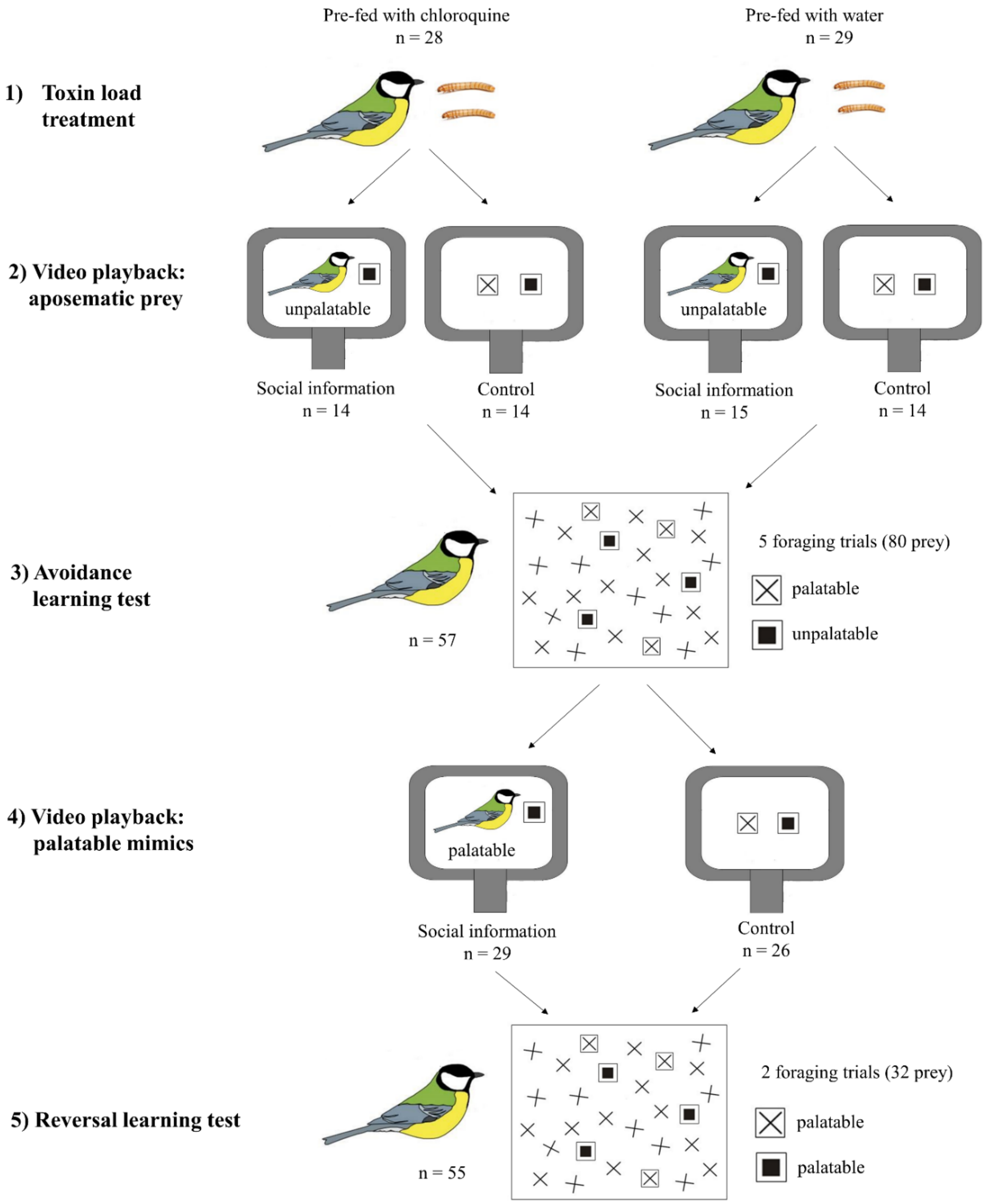


Figure 1. Experimental set-up. In the first part of the experiment, birds were pre-fed with two chloroquine- or water-injected mealworms. Half of the individuals in each treatment were then provided with social information about novel aposematic prey (the other half saw a control video) before five foraging trials with aposematic and palatable prey. In the second part of the experiment, predators (now educated) were provided with social information about palatable mimics (or a control video), and they then encountered same prey items in a palatable environment.

Statistical analyses

We first tested if social information or toxin load affected birds' initial foraging choice (cross/square) using a chi-square test. We then analysed the latency of birds to attack the first prey item and the time taken to complete the first trial. Distributions of these response variables were right-skewed so we used generalised linear models with a negative binomial error distribution. We next analysed predation on aposematic prey in the first trial (number attacked) and avoidance learning across all five trials using generalised linear models with a poisson error distribution. Explanatory variables in models included video playback (social information/control) and toxin load treatments (chloroquine/water), and individuals' sex, age and body condition index as covariates. For each analysis, we tested several models with different interaction terms and covariates, and chose the best-fitting models using Akaike's information criterion corrected for small sample sizes (see Appendix 1 for model selections). When analysing learning across trials, trial number was included as an explanatory variable and bird identity as a random effect.

We analysed reversal learning by calculating the difference between the number of aposematic prey attacked in the last (fifth) foraging trial and the number of palatable mimics attacked in the reversal learning test. This is assumed to measure how well birds retain learned avoidance towards previously unpalatable prey (Skelhorn & Rowe, 2006). We used this difference as a response variable in a generalised linear model with the type of first video presentation (social information about aposematic prey) and second video presentation (social information about palatable mimics) as explanatory variables, and sex, age and body condition as covariates. Next, to indicate how reluctant birds were to sample the previously unpalatable prey we calculated how many cryptic prey (crosses) birds consumed before attacking the first mimic and used this as a response variable in a similar model (with poisson error distribution). To disentangle the effect of social information and birds' previous experience with aposematic prey, we then restricted this model to include only birds that did not receive social information in the first part of the experiment, and used the number of aposematic prey attacked during trials 1-4 as an explanatory variable. All analyses were conducted with the software R.3.3.1 (R Core Team 2016), using *lme4* (Bates *et al*., 2015) and *MASS* (Venables & Ripley, 2002) packages.

RESULTS

Avoidance learning

Most of the birds attacked the aposematic prey (a square) as their first prey choice in the experiment (44/57 individuals), regardless of social information ($\chi^2 = 0.150$, df = 1, $p = 0.70$) or toxin load treatment ($\chi^2 = 0.766$, df = 1, $p = 0.38$). However, there was a trend for birds to attack the first prey item faster when their toxin load was increased (estimate = -0.592 ± 0.346, Z = -1.710, $p = 0.09$; Fig. 2a) but this effect was not significant at alpha level of 0.05. There was also a significant interaction between social information treatment and body condition index (estimate = 1.024 ± 0.378, Z = 2.708, $p = 0.007$). Birds in poorer body condition hesitated longer to attack the first prey item, but only when they did not receive social information. Seven individuals were not motivated to forage during the first trial and did not attack any prey items during the first 20 minutes, so we excluded them when analysing wariness to sample the first prey. Three of these birds were socially educated (all pre-fed with water) and four control birds (one pre-fed with water and three with chloroquine). We continued foraging trials with these birds after giving them a break (approximately 20 min) and after that their first choices were similar to other birds.

Birds that received social information consumed significantly fewer aposematic prey in the first foraging trial (first 16 prey), compared to the control group (estimate = -0.185 ± 0.092, Z = -2.009, $p = 0.045$; Fig. 3a). However, against our prediction, social information use was not influenced by previous experience with toxins (social information * toxin load: estimate = 0.130 ± 0.184, Z = 0.706, $p = 0.48$) and this interaction was removed from the final model. Similarly, toxin load treatment alone did not affect birds' foraging choices in the first trial (estimate = 0.101 ± 0.092, Z = 1.095, $p = 0.27$). However, the time that it took for birds to complete the first trial depended on their toxin load and received social information (social information * toxin load: estimate = -0.688 ± 0.304, Z = -2.263, $p = 0.02$; Fig. 2b). Control birds (no social information) completed the first trial significantly more slowly when they were pre-fed with chloroquine-injected mealworms, compared to the birds pre-fed with water-injected worms (estimate = 0.599 ± 0.219, Z = 2.734, $p = 0.006$). When birds received social information about prey unpalatability, toxin load no longer influenced the time to complete the trial (estimate = -0.090 ± 0.215, Z = -0.417, $p = 0.68$). This means that even though increased toxin load did not influence birds' foraging choices, it increased their wariness to attack novel prey (but only when birds did not have social information). The same trend remained when we excluded the 7 individuals that were very slow to attack the first prey item, although the interaction was no longer significant at alpha level 0.05 (social information * toxin load: estimate = -0.541 ± 0.321, Z = -1.685, $p = 0.09$). Finally, we found that juveniles completed the first trial faster than adults (estimate = -0.370 ± 0.156, Z = -2.368, $p = 0.02$).

All birds learned to discriminate the prey items better over the course of the experiment (the effect of trial number: estimate = -0.326 ± 0.019, Z = -16.723, $p < 0.001$; Fig. 3b). Birds improved at a similar rate across trials, regardless of social information (social information * trial number: estimate = -0.065 ± 0.040, Z = -1.632, $p = 0.10$) or toxin load treatments (toxin load * trial number: estimate = -0.015 ± 0.039, Z = -0.385, $p = 0.70$). Birds that received social information, however, continued to consume fewer aposematic prey than control birds (estimate = -0.341 ± 0.103, Z = -3.312, $p < 0.001$).

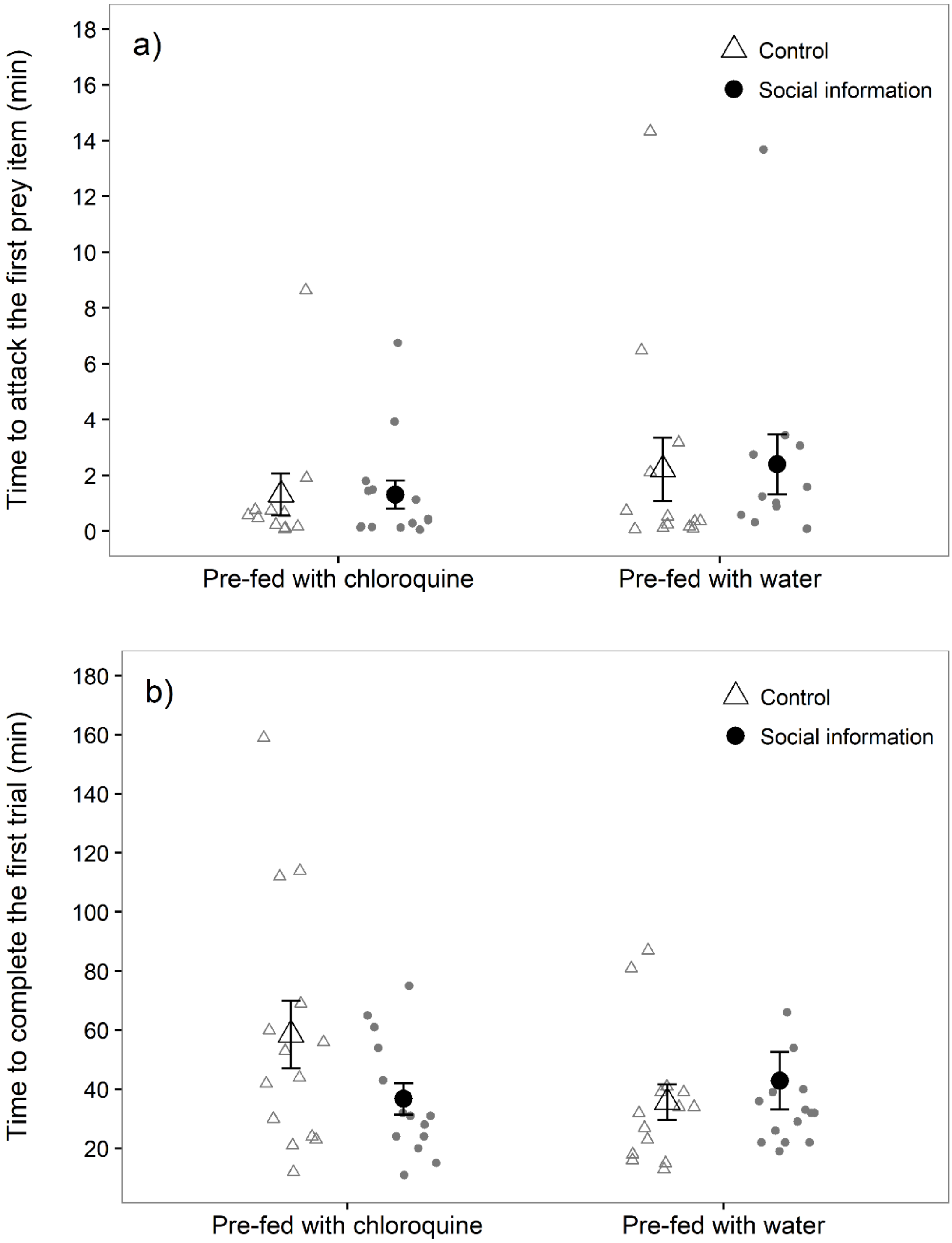


Figure 2. Birds' wariness to attack novel prey in the first foraging trial (first 16 prey items). Birds (n = 57) were pre-fed with two mealworms injected with chloroquine or water. Half of the individuals in both treatments received social information of aposematic prey (circles) and half were presented with a control video (triangles). Big symbols represent mean (± s.e) for each treatment and small gray symbols individual variation within the treatment. (a) Time (min) that it took for birds to attack the first prey item. Seven individuals did not attack any prey during the first 20 minutes and are excluded from the graph (n = 50). (b) Time (min) that it took for birds to complete the first foraging trial (attack the first 16 prey items).

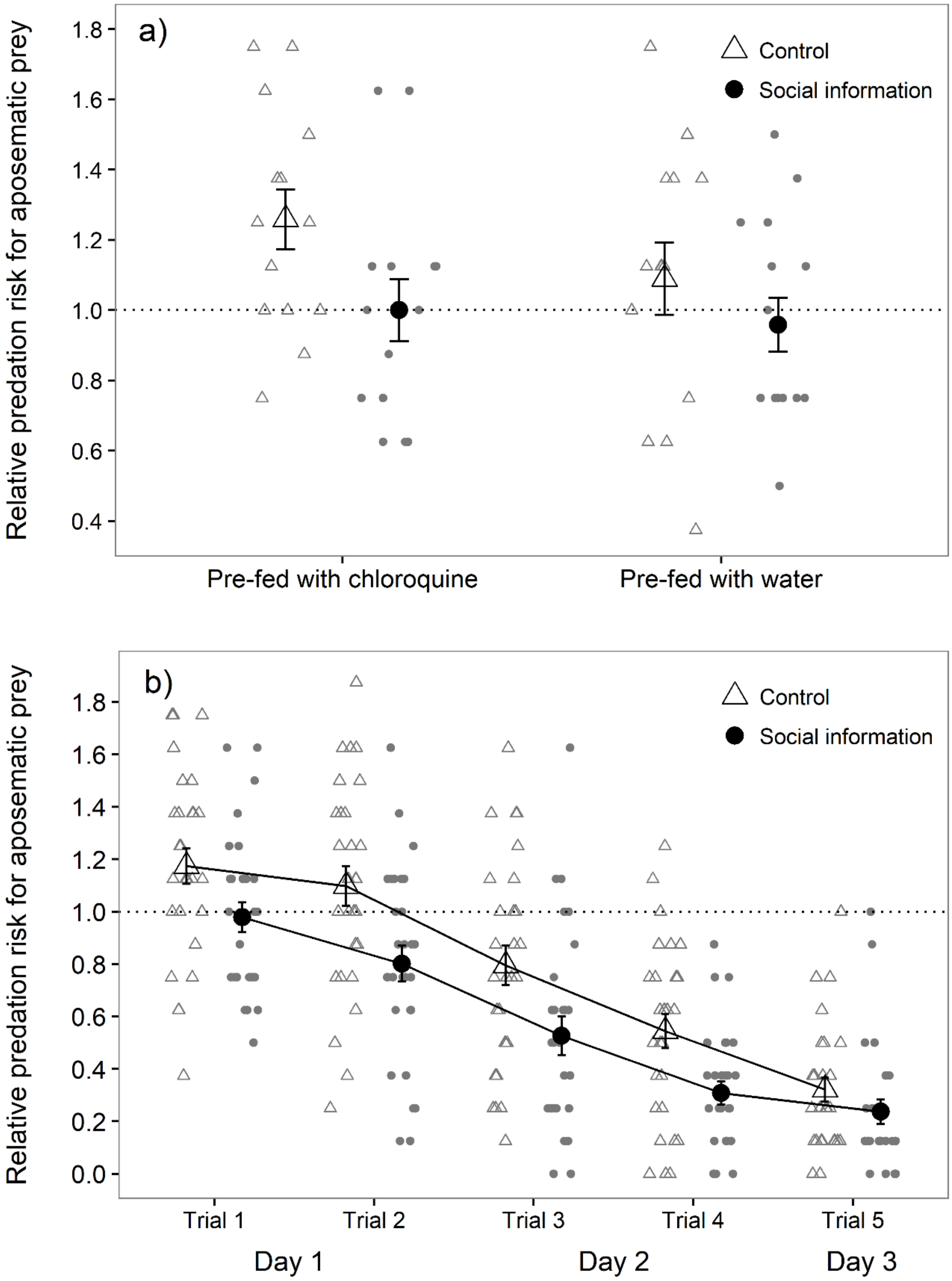


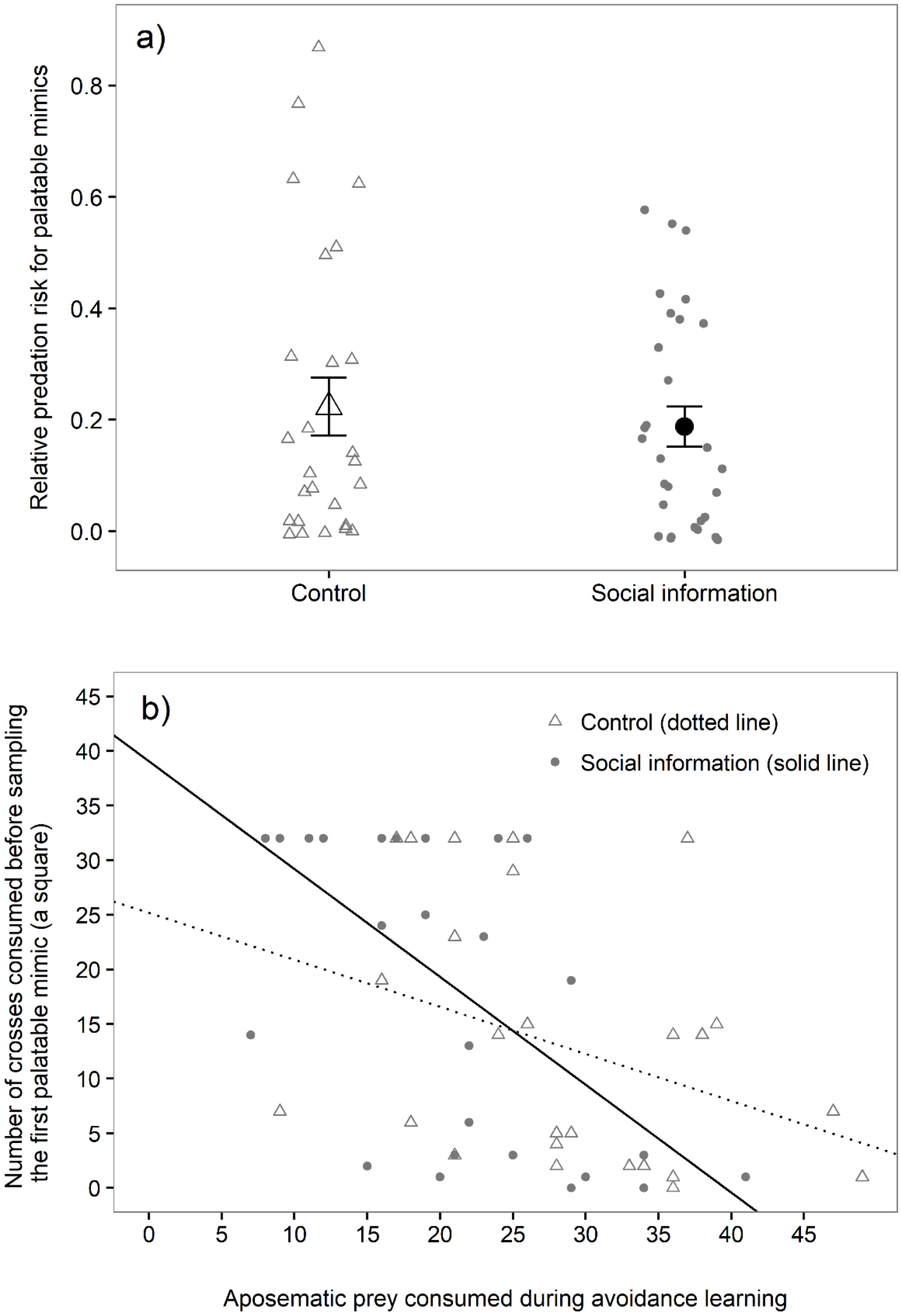
Figure 3. Relative predation risk for aposematic prey (number of aposematic prey attacked/ number expected by chance): (a) in the foraging first trial, and (b) across five foraging trials (conducted over three days). Birds (n = 57) were pre-fed with two mealworms injected with chloroquine or water. Half of the individuals in both treatments received social information of aposematic prey (circles) and half were presented with a control video (triangles). Big symbols represent mean (± s.e) for each treatment and small gray symbols individual variation within the treatment. Because previous consumption of toxins did not affect social information use, chloroquine and water treatments are combined within information treatments in (b).

Reversal learning

Even though birds used social information when learning to avoid aposematic prey, they ignored it in the reversal learning test: social information of previously aposematic prey now being palatable did not influence the number of palatable mimics that birds sampled (estimate = -0.042 ± 0.917, t = -0.046, *p* = 0.96). Instead, all birds were reluctant to attack previously aposematic prey (Fig. 4a). Because birds might value social information differently depending on previously received information, we next investigated whether the first video presentation (social information about aposematic prey on Day 1) influenced the birds' likelihood to use social information about mimics. However, we found no evidence that prior social information influenced the use of social information in the reversal learning test (first video * second video: estimate = -1.300 ± 2.046, t = -0.636, *p* = 0.53), nor did it have an effect on the number of mimics sampled (first video: estimate = 0.055 ± 0.920, t = 0.060, *p* = 0.95).

We predicted that birds would sample palatable mimics faster after receiving social information of their palatability. However, the number of cryptic prey (crosses) consumed before attacking the first mimic did not differ between social information treatments (estimate = -0.056 ± 0.071, Z = -0.782, *p* = 0.43), and this did not depend on an individual's previous experience of social information (first video * second video: estimate = -0.128 ± 0.158, Z = -0.809, *p* = 0.42). Instead, the first video presentation alone had a significant effect: birds that had received social information about aposematic prey (on Day 1) consumed more cryptic prey before attacking the first mimic (estimate = 0.294 ± 0.073, Z = 4.029, *p* < 0.001). However, these birds had also less personal experience of prey toxins because they had consumed fewer aposematic prey during avoidance learning, compared to the control birds without social information.

To disentangle the effect of social information from the number of aposematic prey consumed, we tested how previous experience with aposematic prey influenced the hesitation to attack palatable mimics, including only birds that had not received social information in the first part of the experiment. We found that birds were less hesitant to sample palatable mimics (i.e. consumed fewer cryptic prey before attacking the first mimic) when they had consumed more aposematic prey during avoidance learning (estimate = - 0.022 ± 0.007, Z = -3.388, *p* < 0.001, Fig. 4b). Therefore, the observed effect of the first video presentation on birds' wariness to attack mimics could be caused by differences in personal experience with aposematic prey. Finally, we found that females (estimate = 0.232 ± 0.072, Z = -3.213, *p* = 0.001) and individuals with high body condition index (estimate = 0.112 ± 0.036, Z = 3.157, *p* = 0.002) consumed more cryptic prey before attacking the first mimic. Eleven individuals were excluded from reversal learning analyses because they still consumed more than three aposematic prey in the last (fifth) foraging trial (relative predation risk > 0.5) which indicates weaker avoidance learning towards aposematic prey. Four of these individuals were socially educated (three pre-fed with chloroquine and one with water) and seven were control birds (four pre-fed with chloroquine and three with water). Including these individuals in the analyses did not change our results.



(Figure caption on following page)

Figure 4. Birds' (n = 55) foraging choices in the reversal learning test. (a) Relative predation risk for the palatable mimic (prey with square symbol). Half of the individuals (circles) received social information about palatable mimics and half were presented with a control video (triangles). Big symbols represent mean (± s.e) for each treatment and small gray symbols individual variation within the treatment. (b) Birds that consumed more aposematic prey during avoidance learning (x axis) were less hesitant to attack the palatable mimics, i.e. they consumed fewer cryptic prey before sampling the first mimic. Birds that received social information about aposematic prey in the first part of the experiment (circles + solid line) consumed fewer aposematic prey during avoidance learning, compared to control birds (triangles + dotted line), which could explain why they were more hesitant to attack palatable mimics in the reversal learning test.

DISCUSSION

Social interactions among predators could have important consequences for the effectiveness of prey defences when information is shared about prey palatability. We predicted that previous consumption of toxins would increase the risk to sample novel prey and make social information more valuable (Laland, 2004; Kendal *et al*., 2005), but found that great tits did not rely more on social information when their toxin load was experimentally increased. Instead, we found that birds who observed a conspecific encountering aposematic prey learned to avoid that prey type faster than control birds, regardless of their previous experience with toxins. This indicates that ingesting toxins is costly to predators even when their current toxin load is low, and naïve predators might therefore value social information in all encounters with novel prey. This is the first time that the 'novel world' experimental setup has been implemented in a small test cage, nevertheless our results are consistent with previous experiments in a larger aviary (Lindström *et al*., 1999a; Thorogood *et al*., 2018) and confirm that social cues about prey unpalatability can induce avoidance in great tits (Landová *et al*., 2017; Thorogood *et al.*, 2018) and other species (Mason & Reidinger, 1982; Mason, Arzt & Reidinger, 1984; Fryday & Greig-Smith, 1994; Johnston *et al*., 1998; Skelhorn, 2011). However, we also found that educated birds did not use social information about palatable mimics, which indicates that personal experience with toxic prey may override conflicting social information.

Even though toxin load treatment did not influence how birds used social information, it did influence their foraging behaviour. We found that birds completed their first trial more slowly when the toxin load was increased, but only when they did not have social information. Experience of toxins has been shown to increase wariness also in other studies, with predators biasing their foraging decisions away from novel warningly coloured prey after experiencing chemical defences (Rowe & Skelhorn, 2005; Skelhorn, Griksaitis & Rowe, 2008; Rowland, Ruxton & Skelhorn, 2013). We used artificial symbols instead of typical warning colours, and the experience of chloroquine did not seem to cause hesitation towards the more conspicuous prey. In fact, there was weak evidence that individuals consumed more aposematic prey when their toxin load was increased (Fig. 3a). This differs from a previous study showing that starlings with an increased toxin load decreased consumption of chemically defended prey (Skelhorn & Rowe, 2007). The individuals in Skelhorn and Rowe were, however, educated, whereas in our experiment birds did not have prior personal information about the content of the prey toxins. This indicates that even though toxin load influences the foraging choices of educated predators, it does not affect the number of aposematic prey sampled during initial avoidance learning.

Predators might also use social information to learn about the presence of palatable mimics and therefore allow knowledge of mimics to spread rapidly in a predator population, altering frequency-dependent model-mimic dynamics (Thorogood & Davies, 2012). However, we found that after personally sampling defended prey, great tits ignored conflicting social information about palatable mimics. This is consistent with other studies showing that animals often rely on their personal experience when facing contrasting social information (Fryday & Greig-Smith, 1994; van Bergen, Coolen & Laland, 2004). Social information about palatable mimics is therefore unlikely to increase attacks on models and mimics when predators have recent personal experience of the model's defence. Furthermore, we found that birds avoided mimics even in the absence of the defended models. Palatable mimics might therefore gain protection from predators even if they do not co-occur with their models, as observed in many systems (Pfennig & Mullen, 2010). However, we tested birds' response to mimics only shortly after they had experienced defended models, and more work is needed to investigate how long avoidance towards mimics lasts if models are not present. In our experiment, individuals might have also gained little benefits from using social information about mimics because of abundant alternative prey (Kokko, Mappes & Lindström, 2003; Lindström *et al*., 2004). In nature, alternative prey are likely to be more scarce which could increase predators' willingness to risk sampling previously toxic prey.

Although our results show that social information can influence predators' decisions and reduce the effects of toxin load on wariness, these effects are not absolute and individuals varied in their tendency to attack aposematic prey (also see Thorogood *et al*., 2018 for similar amounts of variation). We did not find evidence that this variation was explained by individuals' toxin load, and it is possible that other factors, such as energetic state (Barnett *et al*., 2007;

Barnett *et al.*, 2012) or personality type (Exnerová *et al*., 2010) have a bigger influence on predators' foraging choices. Interestingly, we found that birds that had consumed more aposematic prey were less hesitant to attack mimics in the reversal learning test. It is possible that these birds were simply less educated and had acquired weaker avoidance towards aposematic prey. Alternatively, they might have gained more feedback on the toxic effects of chloroquine. Even though high concentration of quinine appears to be emetic to birds (Alcock, 1970), we do not know what post-ingestive consequences it has in low doses and how birds learn about these effects (Skelhorn *et al*., 2016). Therefore, birds with more experience of aposematic prey might have learned that consuming them did not have a significant impact on their physiological state, making them more willing to sample the same prey again. Further work is needed where different sources of personal information and social information are modified to better understand why individuals vary.

In conclusion, our study supports the idea that social learning among predators can reduce predation on aposematic prey and help to explain how novel conspicuous warning signals evolve and persist in the prey population (Thorogood *et al*., 2018). However, individuals vary in their personal experience with prey and this might influence their foraging choices and reliance upon social information. We found that birds ignored social information about palatable mimics when they had conflicting personal information about the model's defence. This suggests that social information about mimics is unlikely to increase predation on models and mimics when predators have recently encountered defended models. How predators use social information about mimics in nature, however, could be influenced by many additional factors, such as the accuracy of personal information, the strength of prey defences and the abundance of alternative prey.

CHAPTER 3

Can video playback provide social information for foraging blue tits?

Hämäläinen, L., Rowland, H.M., Mappes, J. & Thorogood, R. (2017). *PeerJ*, 5*,* e3062.

Video playback is becoming a common method for manipulating social stimuli in experiments. Parid tits are one of the most commonly studied groups of wild birds. However, it is not yet clear if tits respond to video playback or how their behavioural responses should be measured. Behaviours may also differ depending on what they observe demonstrators encountering. Here we present blue tits (*Cyanistes caeruleus*) videos of demonstrators discovering palatable or aversive prey (injected with bitter-tasting Bitrex) from coloured feeding cups. First we quantify variation in demonstrators' responses to the prey items: aversive prey provoked high rates of beak wiping and head shaking. We then show that focal blue tits respond differently to the presence of a demonstrator on a video screen, depending on whether demonstrators discover palatable or aversive prey. Focal birds faced the video screen more during aversive prey presentations, and made more head turns. Regardless of prey type, focal birds also hopped more frequently during the presence of a demonstrator (compared to a control video of a different coloured feeding cup in an empty cage). Finally, we tested if demonstrators' behaviour affected focal birds' food preferences by giving individuals a choice to forage from the same cup as a demonstrator, or from the cup in the control video. We found that only half of the individuals made their choice in accordance to social information in the videos, i.e., their foraging choices were not different from random. Individuals that chose in accordance with a demonstrator, however, made their choice faster than individuals that chose an alternative cup. Together, our results suggest that video playback can provide social cues to blue tits, but individuals vary greatly in how they use this information in their foraging decisions.

INTRODUCTION

Potential prey items differ in their nutritional benefits and palatability (Skelhorn, Halpin & Rowe, 2016). Therefore, when foraging, animals face decisions that require an estimation of the profitability of prey (Pyke, Pulliam & Charnov, 1977) in order to maximise their fitness. As well as learning from their own experience with prey (Skelhorn *et al*., 2016), predators can gather social information from observing the foraging experiences of others (Galef & Giraldeau, 2001). For example, observing conspecifics consuming palatable food positively influences food preferences in many avian species (Mason & Reidinger, 1981; McQuoid & Galef, 1993; Fryday & Greig-Smith, 1994). However, the potential for information to be available from observing an encounter with unpalatable prey has received far less attention.

Many bird species show a clear disgust response to aversive food by vigorously wiping their beaks on a perch (Clark, 1970; Ganchrow, Steiner & Bartana, 1990). This cue might provide social information about the profitability of food resources to others. For example, young chicks that observe beak wiping and head shaking are less likely to peck at, or consume, the same foods (Johnston, Burne & Rose, 1998; Skelhorn, 2011), and red-winged blackbirds will avoid feeding cups if demonstrators are induced to vomit after eating from them (Mason & Reidinger, 1982). Parid tits are one of the most studied wild birds in Europe, with an increasing focus on their social behaviour and learning (e.g. Sasvári, 1979; Marchetti & Drent, 2000; Aplin, Sheldon & Morand-Ferron, 2013). While previous studies have shown that parid tits can learn a novel foraging task by observing other individuals (Sasvári, 1979; Aplin *et al*., 2013), it is not yet known how they use social information about food palatability in their foraging decisions.

Our first aim was to investigate how wild-caught blue tits (*Cyanistes caeruleus*) use information from foraging conspecifics, and if their response differs depending on the palatability of food that demonstrators encounter. However, when studies involve experimentally manipulating social behaviour, it can be difficult to control what stimuli focal birds observe (McQuoid & Galef, 1993). Issues can also arise because of social characteristics of the birds themselves (e.g. dominance; Nicol & Pope, 1999). Video playback might circumvent these issues and provide many advantages over live demonstrators. With videos, it is possible to manipulate the characteristics presented and control the timing of the video presentation, thus enabling controlled and standardised stimuli to be presented to focal individuals (D’Eath, 1998; Woo & Rieucau, 2011). Furthermore, use of video playback has ethical implications. For instance, using video playback to study how individuals use social information about food palatability requires fewer demonstrators to be encouraged to eat unpalatable food (e.g. Mason & Reidinger, 1982).

Video playback, however, has potential shortcomings that should be considered when using these stimuli in behavioural studies (D'Eath, 1998; Woo & Rieucau, 2011). For instance, physical interactions between an observer and a demonstrator often play an important role in certain behaviours, such as in aggressive contests and courtship, so the applicability of video playback in these contexts may be limited (D'Eath, 1998). To be able to study focal individuals' responses to specific stimuli, we also need to be sure that individuals pay attention to subtleties in demonstrators' behaviour instead of simply responding to their presence in a video (McQuoid & Galef, 1993). To date, video presentations have been used successfully in both captive (Rowland *et al*., 1995; Ord *et al*., 2002; Bird & Emery, 2008) and field studies (Clark, Macedonia & Rosenthal, 1997; Burford, McGregor & Oliveira, 2000; Gunhold, Whiten & Bugnyar, 2014) across different contexts, including studies of mate preference (e.g. Ophir & Galef, 2003), social learning (e.g. McQuoid & Galef, 1993), and predator recognition (e.g. Evans, Macedonia & Marler, 1993), and for a range of taxa, including mammals (Gunhold *et al*., 2014), fish (Rowland *et al*., 1995), lizards (Ord *et al*., 2002), spiders (Clark & Uetz, 1992), and birds (Rieucau & Giraldeau, 2009; Zoratto *et al*., 2014). Surprisingly, however, the validity of video playback has not been tested for parid tits. Therefore, the second aim of our study was to investigate its applicability.

In this study, we presented focal birds with videos of a demonstrator encountering palatable and aversive prey items in novel, coloured feeding cups. We first quantified variation in demonstrator blue tits' behaviour when encountering these two prey types before presenting standardised videos of these encounters to focal birds. The videos also included a control section that consisted of a different coloured feeding cup in an empty cage; we predicted that individuals would pay more attention to the videos when a conspecific was present. The control section was presented to focal birds both before and after a demonstrator appeared on the screen to investigate if birds' response to control cups would change after they had seen a demonstrator foraging from a different cup. Because demonstrators were more active during the encounter with aversive prey, we also predicted that this might provide more cues and therefore elicit more vigorous response in focal birds, compared to a video of palatable prey.

Recent studies have shown that acquiring information by observing others does not always result in use of that social information (Carter *et al*., 2014; Mesoudi *et al*., 2016). To investigate whether video playback can be used to manipulate social information for blue tits, we used a simple choice test to record if observers preferred to feed from a similarly coloured cup as the demonstrator, or from the different coloured cup (present in the control video). We predicted that focal birds observing a demonstrator encountering a palatable prey would choose to feed from the same cup as the demonstrator, whereas observation of an encounter with aversive prey would lead them to avoid the cup in which the demonstrator found the distasteful prey.

Finally, familiarity with the demonstrator may influence responses to video playback. Previous studies have shown that Japanese quail (*Coturnix japonica*) females identify specific males that they see in videos (Ophir & Galef, 2003) and that rooks (*Corvus frugilegus*) spend more time looking at a video of their partner, compared to a video of a nonaffiliated conspecific (Bird & Emery, 2008). The value of social information may also vary depending on familiarity (Firth, Sheldon & Farine, 2016; Mesoudi *et al*., 2016) or previous experiences (Farine, Spencer & Boogert, 2015) with the demonstrator. We attempted to account for this by including a measure of association strength from our study population's social network, and tested whether the identity of the demonstrator would influence the behavioural responses of observers.

METHODS

Birds and housing

The study was conducted from January to March 2016 at Madingley Wood (0°3.2′E, 52°12.9′N), which is an established study site in Cambridge, UK. There is an ongoing long-term study of great tit (*Parus major*) and blue tit populations in the area and birds have been given British Trust of Ornithology (BTO) ID rings and fitted with radio frequency identification (RFID) tags (fitted to a colour ring) since 2012. In January, five sunflower seed feeders were fitted with RFID antennas and data loggers that scanned birds' unique RFID tag codes when they landed on a feeder. During the winter, great tits and blue tits form loose fission–fusion flocks that move between food sources (Ekman, 1989). This flocking behaviour allows us to use the records from the feeders to identify individuals that forage in the same flock. We used a Gaussian mixture model to detect these gathering events (Psorakis *et al*., 2012), and then calculated social associations (i.e. edge weights in the social network) between individuals based on how often they were present in the same group (gambit of the group approach; Franks, Ruxton & James, 2010).

Wild blue tits (n = 25) were captured with mist nets in February 2016. Individuals were chosen from the population randomly, but RFID tag records enabled us to calculate association strengths for each observer-demonstrator pair used in the experiment. All captured birds were adults (based on plumage), but their sex was unknown. Birds were housed indoors in individual plywood cages (80 × 65 × 50 cm) with a daily light period of 12 hours. Food (sunflower seeds, peanuts and tallow) and water were provided ad libitum except prior and during the experiment when food was restricted for one hour to motivate birds to forage. Birds were kept in captivity for a maximum of four days until released at the capture site, and they were in auditory (but not visual) contact during housing and experiments.

Experimental protocol

Prey types

We created two types of prey: a palatable mealworm and an aversive mealworm that was injected and coated with 2.5% solution of denatonium benzoate (Bitrex). Bitrex tastes bitter to humans (Chandrashekar *et al*., 2000) and elicits beak wiping in birds (Skelhorn & Rowe, 2009).

Video recording

We used six individual blue tits as demonstrators for the videos. Three of these birds were first used as observers in the social information use test before recording them as demonstrators. Birds were moved from their home cage to wooden test cages (66 × 50 × 50 cm) that differed from the home cage in that they had a front wall made of plexiglass. We coated the plexiglass with tinted film that made it possible to observe and film the birds while minimising effects on their behaviour

We first filmed the demonstrators eating a palatable mealworm in a coloured feeding cup (yellow or green). We then filmed the same individual eating a Bitrex mealworm in a different coloured cup (blue or purple). Because an experience of prey with chemical defences was likely to affect birds' response towards palatable prey and their willingness to consume it, we always filmed responses towards palatable prey first.

From the videos, we quantified differences in demonstrators' response to palatable and aversive prey from first contact with the prey item until 10 s after eating. We measured (i) how long demonstrators spent wiping their beaks on a perch (in seconds), (ii) the number of beak wipes they performed, and (iii) the number of times the head was shaken. We then used these videos to create standardised videos to present to observers.

Video presentation

All videos included 45 s of a demonstrator finding a prey item in a coloured cup and a demonstrator's response to that prey. In addition, each video included 60 s of a different coloured cup in an empty cage to make sure that observers were familiar with both cup colours and their foraging choice would depend on the information in the video instead of novelty of cups. Thirty seconds of this control video was shown to observers before a demonstrator appeared on the screen and 30 s was shown after a demonstrator, as we predicted that observers might pay attention to the cups differently after seeing a foraging conspecific. We used green and yellow cups when demonstrators encountered palatable prey (randomising which cup colour was shown with a demonstrator and which in an empty cage), and blue and purple cups when demonstrators encountered aversive prey. We showed each observer (n = 22) two videos, once for each prey type. These two videos were shown on sequential days and the order was randomised among birds. We did not change the demonstrator between different prey types, so observers saw the same demonstrator encounter both palatable and aversive prey. Therefore, we think that any differences in responses of the observers are likely due to the prey type, not the demonstrator's identity.

Observers were moved to a test cage two hours before the video presentations to allow habituation to the cage. We then placed a computer monitor (Dell 1908FPc, 19″) against the plexiglass front wall of the cage for 15 min before showing the video (Fig. 1a). We recorded observers during the video playback (using a DBPOWER 1080P action camera), so that we could classify their behaviour during the different sections of the video: when they were shown (i) a cup (control) before the demonstrator appeared (30 s), (ii) the demonstrator's response to the prey in a differently coloured cup (45 s), and (iii) the control cup once the demonstrator was no longer present (30 s; Fig. 1b). From these recordings, we analysed (i) the time that a bird spent facing the screen or flying, (ii) the number of head turns indicating increased vigilance, and (iii) the number of hops a bird performed on a perch, suggested to indicate increased nervousness such as neophobia (e.g. Heinrich, 1988).

The entire cage was not in the field of view of the camera, so sometimes birds flying close to the roof of the cage, or holding on near the roof, could not be seen in the video. Therefore, we excluded individuals from our dataset that were visible for less than 30 s during the whole 105 s video (60 s of a cup only and 45 s of a demonstrator). After removing these individuals, our dataset included 13 individuals that were shown videos of a demonstrator encountering both palatable and aversive prey, and 3 individuals that were visible only when they were shown a video of a demonstrator encountering palatable prey. The final sample size for video analysis was therefore 16 observers when prey was palatable (mean time that observers were visible = 81 s, range = 38–105 s) and 13 observers when it was aversive (mean time that observers were visible = 90 s, range = 43–105 s).

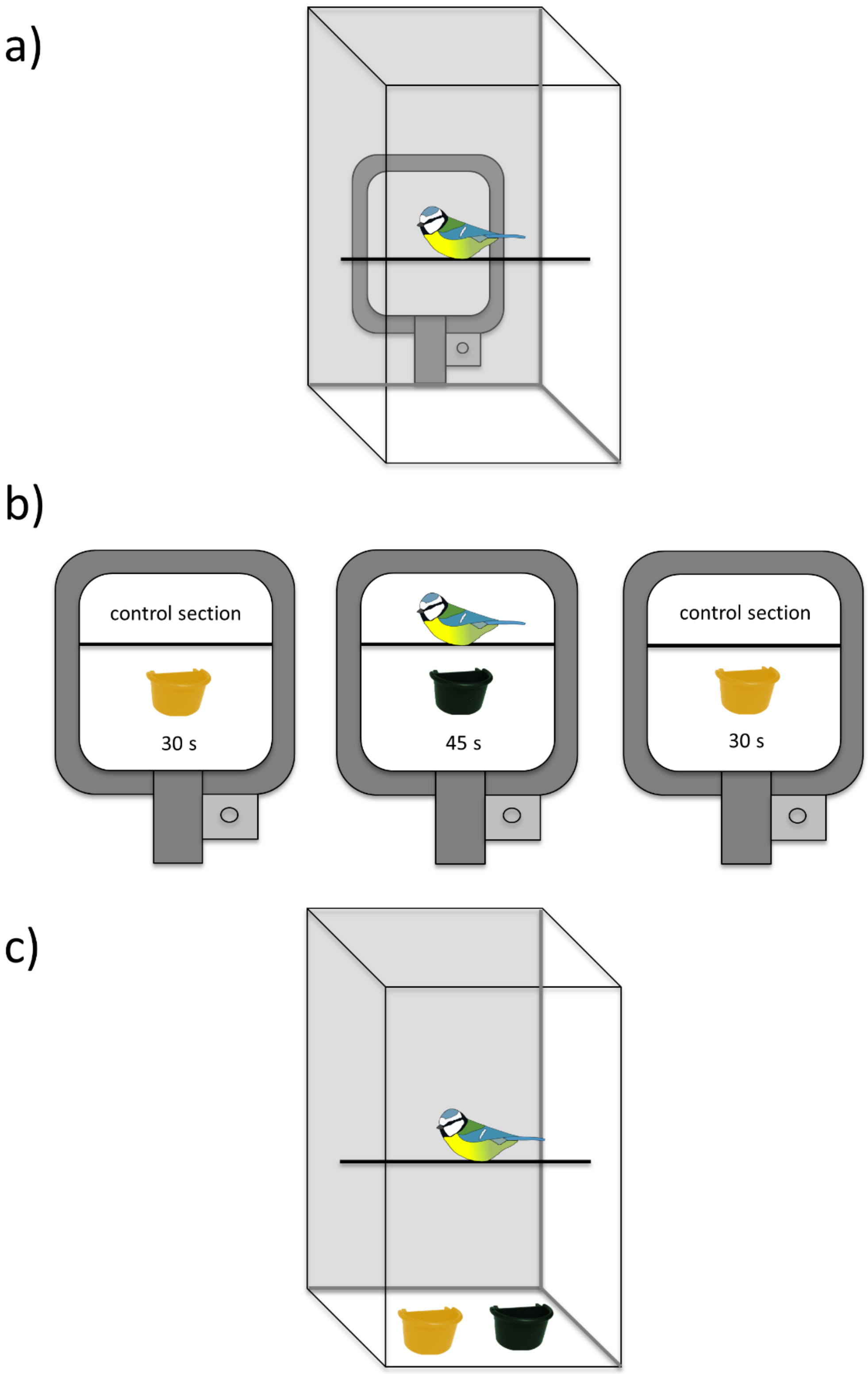


Figure 1. The experimental set-up. (a) The view of the test cage (a computer monitor and a camera recording focal birds' behaviours were placed against a plexiglass wall of the cage). (b) Presentation of video playback including a demonstrator discovering prey from a coloured feeding cup (45 s) and two control sections of a different coloured cup (30 s before and 30 s after a demonstrator). (c) Social information use test, where focal birds had a choice to forage from the same cup as the demonstrator, or from the cup in the control video.

Observer social information use test

Immediately following each session of video playback, we tested if focal birds (n = 22) used social information from the videos by giving them a choice between two different coloured cups: the cup that a demonstrator fed from, and the cup that was shown in an empty cage without a demonstrator (Fig. 1c). Both cups were filled with sand, so that birds could not see their contents and the time cost to search for prey was higher. Before the test, focal birds had been trained in their home cages to search for food hidden in the sand by offering them mealworms in a white feeding cup. Training was done stepwise, by first offering mealworms that were clearly visible, and then covering them partly with sand, until birds learned to search for worms that were completely hidden. Focal birds were therefore familiar with the foraging task in the experiment. We recorded which cup birds landed on first and the latency of this choice (s). The test was finished after birds had landed on both cups, or after 20 min. Two birds in the palatable prey test and one individual in the aversive prey test did not land on either cup in 20 min and were excluded from analyses.

Statistical analyses

All analyses were conducted using software R 3.2.2 (R Core Team, 2015). We used *asnipe* package (Farine, 2013) to construct a social network of wild great tit and blue tit populations. We first tested if the associations in our network of 331 individuals (217 blue tits and 114 great tits) were non-random by conducting permutation tests on the group matrix. The mean weighted degree of our network was significantly greater than values from the permutations ($p = 0.001$), demonstrating that our network differed significantly from random. Association strengths were scaled between 0 (two individuals never observed in the same flock) and 1 (two individuals always observed in the same flock). The associations between observers and demonstrators in our experiment ranged from 0 to 0.070 (mean = 0.018, sd = 0.021). In addition, we calculated the total number of interactions (i.e. times individuals were observed in the same flock) between demonstrators and observers: these ranged from 0 to 107 (mean = 24, sd = 30.803). As both association measures gave similar results when analysing observers' behaviour, we decided to use only association strength in our final analyses.

We used a Wilcoxon signed ranked test to analyse differences in demonstrators' behaviour when encountering aversive or palatable prey, to allow for the small sample size (n = 6). As the time that birds spent on foraging differed among demonstrators (palatable prey: range = 38–170 s, median = 77 s; aversive prey: range = 16–115 s, median = 62 s) we first divided the time spent on beak wiping and a number of beak wipes and head shakes with the total time foraging, and then compared these rates between aversive and palatable prey.

For analyses of observers' behaviour, we used generalised linear mixed effects models with appropriate error distributions, implemented using the *lme4* package (Bates *et al*., 2015). Explanatory variables in all models included an interaction between the effects of a demonstrator being present (cup before/demonstrator/cup after) with the prey type (palatable/ aversive), the observer's association with its demonstrator as determined from the social network, and the test order (first/second test). In addition, we included an observer's identity and a demonstrator video as random effects. The baseline level of each model included an initial cup presentation, aversive prey type, and a first video presentation. As the length of time that birds were visible in videos differed, we modeled the time observers faced the screen or spent flying versus the length of time observers performed other behaviours (i.e. total time visible – time facing a video or flying) as a bound response variable with a binomial error distribution. Similarly, we converted the number of head turns and hops into a rate by dividing the number of times they occurred by the total time a bird was visible. We then converted these rates to integers by multiplying them by 30 s, which was the most common length of time a bird was visible during each section of the videos. We modeled head turns using a Poisson error distribution, but hopping with a negative binomial error distribution because it was right-skewed.

Finally, we analysed if social information in the videos affected which cup observers landed on first and how fast they made their choice, using again generalised linear mixed effects models. To test the effects of video on birds' first choice, we included the choice (same/different cup that a demonstrator fed from) as a response variable, and prey type (palatable/aversive), the observer's association with its demonstrator, and the test order as explanatory variables, using binomial error distribution. The baseline level of the model included the video playback of aversive prey and a first video presentation. Because the distribution of time before birds chose the cup was right-skewed, we modeled it with a negative binomial error distribution, using the time before a choice as a response variable, and an interaction between prey type (palatable/aversive), social information use (0/1, i.e. not matching/matching a demonstrator's behaviour), and the test order as explanatory variables. The baseline level of the model included the video playback of aversive prey, a first video presentation and individuals that did not match a demonstrator's behaviour. Bird identity and a demonstrator video were included as random effects in both models. Most of the birds landed on a cup during the first five minutes after cups were presented. Two individuals, however, were considerably slower at choosing in the aversive prey test and landed on a cup only after 15 min. We therefore considered them as outliers, and removed them from the final analysis.

RESULTS

Demonstrators' response

Demonstrators responded differently to palatable and aversive prey. The time demonstrators spent wiping their beaks on a perch (Wilcoxon signed-ranked test, p = 0.03) as well as the total number of beak wipes (Wilcoxon signed-ranked test, p = 0.03, Fig. 2a) were both significantly greater when demonstrators encountered aversive prey (time spent on beak wiping: median = 14 s, range = 4–23 s; number of beak wipes: median = 49, range = 20–107), compared to palatable prey (time spent on beak wiping: median = 1.5 s, range = 0–5 s; number of beak wipes: median = 5.5, range = 0–17). Demonstrators also performed more head shakes when eating aversive prey (median = 17.5, range = 5–27) than when eating palatable prey (Wilcoxon signed-ranked test, p = 0.03; Fig. 2b; median = 0, range = 0–5).

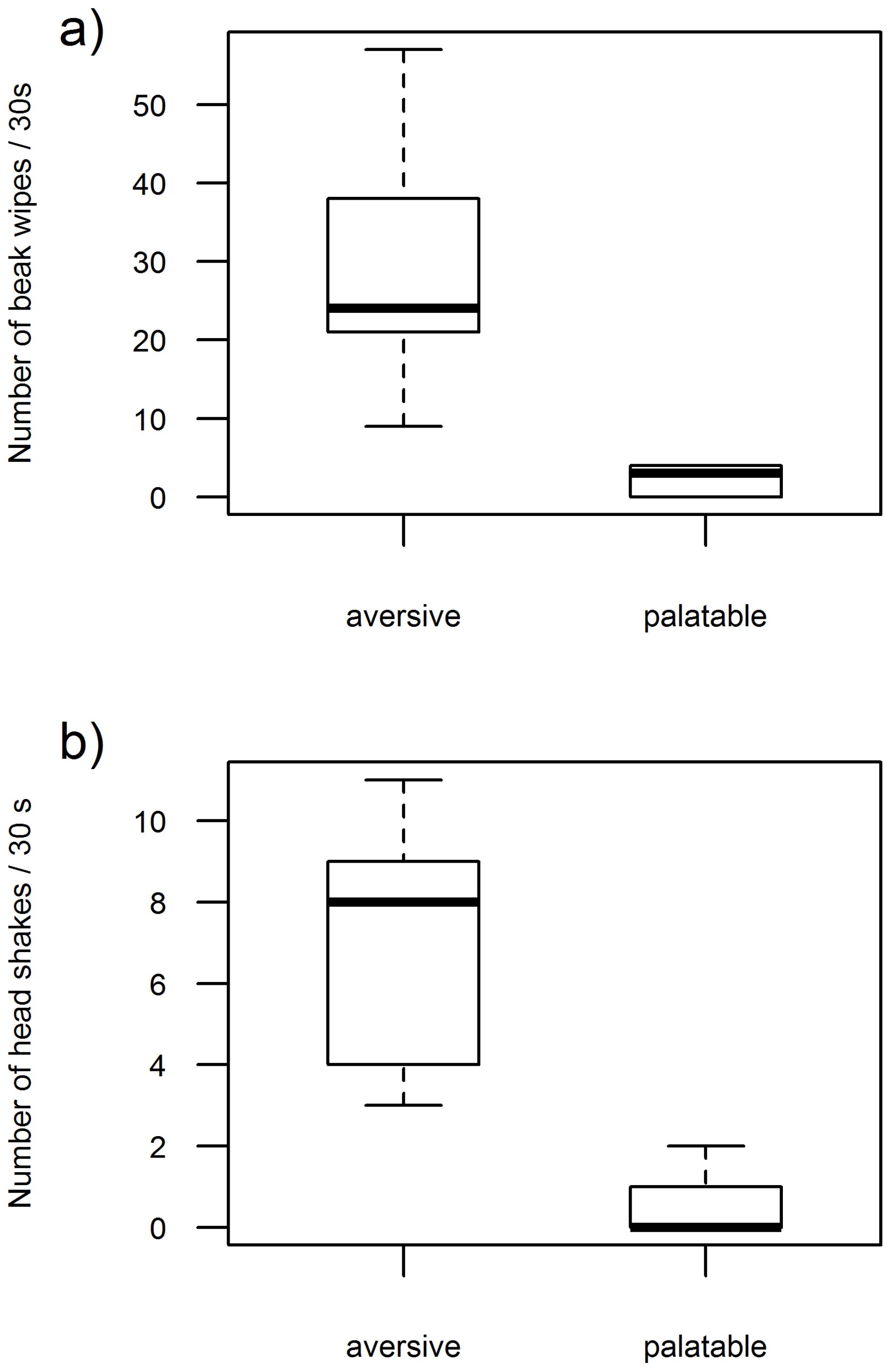


Figure 2. Demonstrators’ response. The rate of (a) beak wipes and (b) head shakes that demonstrators (n = 6) performed when encountering aversive or palatable prey.

Focal birds' response to video-playback

Facing the screen

The time observers faced the video screen depended on the prey type a demonstrator encountered: observers faced the screen less during (demonstrator presence * prey type: estimate = -0.836 ± 0.252, Z = -3.320, $p < 0.001$) and after (cups after demonstrator playback * prey type: estimate = -0.570 ± 0.269, Z = -2.118, p = 0.03) the presentation of palatable prey, compared to aversive prey (Fig. 3a). There were no significant differences between video types in the way observers responded to cups only before the presentation of a demonstrator (estimate = 0.318 ± 0.720, Z = 0.441, p = 0.66), suggesting that it was the behaviour of the demonstrator that influenced how long observers faced the video screen. Observers paid overall less attention to the screen showing cups only following the presentation of any demonstrators (estimate = -0.492 ± 0.170, Z = -2.898, p = 0.004), or compared to cups only before the demonstrator (estimate = -0.392 ± 0.181, Z = -2.167, p = 0.03; Fig. 3a). Focal birds also faced the screen more during the second test (estimate = 0.386 ± 0.144, Z = 2.679, p = 0.007). In addition, association strength with a demonstrator had a significant effect on focal birds' behaviour, showing that individuals faced the screen less when they were more closely associated with a demonstrator (estimate = -28.099 ± 12.296, Z = -2.285, p = 0.02). The distribution of association scores, however, was skewed, as most of the individuals had low association scores with a demonstrator, and it is therefore difficult to interpret this result. Finally, bird identity (variance = 0.674) and demonstrator video (variance = 1.417), included in the model as random effects, explained some of the observed variation. The final model is presented on Table 1 in Appendix 2.

Flying

Although observers varied in how much time they spent flying during video playback (range = 0–29 s, mean = 4.8 s), there was no effect of demonstrator presence and prey type on this behaviour (compared to initial cup presentation, demonstrator present * prey type: estimate = 0.185 ± 0.289, Z = 0.640, p = 0.52; cups after demonstrator playback * prey type: estimate = 0.169 ± 0.310, Z = 0.544, p = 0.59) and their interactions were therefore removed from the final model. The final model showed that a demonstrator's presence, regardless of prey type (estimate = -0.248 ± 0.144, Z = -1.729, p = 0.16), the test order (estimate = 0.114 ± 0.158, Z = = 0.718, p = 0.47) or the association between an observer and a demonstrator (estimate = 14.913 ± 13.957, Z = 1.069, p = 0.29) did not affect the time that observers were flying during video playback, but random effects explained some of the observed variation (variance for bird identity = 0.908; variance for demonstrator video = 0.987; Table 2 in Appendix 2).

Head turns

The number of head turns observers performed depended on a demonstrator's presence in the video and prey type a demonstrator encountered (Fig. 3b). Observers performed fewer head turns during (demonstrator presence * prey type; estimate = -0.393 ± 0.196, Z = -2.002, *p* = 0.045) and after (cups after demonstrator playback * prey type: estimate = -0.543 ± 0.199, *Z* = -2.726, *p* = 0.006) the presentation of palatable prey compared to aversive prey. During the initial cup presentation, observers' responses did not differ significantly between these video types (estimate = 0.015 ± 0.278, *Z* = 0.055, *p* = 0.96). The test order (estimate = 0.188 ± 0.141, *Z* = 1.337, *p* = 0.18) and the association between an observer and a demonstrator (estimate = -8.142 ± 5.062, *Z* = -1.608, *p* = 0.11) had no effect on the number of head turns performed. In addition, the variance estimates for the random effects were small (variance for bird identity = 0.081; variance for demonstrator video = 0.158; Table 3 in Appendix 2).

Hops

The number of hops that observers performed did not depend on the prey type a demonstrator encountered (compared to initial cup presentation, demonstrator present * prey type: estimate = -1.375 ± 0.951, *Z* = -1.446, *p* = 0.15; cups after demonstrator playback * prey type: estimate = -0.636 ± 1.015, *Z* = -0.626, *p* = 0.53), so we removed these interactions from the final model. The final model shows that birds were hopping significantly more in the presence of a demonstrator, compared to initial cup presentation (estimate = 1.967 ± 0.565, *Z* = 3.482, *p* < 0.001) and to the cup presentation after a demonstrator (estimate = 0.953 ± 0.460, *Z* = 2.071, *p* = 0.04; Fig. 3c). Again, the test order (estimate = 0.135 ± 0.452, *Z* = 0.297, *p* = 0.77) and the association with a demonstrator (estimate = 6.237 ± 10.131, *Z* = 0.616, *p* = 0.54) had no effect on an observer's behaviour, and the variance estimates for random effects were small (variance for bird identity < 0.001; variance for demonstrator video < 0.001; Table 4 in Appendix 2). One individual hopped considerably more than the others, but re-running analyses without it did not change the results. In particular, the increase in hopping in the presence of a demonstrator remained significant (hops during presence of a demonstrator versus initial cup presentation: estimate = 1.653 ± 0.415, *Z* = 3.981, *p* < 0.001).

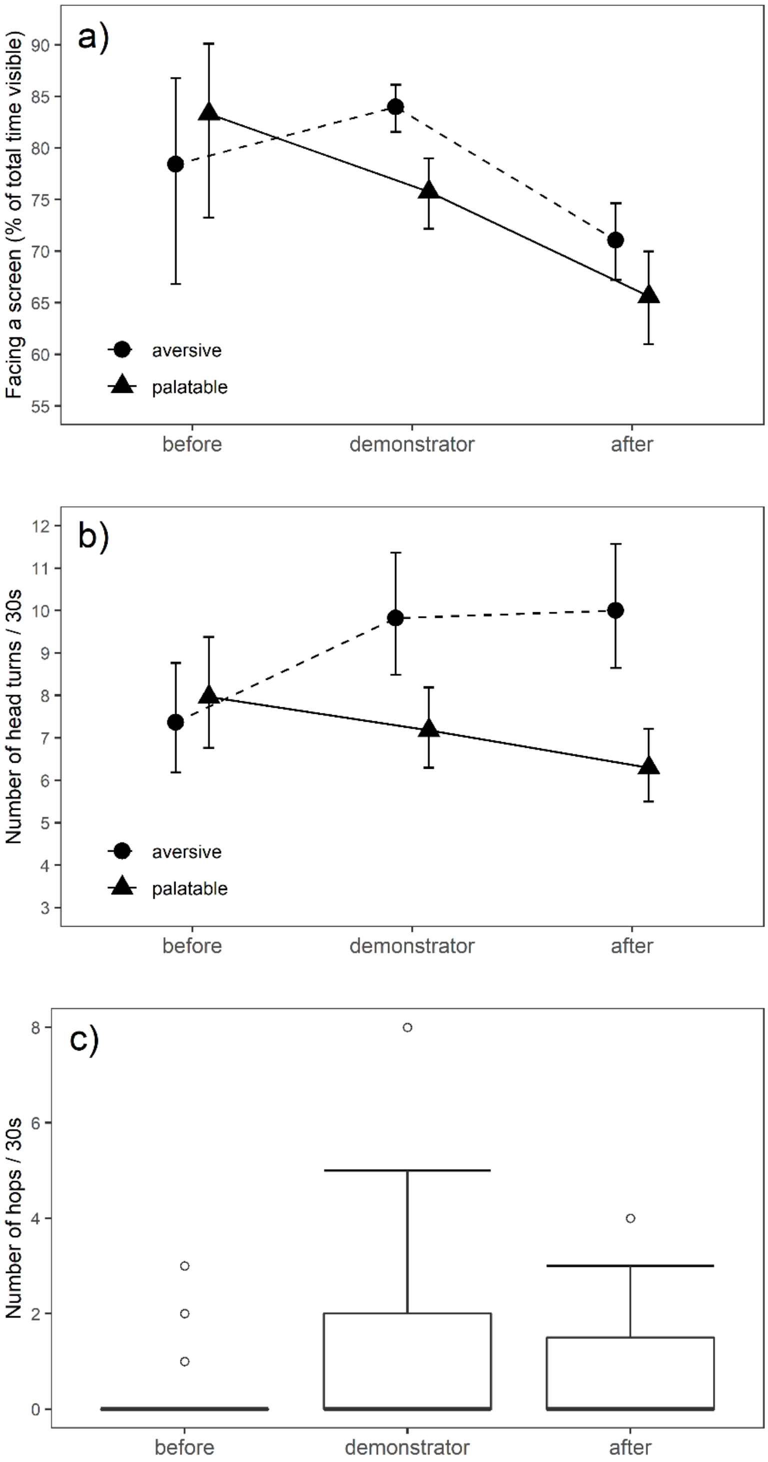


Figure 3. Focal birds' (n = 16) response to video playback. (a) Proportion of time observers faced the screen, and (b) the rate of head turns and (c) hops observers performed when they were presented with (i) an empty cage with a feeding cup before a demonstrator, (ii) a demonstrator or (iii) an empty cage with a feeding cup after a demonstrator. The time observers faced the screen, and the number of head turns differed between palatable (triangles + solid line) and aversive prey (circles + dashed line). Graphs (a) and (b) show the means and standard errors. Graph (c) shows the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range, and circles are outliers (included in the analyses).

Social information use

Prey type in the video (estimate = 0.372 ± 0.814, *Z* = 0.457, *p* = 0.65), the test order (estimate = 0.829 ± 0.745, *Z* = 1.113, *p* = 0.27), or the association score with a demonstrator (estimate = -17.137 ± 14.739, *Z* = -1.163, *p* = 0.25) did not influence an observer's cup choice (i.e. their decision to choose the same or a different cup than a demonstrator), but demonstrator video, included as a random effect, explained some of the observed variation (variance for bird identity = 0.031; variance for demonstrator video = 0.442; Table 5 in Appendix 2). After observing a demonstrator discover palatable prey in a coloured cup, only 10 birds landed first on that cup, whereas 10 birds chose the alternative coloured cup (binomial test, 10/20 compared to equal probability, *p* = 1). Similarly, after video-playback of a demonstrator's response towards aversive prey, only 12 birds avoided the cup that the demonstrator fed from, whereas nine birds landed on it first (binomial test, 9/21 compared to equal probability, *p* = 0.66). Only five birds matched our predictions in both tests, choosing the same cup colour as a demonstrator after receiving information about palatable prey, and avoiding that colour after seeing a demonstrator's disgust response. Again, this was not different from what would be expected if birds foraged randomly (binomial test, 5/20 compared to probability of 0.25, *p* = 1).

Information in the video, however, did appear to affect the latency of observers' cup choice. Observers made their choice faster when they chose a cup matching the social information provided in the video (compared to birds that did not match our predictions, estimate = -0.837 ± 0.265, *Z* = -3.154, *p* = 0.002; Fig. 4). This did not vary between the prey types observed (estimate = -0.024 ± 0.262, *Z* = -0.092, *p* = 0.93), or between the first and the second test (estimate = 0.009 ± 0.226, *Z* = 0.043, *p* = 0.97). Therefore, in both tests birds chose the cup faster when their decision matched a demonstrator's behaviour. The variance estimates for random effects were small (variance for bird identity = 0.167; variance for demonstrator video = 0.062; Table 6 in Appendix 2).

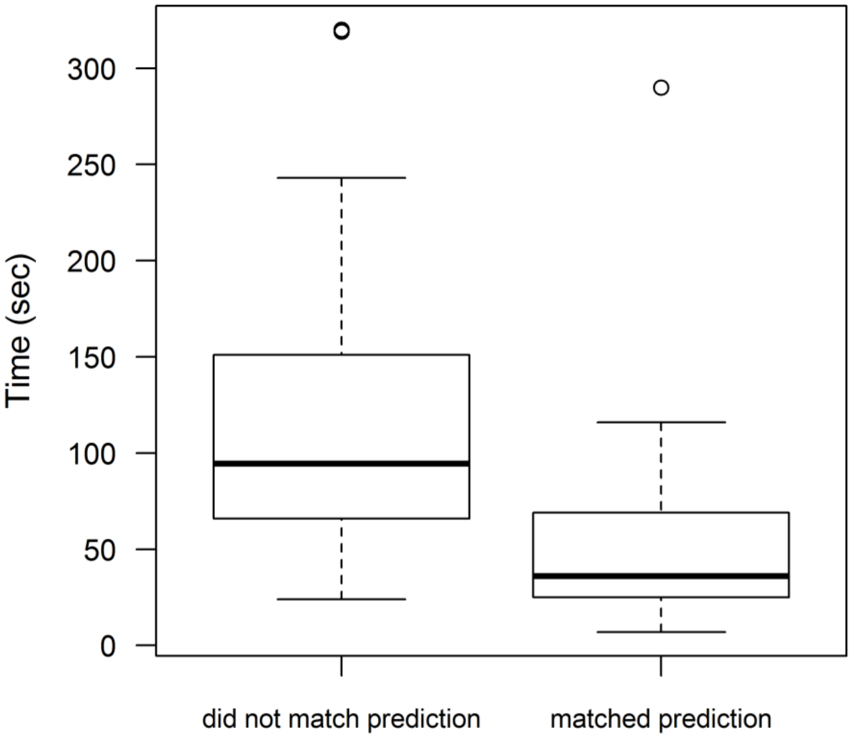


Figure 4. Time before birds chose a cup in a two-choice test. Time (s) before individuals made their cup choice when they (i) chose a different cup than predicted (i.e. did not use social information, n = 19), or (ii) chose the predicted cup (n = 21). The interaction between prey type and social information use did not have a significant effect on time that it took birds to choose a cup (estimate = 0.218 ± 0.532, $Z = 0.410$, $p = 0.68$), so responses are plotted across prey types. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range, and circles are outliers (included in the analyses).

DISCUSSION

Our experiment shows that blue tits, like many other species tested (e.g. McQuoid & Galef, 1993; Rieucau & Giraldeau, 2009; Zoratto *et al*., 2014) pay attention to video playback of a conspecific. Focal birds were more active in the presence of a demonstrator than when videos showed a cage without a conspecific present, and observers' behaviour differed depending on which prey type was being sampled in the demonstration video. Furthermore, the identity of the demonstrator explained some variation in observers' behaviour. Despite our predictions, however, we found that only half of the focal birds then chose to forage from the cup according to the information that demonstrators had provided, the same as if birds foraged randomly. Information from the video, however, did influence how quickly birds made a choice: those that chose in accordance with the demonstrator did so more quickly. Together, these results suggest that social cues in video playback could provide blue tits with information about prey profitability, but the birds either did not acquire or chose not to use this social information in their decision making.

Similar to previous studies, (Clark, 1970; Skelhorn, 2011), we found that demonstrators responded to aversive prey by performing beak wipes and head shakes. Head shaking and beak wiping has been proposed to provide observers with information about potentially toxic prey (Johnston *et al*., 1998; Skelhorn, 2011). This kind of 'disgust' behaviour could increase the benefits for paying attention to a demonstrator, as encounters with aversive prey can elevate internal toxin levels (Skelhorn *et al*., 2016) or even increase the risk of mortality when prey are lethal (Longson & Joss, 2006). Perhaps this explains why we observed differences in focal birds' behaviour between different video types, and why observers continued to pay more attention to a cup in an empty cage after observing a demonstrator encountering aversive prey. Alternatively, it is possible that focal birds faced the video screen and made more head turns when demonstrators discovered aversive prey simply because demonstrators were more active during this presentation. This could be investigated further by presenting focal birds with videos that contain different cues but show similar amounts of activity.

Other research on social information use by blue tits also finds that use of social information is low: only approximately 50% of individuals learn to solve a novel feeding task after observing a conspecific solve it (Sasvári, 1979; Aplin *et al*., 2013). These studies differ from our experiment because in task solving tests, none of the individuals are expected to solve the task without demonstration or training; in our experiment, individuals had a 50% probability to choose the predicted cup just by chance. Therefore, our result, that focal birds' foraging decisions do not differ from what would be expected if birds were choosing the cup by chance, is difficult to interpret. Individuals that chose the predicted cup in our experiment may have used social information, or may have just chosen by chance a cup that matched a demonstrator's behaviour. However, we found that individuals made their choice faster when choosing a cup that matched the information in the video. It has been suggested that one of the costs of personal information use is time and energy that individuals need for information gathering (Dall *et al*., 2005), and the observed time difference in our experiment indicates that the time cost to make a decision might be higher if individuals do not use social information. However, if we assume that all birds that chose the cup according to our predictions used social information because they made their choices more quickly, it is difficult to explain why all the other birds would have chosen an alternative cup, as we would expect their choices to be random. Alternatively, if we assume that none of the birds used social information from the videos, it is difficult to explain the observed difference in their decision times.

One possibility is that some of the focal birds used the cues from videos differently than others. For example, neophobia or competition could have affected observers' foraging choices (Gibelli & Dubois, 2017). After seeing a demonstrator eating palatable prey from a coloured cup, some observers might interpret that cup to be empty and therefore choose an alternative cup to avoid competition. On the other hand, observers might interpret the video of a cup in an empty cage so that demonstrators did not want to forage from that cup. Individuals might therefore choose the same cup as a demonstrator just to avoid novelty, even after seeing a demonstrator eating aversive prey. Furthermore, birds were pre-trained to locate favourable prey items from food cups, albeit of different colour, so instead of using social information about food unpalatability, they might have relied on their previous experience with prey (e.g. Kendal, Coolen & Laland, 2004). In addition, individuals might have had preferences for different cup colours, but we did not find that they chose any of the coloured cups more often than others, and the cup colours for demonstrator and control videos were randomised.

It has been suggested that individuals are more likely to rely on social information when the costs to acquire personal information increase (Kendal *et al*., 2004; Kendal *et al*., 2005), and it is possible that in our experiment the cost of foraging from the 'wrong' cup was too low to detect information use. In addition, some characteristics of observers such as sex and age (Loukola, Seppänen & Forsman, 2012; Aplin *et al*., 2013; Guillette & Healy, 2014), personality (Marchetti & Drent, 2000), or dominance status (Nicol & Pope, 1999), could have made it more difficult for us to detect an effect of social information on cup choice. In a previous study of social learning in blue tits, juvenile females were almost twice as likely to learn the novel foraging task as other age/sex classes, and only 37.5% of adults overall learned by observing others (Aplin *et al*., 2013). In our study, all observers were adult birds but we do not know their sex. Future work should therefore present blue tits with more complicated tests with higher foraging costs (e.g., Aplin *et al*., 2013), and ensure sex and age are known. Still, in our experiment only five birds made their choice in accordance with the demonstrator in both tests, so individuals were not consistent in their information use and it is therefore unlikely that their sex would explain the observed variation. The variation in information use between the two tests, however, is not surprising, as individuals might value different types of social information differently. For instance, individuals' current toxin levels and energetic state might influence their decision to attack aversive prey (Skelhorn *et al*., 2016) and increase the value of social information about prey unpalatability.

To further investigate the effectiveness of video playback in parid tits, it could be useful to compare focal birds' responses to videos to their response to live demonstrators. This, however, would be difficult to conduct as live demonstrators vary in when and how they perform behaviours. For example, individuals' propensity to eat aversive prey could depend on intrinsic differences, such as their current energetic state (Skelhorn *et al*., 2016) that might vary over time. In our experiment, the time that demonstrators spent eating aversive prey differed considerably among individuals, and some of the demonstrators showed a stronger disgust response (more beak wipes and head shakes) than others. With video playback, we could present focal birds standardised videos of demonstrators' responses but the use of live demonstrators would include more variation, and therefore require a high number of individuals to be tested. A second potential problem with our experiment was that vocal communication between an observer and a demonstrator was impossible. However, we did not hear any of the focal birds vocalise during playback, nor did any of the demonstrators vocalise during filming. We therefore suggest that our results of focal birds' behavioural changes during video playback, the different responses depending on demonstrator identity, and the effect we detected on the latency to forage, provide adequate evidence that blue tits pay attention to video playback. We assert that this could be a valid method for studying social information use.

In conclusion, our study showed that blue tits respond to video playback of a conspecific, and that individuals paid more attention to demonstrators encountering aversive prey. This indicates that they did not only respond to the presence of a demonstrator but also observed differences in a demonstrator's behaviour. The cues from videos then influenced focal birds' behaviour in a foraging task, as individuals that chose to forage in accordance with a demonstrator made their foraging choice faster. The proportion of birds that made their choice according to information from videos, however, did not differ from random, and we are therefore unable to explain the differences in these two measures of foraging. Together, our results suggest that video playback of a conspecific can provide social cues to blue tits, and video playback therefore provides a promising method for studying social behaviour and learning in parid tits, with potential application for studies in both captivity and the wild. However, we do not know how these social cues are later used in decision making, and this seems to vary greatly among individuals.

CHAPTER 4

The effect of social information from live demonstrators compared to video playback on blue tit foraging decisions

Hämäläinen, L., Rowland, H.M., Mappes, J. & Thorogood, R. (2019). *PeerJ,* 7, e7998.

Video playback provides a promising method to study social interactions, and the number of video playback experiments has been growing in recent years. Using videos has advantages over live individuals as it increases the repeatability of demonstrations, and enables researchers to manipulate the features of the presented stimulus. How observers respond to video playback might, however, differ among species, and the efficacy of video playback should be validated by investigating if individuals' responses to videos are comparable to their responses to live demonstrators. Here we use a novel foraging task to compare blue tits' (*Cyanistes caeruleus*) responses to social information from a live conspecific versus video playback. Birds first received social information about the location of food, and were then presented with a three-choice foraging task where they could search for food from locations marked with different symbols (cross, square, plain white). Two control groups saw only a foraging tray with similar symbols but no information about the location of food. We predicted that socially educated birds would prefer the same location where a demonstrator had foraged, but we found no evidence that birds copied a demonstrator's choice, regardless of how social information was presented. Social information, however, had an influence on blue tits' foraging choices, as socially educated birds seemed to form a stronger preference for a square symbol (against two other options, cross and plain white) than the control birds. Our results suggest that blue tits respond to video playback of a conspecific similar to a live bird, but how they use this social information in their foraging decisions, remains unclear.

INTRODUCTION

The number of studies investigating social information use in animals has been expanding during the last few decades, and it is now well documented that many species use social information in their decision making (Galef & Laland, 2005). Acquiring social information can be beneficial in many different contexts. Animals can, for example, use social information in their foraging decisions, mate choice, breeding habitat selection, or when avoiding predators (Danchin *et al.*, 2004). Social transmission is taxonomically widespread, with evidence of social information use found in birds (Aplin, 2019), mammals (Whiten, 2000), fish (Brown & Laland, 2003), reptiles (Noble, Byrne & Whiting, 2014; Kis, Huber & Wilkinson, 2015) and even insects (Dawson & Chittka, 2012; Baracchi et al., 2018). Social information is predicted to benefit individuals by reducing the costs of personal learning (Laland, 2004; Kendal *et al.,* 2005; Kendal *et al.*, 2018). When foraging, for example, individuals can gather social information about the location of food sources or food palatability, and learn novel foraging skills (reviewed in Galef & Giraldeau, 2001), which could increase their foraging efficiency.

As the number of social learning studies has grown, also the number of techniques to study social interactions has increased. A common method is to use artificial stimuli that enables researchers to control and standardise what information is presented (D'Eath, 1998; Woo & Rieucau, 2011). Artificial stimuli have been used for a long time in animal behaviour research, starting from simple dummies and leading up to robotic animals. Cardboard models were first used by Tinbergen & Perdeck (1950) to investigate the importance of various stimulus characteristics on the begging response of herring gull chicks. Subsequently, simple models have been used in many experiments, including studies investigating mate choice (Halnes & Gould, 1994; Höglund *et al.*, 1995), or individuals' responses to predators (Powell, 1974; Petersson & Järvi, 2006) and brood parasites (Thorogood & Davies, 2016). Over the recent years, new technology has enabled researchers to use also more sophisticated techniques, such as robotic animals (Taylor *et al.*, 2008; Krause, Winfield & Deneubourg, 2011). For example, male satin bowerbirds were found to adjust their displays in response to signals from robotic females (Patricelli *et al.*, 2002), and wild grey squirrels were shown to respond to a robotic model of a conspecific displaying alarm behaviour (Partan, Larco & Owens, 2009).

Another promising technique to study social interactions is video playback. Videos can be easily edited and manipulated, allowing researchers to alter the stimulus features that are presented to observers and reduce the variation among presentations (D'Eath, 1998). Video presentations can be used to study animals' responses to simple animations, such as point-light displays, and domestic chicks (*Gallus gallus domesticus*) have been demonstrated to prefer biological motion patterns when exposed to these displays (Vallortigara, Regolin & Marconato, 2005; Vallortigara & Regolin, 2006). Furthermore, with technological advances it is now possible to create realistic computer-generated animations of animal models to study social interactions (Woo & Rieucau, 2011). However, a more common method in behavioural studies is to record a video of a live animal and video playback has now been used successfully in many bird species (Ikebuchi & Okanoya, 1999; Ophir & Galef, 2003; Bird & Emery, 2008; Rieucau & Giraldeau, 2009; Guillette & Healy, 2017; Thorogood, Kokko & Mappes, 2018; Carouso-Peck & Goldstein, 2019; Smit & Oers, 2019), as well as across a range of other taxa, including mammals (Hopper, Lambeth & Schapiro, 2012; Gunhold, Whiten & Bugnyar, 2014), fish (Rowland *et al*., 1995; Trainor & Basolo, 2000), reptiles (Clark, Macedonia & Rosenthal, 1997; Ord et al., 2002) and spiders (Clark & Uetz, 1992). Video playback does, however, have limitations such as the lack of depth cues, the lack of interaction between an observer and an individual on the video, and differences between animal and human visual systems (D'Eath, 1998; Zeil, 2000; Ware, Saunders & Troje, 2015). Birds, for example, have higher critical flicker-fusion frequencies (> 100 Hz) than humans (60 Hz) and they might therefore perceive the video image as flickering, instead of continuous motion (D'Eath, 1998; Bird & Emery, 2008). However, this degree of visual resolution often occurs when light stimuli are very bright (e.g. 1500 cd/m^2 in blue tits, (Boström *et al*., 2016)) and beyond the normal brightness of most video screens. Furthermore, the use of liquid crystal display (LCD) monitors instead of older cathode ray tube (CRT) displays can help to overcome the problem of flicker, and especially a flickerless thin film transistor (TFT) LCD has provided a good method to present videos for birds (Ikebuchi & Okanoya, 1999). Another important aspect to take into account is image presentation rate (IPR) which influences how realistic the motion on the video appears (Ware *et al*., 2015). Ware *et al.* (2015) demonstrated that pigeons (*Columbia livia*) responded to videos of a conspecific more strongly when IPR was 60 frames per second, compared to lower presentation rates (15 or 30 frames/s) and the authors therefore suggest researchers to use the highest frame rate available when using video playback.

Although videos have been used successfully in many studies, video playback does not always generate the same responses in observers when compared to studies using live demonstrators (see Schlupp, 2000). For example, a recent study with California scrub-jays (*Aphelocoma californica*) found that observing a video of a conspecific eavesdropping on a caching event did not influence focal individuals' caching and re-caching behaviour, in contrast to previous studies with a live conspecific (Brecht *et al*., 2018). The strength of the responses to video and live demonstrations may also differ even when observers are found to respond to videos.

Zebra finch (*Taenopygia guttata*) males, for example, copy the nest material choice from a video demonstrator but this preference is stronger when birds observe a live demonstrator (Guillette & Healy, 2019). Most of these studies, however, have compared individuals' responses to video playback to previous experiments with live demonstrators, and therefore have not accounted for possible differences in test conditions, such as individual differences among the demonstrators. Here our aim was to compare these two methods in one study by investigating whether blue tits' response to the same demonstrator differs between video and live presentation.

The applicability of video playback in studies with blue tits is so far unclear. We found recently that blue tits' behaviour changed when they were presented with video playback of a conspecific, but social information from videos did not influence their foraging decisions in a later foraging task (Hämäläinen *et al*., 2017). In contrast, great tits (*Parus major*) have been demonstrated to respond to videos of a conspecific (Snijders, Naguib & van Oers, 2017), and use social information from videos in their foraging decisions (Thorogood *et al*., 2018; Smit & Oers, 2019; Hämäläinen *et al*., 2019a), suggesting that video playback can be used successfully in other parid tit species. It is, however, possible that even closely related species differ in their response to video stimuli. For example, Roberts, Gumm & Mendelson (2017) tested the efficacy of video playback in two species of darters, *Etheostoma barrenense* and *Etheostoma zonale,* and found that despite the same experimental set-up and close relatedness of the species, only *E. zonale* females' responses to video playback of conspecific males were comparable to live males, whereas *E. barrenense* females showed a preference only for live males. Similarly, blue tits might respond to videos differently than great tits. Alternatively, our previous result of blue tits not copying a demonstrator (Hämäläinen *et al*., 2017) might be because blue tits were simply not using acquired social information, regardless of how it was presented. Indeed, studies using live demonstrators have found that only about half of the tested blue tits learn a novel foraging task socially (Sasvári, 1979; 1985; Aplin, Sheldon & Morand-Ferron, 2013), compared to great tits that are more likely to solve the task after observing others (Sasvári, 1979; 1985). To disentangle the effect of video playback and blue tits' tendency to use social information, we designed an experiment where we investigated whether birds were more likely to use social information from a live demonstrator, compared to a video presentation.

In this experiment, we presented blue tits with a three-choice foraging task: an ice cube tray with three wells covered and marked with different symbols (cross, square and plain white). One group of the birds received social information about the location of food from a live conspecific, whereas another group saw a video playback of a conspecific demonstrator. In addition, we had two control groups that saw a foraging tray only (live/video presentation) and no information about the location of food. We predicted that the birds in the control group would not have a preference for any of the symbols and would choose each of them equally often. Socially educated birds were predicted to choose the same symbol and location where they had observed a demonstrator foraging. We predicted that blue tits would copy a demonstrator's choice equally often regardless of how social information was presented (live/video demonstrator). However, finding that blue tits were less likely to copy a demonstrator's choice from videos would indicate that video playback might not be a suitable method for social learning studies in the species. Finally, we predicted that birds that received social information would start the foraging task faster than control birds (Hämäläinen *et al.*, 2017; Thorogood *et al.*, 2018).

METHODS

Birds

The experiment was conducted at Konnevesi Research Station in Central Finland during January and February 2017. We tested social information use in 40 juvenile blue tits. In addition, five adult birds were used as demonstrators. Birds were caught from the feeding site and housed in individual plywood cages (80 × 65 × 50 cm) with a daily light period of 12.5 hours, and free access to food (sunflower seeds, tallow and peanuts) and fresh water. Before and during the experiment food was restricted to make sure that birds were motivated to forage. Birds were kept in captivity for approximately one week and then released back at the capture site. Before this, each bird was weighed and ringed for identification purposes.

Foraging task and pre-training

We investigated whether blue tits used social information about the location of food by presenting them with a three-choice foraging task where they had to find mealworms from a white plastic ice cube tray (modifying a protocol used in Hodgson & Healy, 2005). The tray had 21 wells in three rows and we covered three of these (in the middle row) with a piece of white paper that had either (i) a black cross symbol, (ii) a black square symbol, or (iii) no symbol (plain white) printed on top (Fig. 1a). The same symbols were attached in front of the foraging tray to increase their visibility to the observers during demonstration. In the experiment birds had to lift up the paper covers to find a food reward and we investigated whether social information influenced their first choice.

Before the experiment, we trained birds in their home cages to forage from an ice cube tray. Training was done step-wise by first offering birds a tray with four of the wells (randomly selected) containing a mealworm. After birds had eaten these, we next presented them with a tray with four wells partly covered (again randomly selected), so that the mealworms were still visible. During training, the wells were covered with brown paper to prevent birds associating a food reward with white colour that was used in the main experiment. In the next step birds received a tray where four wells were covered with brown paper, so that the mealworms were completely hidden. After birds had completed these steps (i.e. found and consumed all mealworms), we finally presented them with a tray with seven wells covered but only four of them containing a mealworm. This was done to increase individuals' uncertainty about a food reward, which might increase their likelihood to use social information in the experiment. Training was completed once individuals had found and consumed all mealworms. All birds finished training in one day.

Demonstrators

We used five individuals (all adults, i.e. > 1 year old) as demonstrators in the experiment. Each individual was used twice in the live demonstration and also filmed for the video playback that was presented to two observers (i.e. each individual was a demonstrator for four observers). Demonstrators were first trained to forage from an ice cube tray in their home cages, following a similar step-wise protocol that we used with the observers (see above). However, instead of covering the wells with brown paper, we presented demonstrators with a similar tray used in the main experiment, with three wells covered with different symbols (cross, square, plain white; Fig. 1a). The food reward was placed only under one of the symbols (cross or square) whereas the other wells were always empty. Demonstrators therefore learned to associate a food reward with one of the symbols and searched for food from that location during the demonstrations. We trained two of the demonstrators to associate a food reward with a cross symbol, and two with a square symbol. To ensure that the number of demonstrations for each symbol were balanced, the last of the five demonstrators was trained first with a square and then with a cross.

For the video playback, we filmed each demonstrator performing the foraging task (i.e. finding a mealworm by lifting up the paper cover) through the plexiglass wall of the test cage (a 50 × 66 × 50 cm sized plywood cage with a plexiglass front wall) using an HD camcorder Canon Legria HF R66 (with 50 frames/s progressive recording mode). Three mealworms were hidden in the well (with either a cross or a square symbol), and birds were filmed finding and eating all of them, so the demonstration was repeated three times. We then edited these videos (using

Windows Movie Maker), so that they were all 150 s long. We also filmed a five-minute long video of a demonstrator in the cage without a tray, which was presented to observers before the foraging task demonstration. Finally, we filmed control videos that contained a tray only (with different symbols) but no bird (150 s). We filmed six different control videos with all possible symbol orders on the tray to ensure that the location on the tray would not influence our results.

Experimental protocol

In the experiment observers were randomly allocated to four treatments (n = 10 in each): (i) social information from a live demonstrator, (ii) social information from video playback, (iii) live control (the feeding tray only), (iv) video playback control (video of the feeding tray only). In all treatments, birds were first allowed to habituate to the test cage for two hours. During this time, we repeated the foraging task training one more time by presenting birds with an ice cube tray with seven wells covered with brown paper and four of these containing a mealworm. After this food was restricted for one hour which is a moderate level of deprivation for blue tits and increases their motivation to search for food during the experiment.

The live demonstration was conducted in a plywood cage that was divided into two individual compartments (each 50 × 66 × 50 cm) that were separated by a plexiglass wall (Fig. 1b). An individual that was tested was placed on one side of the wall, and a demonstrator bird (or a tray only for the control group) on the other side. Outside the experiment, the plexiglass was covered (with a cardboard sheet), so that the birds could not see each other, and the cover was removed only for the duration of the demonstration. The front wall of each compartment was similarly made of plexiglass, so that we could observe the birds during the experiment. The demonstrator was placed in the test cage two hours before the test (with plexiglass between the two cage compartments covered). Demonstrators were then given one more training session with the symbols to ensure that they were foraging in the test cage, and that they were choosing the right symbol (the symbol they had been trained to associate with a reward). After this, demonstrators were food-deprived for one hour, so that they were motivated to forage during the demonstration. We then removed the cover of the plexiglass between the observer and the demonstrator, and let the birds to habituate to this new situation for five minutes before presenting the foraging tray to the demonstrator. The tray had three wells covered and one of them (the well with either a cross or a square symbol) contained three mealworms. The order of the symbols was randomised across presentations. We waited until the demonstrator found and ate all three mealworms which took on average 230 s (range = 154–492 s).

Once the demonstration was finished (i.e. the demonstrator had consumed all three mealworms), we covered the plexiglass between the cages, so that the birds could not see each other. We then presented observers with a foraging tray with the same three symbols. The order of the symbols in the presented tray was the same as in the demonstration, so that observers could use both symbol and spatial cues about the location of the food reward. This time all wells were empty to make sure that birds could not get any additional cues about food. We recorded observers' first choice to search for food (i.e. the well where they first lifted up the cover) and the test was finished after this. To investigate whether social information influenced birds' latency to start the task, we also recorded the time before the choice (s). The live control treatment was conducted in a similar way but instead of seeing a demonstrator, birds saw only the tray in an empty cage for 150 s.

When birds received information from videos, the experiment was conducted in a 50 × 66 × 50 cm sized plywood cage with a plexiglass front wall. We presented birds videos by placing an LCD monitor (Dell E198FPF, 19", resolution 1280 × 1024, 75 Hz refresh rate, 300 cd/m^2) against the plexiglass (Fig. 1c), following previously validated methods (Hämäläinen *et al.*, 2017; Thorogood *et al.*, 2018; Hämäläinen *et al.*, 2019a). The size of the demonstrator on the screen was smaller than the size of the live bird (approximately 70 % of the real size). How birds perceive the demonstrator's size is, however, difficult to estimate because of depth cues (Zeil, 2000) and differences in viewing distance depending on an observer's position in the cage. Nevertheless, previous studies have demonstrated that great tits use social information from the videos with a similar sized demonstrator (Thorogood *et al.*, 2018; Hämäläinen *et al.*, 2019a). Birds were first let to habituate to the monitor for 15 min before starting the video. Birds that received social information were then presented with a five-minute video of a demonstrator in the cage without the foraging tray, so that the protocol was similar to the live demonstration treatment where birds could observe each other for five minutes before the demonstration. Birds were then presented with a 150 s long video of a demonstrator finding and consuming three mealworms under one of the symbols. Birds in the control group saw a video of the feeding tray only (150 s). After this, the computer monitor was removed and we presented birds with the foraging task, following the same protocol as in live demonstration. Again, the order of the symbols was the same as in the demonstrator videos, and we recorded birds' first choice and the time before they started the task.

Statistical analyses

We first investigated whether birds had an overall preference towards any of the symbols using a binomial test (compared to equal probability of choosing any of the three symbols). We then investigated whether these preferences differed between socially educated and control birds. Because we did not find differences in information use between video and live demonstration treatments (see results), we combined these treatments and used a G-test to compare distributions of the preferences between all socially educated birds (live and video treatment; n = 20) and control birds (live and video treatment; n = 20). We also used a G-test to investigate (i) if birds had a preference for the spatial location on the tray (left/middle/right), i.e. if they chose any of the locations more often than expected by chance (1/3 probability), and to (ii) compare the choices of socially educated birds that saw a demonstrator choosing a square to those seeing a demonstrator choosing a cross (video and live treatments combined). Because birds seemed to prefer a square symbol (see results), we did this by testing if birds chose a square (over alternative options cross/white) more often after seeing a demonstrator choosing it, compared to seeing a demonstrator choosing a cross. We next used a Fisher's exact test to investigate if birds were more likely to copy a demonstrator's choice when they were (i) presented with a live demonstrator, compared to video playback, and (ii) when a demonstrator chose a square, compared to a cross. This was done by simply comparing the number of birds whose choice matched that of a demonstrator to those who chose a different symbol. Finally, we tested if social information influenced the latency to start the foraging task using a Cox regression analysis. The time to choose the well (s) was used as a response variable and this was explained by an interaction between social information treatment (social information/ control) and the way information was presented (live/video demonstration). Other explanatory variables in the model included the symbol (cross/square/white) and tray location (left/middle/right) that the birds chose. To investigate whether birds that matched a demonstrator's choice started the foraging task faster than those that did not, we also conducted the analysis including only socially educated birds (live and video treatment; n = 20). The latency to choose was again used as a response variable and this explained by an interaction between information type (live/video demonstrator) and whether birds chose a same symbol as a demonstrator or not. All analyses were conducted with the software R.3.3.1 (R Core Team, 2016), using *survival* package (Therneau, 2015).

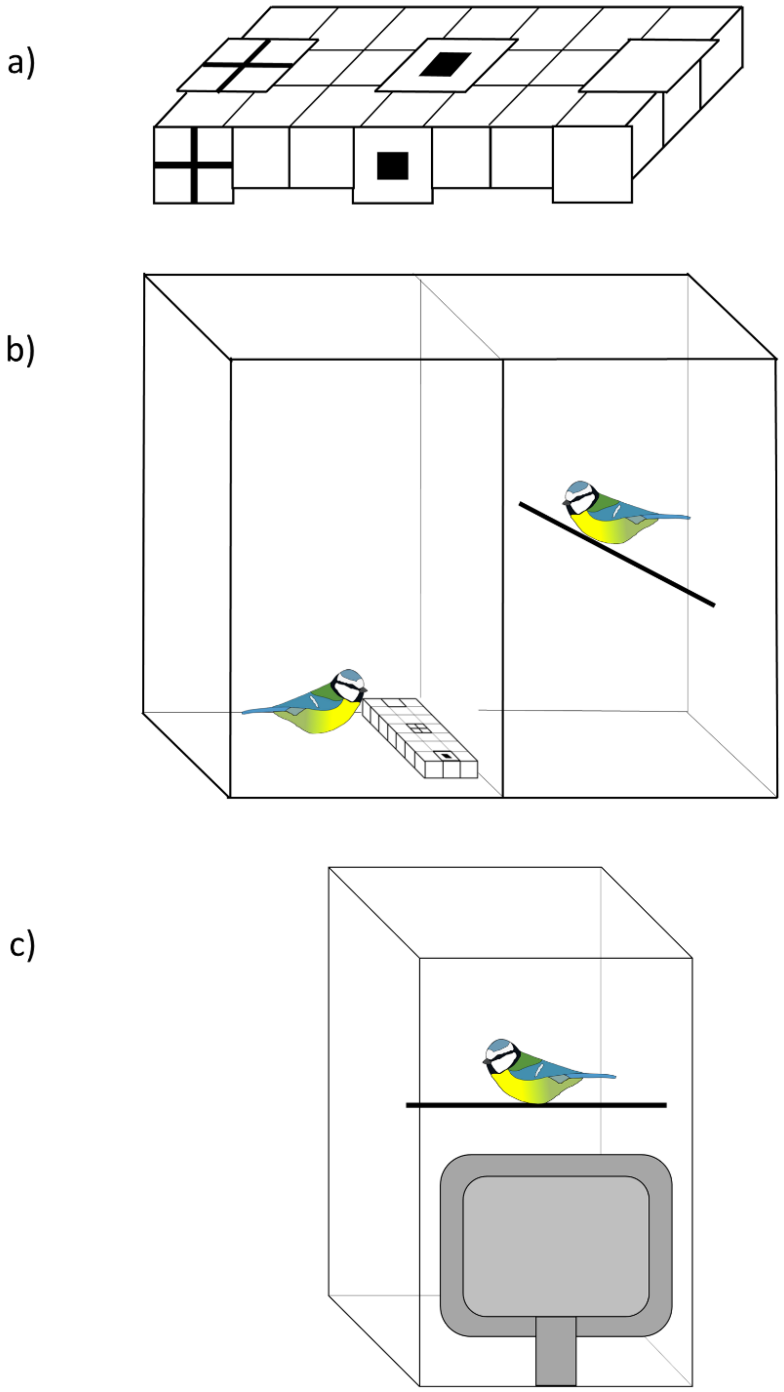
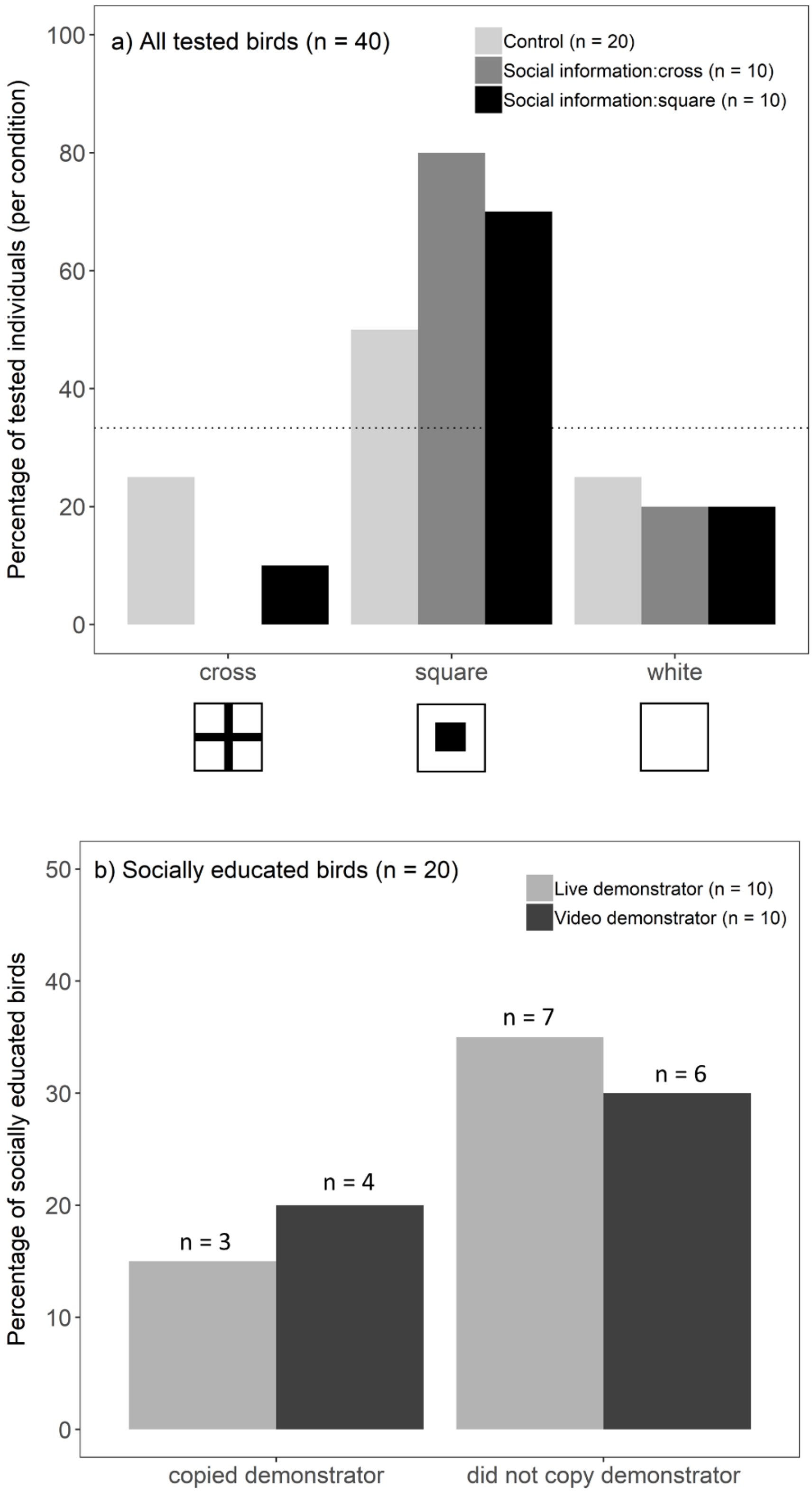


Figure 1. The experimental set-up. (a) An example of the ice cube tray that was presented to birds. The tray had 21 wells and three of them (left, middle and right well in the middle row) were covered with a piece of white paper that had either a black cross or a square printed on top, or no symbols (plain white). The same symbols were attached in front of the tray to increase their visibility to observers. The order of the symbols was randomised among birds. (b) The set-up of the live demonstration. The demonstrator (left) and the observer (right) were in individual cages that were separated by plexiglass, so that birds could see each other. In the control treatment the birds saw only the tray. (c) The set-up of the video playback. A computer monitor was placed against a plexiglass front wall of the test cage. Birds were then presented with a video of a demonstrator or a control video of the tray.

RESULTS

Overall, birds chose the well with a square symbol more often than predicted by chance (binomial test, 25/40, $p < 0.001$). This preference, however, differed between socially educated and control birds (G-test, G = 7.16, $p = 0.03$; Fig. 2a): individuals that received social information (live and video treatments combined) showed a strong preference towards a square symbol (binomial test, 15/20, $p < 0.001$), whereas this preference was not significant in the control groups (binomial test, 10/20, $p = 0.15$). Against our prediction that socially educated birds would choose the same symbol as a demonstrator, we did not find evidence that a demonstrator's choice (cross/square) influenced an observers' likelihood to choose a square symbol (G-test, G = 0.51, $p = 0.47$). Instead, socially educated birds seemed to prefer a square, regardless of a demonstrator's choice (Fig. 2a). This did not differ between live and video presentations, i.e. birds were not more likely to copy the choice of a live demonstrator compared to video playback (Fisher's exact test, $p = 1$; Fig. 2b). Because socially educated birds preferred a square symbol, they were found to be more likely to match a demonstrator's choice when a demonstrator chose a square symbol, compared to a demonstrator choosing a cross (Fisher's exact test, p = 0.003). The location on the tray (left/middle/right) did not influence birds' choices (location that birds chose did not differ from that expected by random chance; G-test, G = 3.62, $p = 0.16$).

Both control and socially educated birds started the foraging task faster after seeing a video demonstration, compared to live demonstration groups (effect of video presentation: estimate = 1.072 ± 0.420, Z = 2.553, $p = 0.01$). Birds that chose the right side of the tray also initiated the task faster than birds that chose the left location (effect of location (right): estimate = 1.086 ± 0.458, Z = 2.372, $p = 0.02$). Birds tended to choose a square symbol faster than a cross symbol (effect of symbol (square): estimate = 0.918 ± 0.526, Z = 1.745, $p = 0.08$), but this effect was not significant at alpha level of 0.05. Received social information did not influence how fast birds started to forage (effect of social information: estimate = -0.210 ± 0.382, Z = -0.549, $p = 0.58$), regardless of the way the information was presented (social information * type of presentation (video): estimate = 0.265 ± 0.726, Z = 0.366, $p = 0.71$), and these non-significant terms were removed from the final model. However, when investigating only socially educated birds, we found that birds that matched a demonstrator's choice started the foraging task more quickly (mean = 81 s, range = 12–253 s) than those that did not (mean = 768 s, range = 35–2640 s; matching a demonstrator: estimate = 1.058 ± 0.539, Z = 1.962, $p = 0.049$). This did not depend on the way information was presented (matching a demonstrator * type of presentation (video): estimate = -0.635 ± 0.970, Z = -0.655, *p* = 0.51), and this interaction was excluded from the final model.



(Figure caption on following page)

Figure 2. Birds' foraging choices in the experiment. (a) The percentage of birds (n = 40) choosing each symbol when they were presented with (live and video demonstrations combined) (i) a tray only (light grey bars, n = 20), (ii) social information of a demonstrator choosing a cross (dark grey bars, n = 10), or (iii) social information of a demonstrator choosing a square (black bars, n = 10). In the absence of any symbol preference, each symbol was predicted to be chosen with 1/3 probability. This is represented by the dotted line (33 %) and the bars above the line indicate birds' preference towards that symbol. (b) Percentage of socially educated birds (n = 20) that copied the demonstrator (i.e. chose the same symbol as a demonstrator vs. one of the other two symbols) after seeing a live demonstrator (light grey bars, n = 10) or video playback of a demonstrator (dark grey bars, n = 10).

DISCUSSION

In this experiment, we tested whether blue tits were more likely to copy the food choice of a live conspecific, compared to video playback. However, we found that blue tits did not copy a demonstrator's choice of symbol, regardless of how social information was presented. Instead, individuals chose the well with a square symbol more often than other options (Fig. 2a). Because of this preference and the lack of evidence that observers copied a demonstrator's choice, it is difficult to compare the effectiveness of video playback and live demonstration. However, birds' preference for a square symbol was stronger after they received social information, compared to the control groups, and birds whose choice matched that of their demonstrator were quicker to initiate foraging. These responses were consistent across both social information treatments, indicating that even if birds did not often choose the same symbol as a demonstrator, they responded to video playback similarly as to a live demonstrator.

Blue tits might not value social information when the foraging task is relatively simple. Similar to our previous video playback study (Hämäläinen *et al*., 2017), we did not find evidence that blue tits copied the foraging choice of a conspecific from the video, and neither did they copy the choice of a live demonstrator. Other studies with live demonstrators have similarly failed to find a strong effect of social information in blue tits, showing that only approximately 50 % of tested birds learn a novel foraging task socially (Sasvári, 1979; 1985; Aplin *et al.*, 2013). Social learning seems to also be age- and sex-biased with juveniles (Sasvári 1985) and especially juvenile females being most likely to learn socially (Aplin *et al.*, 2013). To increase the chances of detecting social information use, we therefore decided to test only juveniles, but we were not able to determine the sex of the tested individuals. Furthermore, birds were provided with both visual and spatial cues about the food reward (the location of the symbols in the foraging task mirrored that in the demonstration), so individuals could have used either type of information. Despite this, we failed to find evidence of blue tits copying a demonstrator's foraging choice. However, similar to our previous study (Hämäläinen *et al*., 2017), we found that birds that matched a demonstrator's choice started the foraging task more quickly than birds that chose an alternative symbol, suggesting that social information might have influenced their behaviour. In addition, birds started the task faster after seeing video playback (either control or social information) compared to seeing live stimuli. This probably results from slight differences between the test conditions (i.e. different test cages). After the live demonstration, we covered the observer's view of the demonstrator's cage by sliding a cardboard sheet between the two cage compartments, and this disturbance might have affected the observers more than simply removing the computer monitor following the video demonstration. Therefore, the test with live stimuli might have been slightly more stressful for the birds which could explain the longer hesitation to start the foraging task.

Despite failing to find evidence that blue tits copied the foraging choice of a demonstrator, social information did have an influence on their foraging choices. In all treatments, birds chose the square symbol more often than other two options (cross or white). However, this preference for squares was even stronger when birds received social information from a live or video demonstrator, regardless of the demonstrator's choice. This indicates that simply seeing a demonstrator foraging from the tray enhanced blue tits' preference towards the square symbol. This result is difficult to explain, but it is possible that birds saw a demonstrator as a competitor, which led them to choose the most visible and preferred prey item. Blue tits were similarly found to prefer squares in our other experiment, where birds were allowed to choose between two prey items with cross and square symbols (Hämäläinen *et al*., in review). Conspicuous square therefore seems to be a more salient cue for blue tits, and contrasting social information about food location did not override this preference. Great tits were recently found to have a high level of self-control ability (Isaksson, Urhan & Brodin, 2018), but to our knowledge this has not been tested in blue tits, and it is possible that blue tits were simply too impulsive to inhibit their response to the preferred signal. This initial preference makes our results difficult to interpret, and different symbols might have provided us better evidence of social information use. Interestingly, the preference for square symbols has not been found in great tits (Lindström *et al*., 2001a; Hämäläinen *et al*., 2019a), and artificial prey with cross and square symbols have been used in many avoidance learning experiments (e.g. Alatalo & Mappes, 1996; Lindström *et al*., 1999a; Lindström *et al*., 2001a; Thorogood *et al.*, 2018). In these experiments squares often represent unpalatable aposematic prey and great tits acquire avoidance to squares faster after receiving social information about their unpalatability (Thorogood *et al.*, 2018; Hämäläinen *et al*., 2019a). Despite the initial preference for squares, blue tits similarly learn to avoid them faster after observing a negative foraging experience of a conspecific (Hämäläinen *et al*., in review) which shows that blue tits can switch their foraging preferences according to acquired social information. However, our experiment suggests that this is context-dependent, and blue tits do not change their preferences when they receive positive social information and the foraging task is relatively simple.

Our study highlights the importance of comparing animals' response to real and video stimuli when testing the applicability of video playback (D'Eath, 1998). Without the live demonstrator treatment, it would have been difficult to separate the effect of video presentation from blue tits' tendency to use social information. However, because birds were not more likely to copy the choices of live demonstrators, we can now be more confident that our result is not explained only by the lack of response to video playback. Comparing individuals' responses between video and live demonstrations might be important even when videos are found to have an effect on observers' behaviour, as these responses could be different compared to live stimuli. The responses to videos might also be context-dependent: zebra finch males showed a stronger preference for the nest material choice of a live conspecific (Guillette & Healy, 2019), whereas female zebra finches courted video images of males more actively than live males, possibly because of the lack of reciprocal response from males on the video (Swaddle, McBride & Malhotra, 2006). The efficacy of video playback seems to also depend on the features of the video presentation, such as the sound on the video. Zebra finches were found to copy foraging choices from video playback only when videos did not have sound (Guillette & Healy, 2017), whereas the opposite was true in Burmese red junglefowl (*Gallus gallus spadecius*) that used social information only from videos with sound (McQuoid & Galef, 1993). Together, these studies indicate that video playback can be a useful tool in behavioural studies but its applicability might vary among species and different contexts.

The aim of our study was to test the effectiveness of video playback in social learning studies in blue tits by comparing social information use between live and video demonstrations. This comparison proved to be difficult, as we did not find strong evidence of social learning from either live or video demonstrators, indicating that blue tits do not rely on social information in simple foraging tasks. In our experiment the cost to search for food (i.e. lift up the paper cover) was probably low and birds might have ignored social information because personal information was easy to acquire (Laland, 2004; Kendal *et al*., 2005). It is also possible that birds would have needed to observe several demonstrations from different individuals before relying on social information. In our experiment individuals received information from one demonstrator only, whereas in nature blue tits form foraging flocks and have opportunities to gather information from both conspecifics and heterospecifics (Farine *et al*., 2015). Individuals are also likely to vary in their tendency to use social information (Sasvári, 1979; Aplin *et al.*, 2013) and we might have needed a bigger sample size to detect social learning. Furthermore, instead of using positive social information about the location of food, some observers might have seen the demonstrator as a competitor and therefore avoided the same symbol. Nevertheless, we found that blue tits responded to video playback similarly as to a live demonstrator, as both demonstrations enhanced observers' preference towards squares, indicating that videos had the same effect on birds' behaviour as live demonstrators. However, because of the difficulties to detect social learning in blue tits, the efficacy of videos should be tested in other contexts before making conclusions of its applicability for this species.

CHAPTER 5

Social learning within and across predator species facilitates the evolution of aposematic prey

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Aposematic prey advertise their unprofitability to predators with conspicuous warning signals. These signals are only effective once predators learn to recognise them, which sets up an evolutionary paradox – the defence initially increases predation risk, rather than protecting the prey. Recent research suggests that if multiple predator individuals can learn by observing single predation events, then this cost of conspicuousness will be reduced just enough for aposematism to evolve. Most experimental evidence is currently limited to within-species learning, but predator communities are complex. While heterospecific observations could increase learning opportunities and further enhance protection for novel aposematic prey, we know little about how social information use varies across different species. Here we test conspecific and heterospecific information use across a predator community with wild-caught blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*). We used video playback to manipulate social information about novel aposematic prey and then compared birds' foraging choices in 'a small-scale novel world' that contained novel palatable and aposematic prey items. We expected that blue tits would be less likely to use social information compared to great tits, and that the initial predation cost for aposematic prey would therefore be higher with blue tit predators. However, we found that both blue tits and great tits consumed fewer aposematic prey after observing a negative foraging experience of a demonstrator. In fact, this effect was stronger in blue tits compared to great tits. Interestingly, blue tits also learned more efficiently from watching conspecifics, whereas great tits learned similarly regardless of the demonstrator species. Together, our results indicate that social transmission about novel aposematic prey occurs in multiple predator species and across species boundaries. Social interactions among predators are therefore likely to be a strong selective agent in the evolution of aposematic prey.

INTRODUCTION

Aposematic species signal their unprofitability to potential predators with conspicuous warning colouration (Poulton, 1890). The evolution of aposematism, however, is still a puzzle: even though conspicuous signals facilitate the avoidance learning of predators (Roper & Redston, 1987; Lindström *et al*., 1999a), they are assumed to have a high initial mortality cost because they are easily detected by uneducated predators (Mappes *et al.*, 2005). This evolutionary paradox has received wide theoretical and experimental interest, and several different mechanisms might play a role in facilitating the survival of aposematic prey (reviewed in Ruxton *et al.,* 2018). Predators might, for example, show an increased wariness to attack (Thomas *et al.,* 2004; Marples, Kelly & Thomas, 2005) or handle novel prey (Guilford, 1994), or have innate aversion to typical warning colours (Lindström, Alatalo & Mappes, 1999b). Aposematic prey is also suggested to benefit from aggregation (Mappes & Alatalo, 1997; Riipi *et al*., 2001) and kin selection (Mallet & Singer, 1987). Most of this research has, however, focused on how predators learn individually about prey defences (Ruxton *et al*., 2018), and we still know little about how social transmission of information in the predator community influences the selection for aposematic prey.

In addition to directly interacting with prey, predators can acquire information about prey defences by observing the foraging behaviour of both experienced and naïve individuals. This has been suggested to provide one resolution to the paradox of aposematic signal evolution, with mathematical models (Thorogood, Kokko & Mappes, 2018) and experiments (Thorogood *et al.*, 2018; Hämäläinen *et al*., 2019a) showing that observational learning by predators can reduce predation risk just enough for novel aposemes to reach fixation in a prey population. This 'social avoidance learning' has been demonstrated in several avian species, including red-winged blackbirds (Mason & Reidinger, 1982), common grackles (Mason, Arzt & Reidinger, 1984) and domestic chicks (Johnston, Burne & Rose, 1998; Skelhorn, 2011) that avoid unpalatable foods after observing a negative foraging experience of others. In contrast, other studies have found that hens (Sherwin, Heyes & Nicol, 2002) and blue tits (Hämäläinen *et al*., 2017) did not use social information about food unpalatability in their foraging decisions. However, only recent experiments with great tits have specifically tested social learning about aposematic prey and investigated its effects on prey survival (Landová *et al*., 2017; Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a).

Like many studies of social learning (Danchin *et al*., 2004; Galef & Laland, 2005), most previous work on social transmission of avoidance has thus far been limited to learning within predator species. However, predator communities are often complex and consist of several species, therefore providing multiple sources of social information. Predator species may vary in how likely they are to try unpalatable prey and while this is thought to create heterogeneity in selection pressures for prey warning signals (Endler & Mappes, 2004; Valkonen *et al*., 2012; Nokelainen *et al*., 2014); it may also enhance opportunities for social learning when some predators are more likely to try novel prey than others (Exnerová *et al*., 2003; 2007). Indeed, the risk of consuming toxins might make social information about prey defences valuable to a broad range of predators, regardless of the identity of the demonstrator. Heterospecific social avoidance learning could therefore increase the strength of positive selection previously suggested to facilitate the evolution of novel aposematic prey (Thorogood *et al.*, 2018).

Previous studies on social avoidance learning have manipulated the strength of the demonstrator's response from the complete avoidance of prey (Landová *et al*., 2017) to disgust responses ranging from very strong aversive responses, generated by intubating demonstrators with a methiocarb solution (Mason & Reidinger, 1982; Mason *et al*., 1984), to less severe responses with beak wiping and head shaking after experiencing a bitter taste (Johnston *et al*., 1998; Skelhorn, 2011; Thorogood *et al*., 2018). Similarly, tests of the effect of social information have varied from choice tests (Mason & Reidinger, 1982; Mason *et al*., 1984; Hämäläinen *et al*., 2017) to more complex avoidance learning experiments with novel aposematic prey (Landová *et al*., 2017; Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a), which makes the comparison of different studies difficult. Indeed, only one previous study has investigated species-specific differences in social avoidance learning within the same experimental set-up, showing that red-winged blackbirds and common grackles developed an aversion to coloured food after observing a distress response of either a conspecific, or a heterospecific (Mason *et al*., 1984). Although heterospecific information use has been documented in other contexts (reviewed in Seppänen *et al*., 2007), a study by Mason *et al.* (1984) also provides the only evidence so far of avoidance learning across predator species, and we do not know how important this is in other predator communities.

Here we investigated how wild blue tits and great tits use conspecific and heterospecific information when learning about prey defences. Outside the breeding season parid tits form mixed species foraging flocks (Ekman, 1989), which provide good opportunities for social learning within and between species. Great tits have been shown to use conspecific information about both palatable (Marchetti & Drent, 2000) and unpalatable food (Landová *et al*., 2017; Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a) and novel foraging skills have been found to spread through wild great tit populations (Aplin *et al*., 2015b). In addition, great tits have been demonstrated to use heterospecific information (Brodin & Urhan, 2014), although there is evidence that adult birds might learn a novel foraging task better from a conspecific than from a heterospecific (blue tit) demonstrator (but this difference was not observed in juveniles; Sasvári, 1979; 1985). In blue tits, the evidence for social information use is less clear. Aplin, Sheldon & Morand-Ferron (2013) demonstrated that blue tits used social information to learn a novel foraging task, but individuals varied with only approximately 50 % of birds learning the task by observing others. In our recent research, we also found no evidence of blue tits using social information in their foraging decisions (Hämäläinen *et al*., 2017; Hämäläinen *et al*., 2019b). This indicates that the two species might differ in their information use, which sets up an interesting paradigm to study social learning across a predator community.

Research comparing information use between blue tits and great tits in the same experimental set-up is, however, limited. To date, the best evidence comes from experiments by Sasvári (1979; 1985) who found that adult great tits were more likely to learn a novel foraging skill socially, compared to adult blue tits (Sasvári, 1979), whereas there was no difference in social learning between juveniles of the two species (Sasvári, 1985). In addition, cross-fostering experiments in the wild have provided evidence that both species acquire social information about prey types and foraging niches from their parents, but this effect seems to be stronger in great tits (Slagsvold & Wiebe, 2007; 2011). Experiments with wild parid tit populations have also demonstrated heterospecific information use (Farine *et al*., 2015). Farine *et al.* (2015) showed that blue tits and great tits acquired information about novel foraging sites from both conspecifics and heterospecifics, but associations among heterospecifics were found to be weaker than among conspecifics, which suggests faster information transfer within species. These studies, however, have all investigated how birds learn about positive foraging experiences of others, and we do not know how parid tits differ in their use of social information about unpalatable prey.

We presented blue tits and great tits with social information using video playback of a demonstrator bird (blue tit or great tit) responding to novel aposematic prey. When tasting unpalatable food, birds usually perform vigorous beak wiping and head shaking (Clark, 1970; Rowland, *et al*., 2015; Hämäläinen *et al*., 2017) which can provide information for others (Johnston *et al*., 1998; Skelhorn, 2011; Thorogood *et al*., 2018). Video playback has been used previously with both blue tits (Hämäläinen *et al*., 2017) and great tits (Snijders, Naguib & van Oers, 2017; Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a; Smit & van Oers, 2019), and it provides a good method to control the information that is presented to observers. In both species, we had three treatment groups that received either (i) conspecific or (ii) heterospecific information about novel aposematic prey, or (iii) saw a control video with prey items only, but no information of their palatability. We then conducted foraging trials in 'a small-scale novel world' that contained cryptic palatable and conspicuous aposematic prey that were evolutionary novel to the birds (Alatalo & Mappes, 1996; Hämäläinen *et al*., 2019a). We investigated if receiving social information influenced birds' foraging choices, and whether information use differed between the species or depended on the demonstrator's identity. As great tits have been found to be more sensitive for social information (Sasvári, 1979; Slagsvold & Wiebe, 2007), we predicted that 1) social information would reduce the attacks on the aposematic prey in both species, but 2) great tits would rely on social information more than blue tits, i.e. social information would reduce predation risk for aposematic prey more in great tit treatments. Because parid tits have been demonstrated to learn more efficiently from conspecifics (Sasvári, 1979; Farine *et al*., 2015), we also predicted that 3) individuals would rely more on conspecific information compared to heterospecific information and therefore learn to avoid aposematic prey faster after observing conspecifics.

METHODS

Birds and housing

The experiment was conducted at the Konnevesi Research Station in Central Finland from October to December 2017. We tested 39 great tits (7 female juveniles, 12 male juveniles, 8 female adults, 12 male adults) and 48 blue tits (19 juveniles, 29 adults). Birds were caught from the feeding site in Konnevesi and housed individually in indoor plywood cages (80 × 65 × 50 cm), with a daily light period of 12.5 hours. Fresh water and food (sunflower seeds, tallow and peanuts) were provided ad libitum, except during training and the experiment when food restriction was necessary to motivate birds to forage. After the experiment (approximately one week) birds were ringed and released at their capture site. They were weighed (after capture and before the release) and their wing and tarsus lengths were measured. Both species were aged based on their plumage and great tits were sexed (Svensson, 1992). We also classified blue tits to males and females based on their morphological measurements and plumage, but because genetic samples are required to sex the species confidently, we did not include this measure in any of the analyses.

Prey items

We used ‘a small-scale novel world’ method (Alatalo & Mappes, 1996; Hämäläinen *et al*., 2019a) to investigate predation risk of novel palatable and aposematic prey. Prey items were small pieces (approximately 0.1g) of almond flakes that were glued inside a white paper packet (8 × 8 mm) using non-toxic UHU glue. We used two black symbols (printed on both sides of paper packets) to indicate prey palatability. Palatable prey had a cross symbol that was cryptic to the background, whereas aposematic prey were printed with a conspicuous square symbol. Aposematic prey were made distasteful by soaking almond pieces in bitter-tasting chloroquine phosphate solution (2g of chloroquine in 30 ml of water) for one hour (e.g. Lindström *et al*., 2001b).

Previous studies have shown that great tits do not have a preference for a cross or square symbol (Lindström *et al*., 2001a; Hämäläinen *et al*., 2019a). We followed the same protocol to investigate initial preference in blue tits using 10 individuals that did not participate in the main experiment (see Appendix 3 for details of the preference test). We found that when given a choice between a cross and a square symbol (both palatable), blue tits preferred squares. This strong initial preference for squares means that it might be more difficult to detect an effect of social avoidance learning (acquiring avoidance to squares) in blue tits, compared to great tits that do not have preferences towards the symbols (Lindström *et al*., 2001a; Hämäläinen *et al*., 2019a). However, it also means that finding an effect of social information use would provide even stronger evidence of social avoidance learning, as it would indicate that birds switched their initial preferences after observing others.

Experimental set-up

The foraging trials were conducted in a 50 × 66 × 49 cm sized wooden cages that had the front wall made of plexiglass, enabling us to observe birds during the experiment. In each trial, we presented birds with novel world backgrounds that contained 8 cryptic palatable prey items (cross symbol) and 8 conspicuous aposematic prey items (square symbol). Backgrounds were made of A1 sized white paper sheets that had 140 crosses printed in random positions to make palatable prey cryptic. To increase the difficulty to find cryptic prey, we made the background three-dimensional by adding in each sheet 20 fake cryptic prey items (a piece of double-sided mounting tape with a cross symbol), following previously established methods (e.g. Lindström *et al*., 2001b; Hämäläinen *et al*., 2019a). Backgrounds were covered with adhesive plastic, and prey items (8 of each type) were randomly distributed and glued to them.

Previous studies have tested the symbol visibility with great tits, showing that squares are approximately four times more visible against the background in a large aviary (Lindström *et al.,* 1999a) and in our 'small-scale novel world' set up (Hämäläinen *et al*., 2019a). Before the main experiment, we conducted the visibility test with blue tits, using the same 10 individuals that were tested for symbol preference (see Appendix 3 for details). Birds were required to attack 20 prey, and similar to great tits (Lindström *et al*., 1999a; Hämäläinen *et al*., 2019a), blue tits were found to attack more squares than crosses (on average 15 squares and 5 crosses), which suggests that squares are more visible against the background. However, because blue tits also preferred squares before the visibility test, it is difficult to disentangle this preference from the visibility of the symbols.

Video playback

Birds were provided social information using video playback of a foraging demonstrator (a conspecific or a heterospecific). We filmed four adult great tits and four adult blue tits as demonstrators for the videos. To reduce variation among demonstrations, all demonstrators were males (although the sex of blue tits could not be determined with 100 % confidence without genetic sampling). Some of the demonstrators (all blue tits and one great tit) participated in the experiment also as observers, and they were filmed as demonstrators for others after they had finished the avoidance learning trials. Demonstrators' responses to aposematic prey were filmed through the plexiglass wall of the cage with an HD camcorder (Canon Legria HF R66), following previously established methods (Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a). An aposematic prey item was similar to the prey used in the main experiment (a square symbol) but bigger in size (20 × 20 mm) to ensure that it was visible to observers.

We filmed a demonstrator taking the aposematic prey item from the cage floor, opening it on the perch and tasting it. Following this, birds showed a clear disgust response by wiping their beak on the perch and shaking their head. The length of these responses varied among demonstrators and we aimed to standardise their strength by editing the videos (using Windows Movie Maker) so that they all consisted of 80 s of a demonstrator's response to aposematic prey (see Appendix 3 for details about variation among videos). Videos also included 80 s of an alternative prey with a cross symbol in an empty cage (40 s before and 40 s after a demonstrator) to make sure that birds had seen both prey types before the foraging trials, so that the familiarity of symbols would not influence their preferences. We filmed and edited eight different videos (one of each demonstrator) and each video was used in six demonstrations (for three blue tit and three great tit observers). In addition, we recorded a control video that showed only prey items in an empty cage (80 s each). This was presented to the control groups that did not receive information about prey palatability. A demonstrator bird was not included in control videos, as this could have provided observers unintended social information of the demonstrator rejecting the prey via avoidance.

Foraging trials

Before the experiment birds were trained to consume artificial prey items, following previously established methods (e.g. Lindström *et al*., 2001b; Hämäläinen *et al*., 2019a). The first training phase was done in home cages, where birds were trained to open brown paper packets and to detach them off the training background that was printed with >? symbols. During training birds did not have access to other food (for detailed methods see Hämäläinen *et al*., 2019a). The last training phase was conducted in the test cage on the same day when the experiment started. We presented birds with a training background that resembled the backgrounds that they later encountered in the foraging trials (i.e. with cross symbols). This background contained three brown and three cryptic (cross) prey items and we waited for birds to find and eat all of them before starting the experiment. The same protocol has been used in previous experiments (Thorogood *et al*., 2018, Hämäläinen *et al*., 2019a) and it ensures that birds learn to forage in the novel world environment before the learning trials. Other food was restricted for two hours before the experiment to ensure birds' motivation to forage.

After birds had completed the last training phase (i.e. consumed 3 brown and 3 cryptic prey), we provided them information about aposematic prey via video playback. In both species, individuals were randomly allocated to three treatments that (i) received social information from a conspecific (n = 12 in both species), (ii) received social information from a heterospecific (n = 12 in both species) or (iii) did not receive any social information (control group) before four foraging trials (great tits: n = 12; blue tits: n = 14). Two blue tits in the control group completed only the first trial, with one of them refusing to attack any prey in the second trial, and another one getting injured (this was not related to the experiment, and the bird recovered and was released afterwards). The blue tit control group therefore includes 14 individuals that completed the first trial and 12 individuals that completed all four trials.

Video playback was shown from a computer monitor (Dell E198FPF) that was positioned against the plexiglass wall of the cage. Birds were first allowed to habituate to the monitor for 15 min, and then presented with a video of a conspecific or a heterospecific demonstrator, or the prey only (Fig. 1). Even though these videos were not capturing the UV cues in birds' plumage, observers were likely to recognise conspecifics and heterospecifics easily based on other species-specific visual characteristics (such as plumage patterns). Immediately after the video, the monitor was removed and birds were presented with a first novel world background that contained 8 palatable crosses and 8 aposematic squares. Birds were allowed to attack 4 prey items before the background was removed and replaced with a new one. In each trial, birds were sequentially presented 4 different backgrounds, allowing them to attack 16 prey items in total (4 from each background). Sometimes birds took the prey from the background but did not open them. We did not count this as an attack because birds did not taste prey items and therefore did not receive any information about their palatability. Previous studies have also demonstrated that aposematic insects often survive an encounter with avian predators (Wiklund & Järvi, 1982; Exnerová *et al.,* 2003), and we assumed that picking up the prey without further handling would not 'kill' it and would therefore not influence prey fitness. If birds failed to attack all 4 prey items during the first 20 minutes, we removed the background and waited for birds to be more motivated to forage before continuing the trial with the same background. We conducted two foraging trials on the first day of the experiment (with at least 30 min break between the trials) and two trials on a following day. Birds were not provided with further social information on the second day to investigate if the effect of social information persisted across days. During the experiment, birds attacked in total 64 prey items (16 in each of the four trials) and we recorded their foraging choices. In addition, we recorded how fast birds started the first foraging trial to see if this was influenced by received social information.

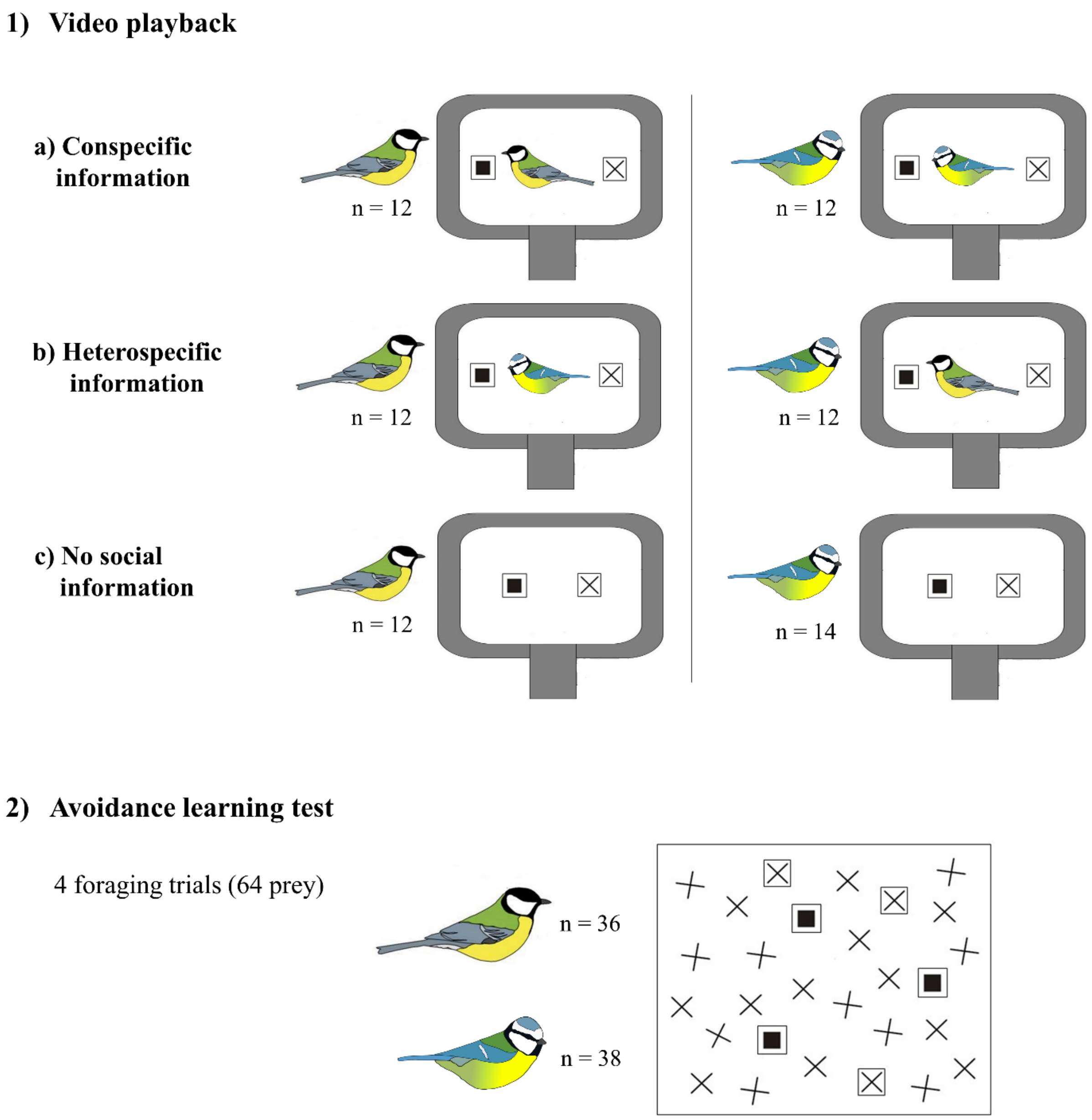


Figure 1. Experimental set-up. Great tits and blue tits were first presented with video playback of (a) a conspecific or (b) a heterospecific attacking a novel aposematic prey (prey with a square symbol) and an alternative prey (a cross symbol) in an empty cage, or (c) prey items only (control group with no information about prey palatability). We then conducted an avoidance learning test in ‘a small-scale novel world’, where birds encountered cryptic palatable prey (crosses) and conspicuous aposematic prey (squares). We investigated avoidance learning across four foraging trials (conducted over two consecutive days), in each of which birds were allowed to attack 16 prey items.

Statistical analyses

We first tested whether birds' first foraging choice depended on received social information using a chi-square test. Differences in the latency to start foraging (i.e. to attack the first prey item) were then analysed using a Cox regression model, as the response variable (time before attacking the first prey item) was time before an event type. This was explained by an interaction between information treatment (conspecific/heterospecific/control) and species (blue tit/great tit), and individuals' age and body condition index as covariates. Body condition index was assumed to indicate individuals' energetic reserves and it was calculated for each individual based on the relationship of their weight and tarsus measures (Peig & Green, 2009). Because of the different size of blue tits and great tits, we calculated body condition index separately for each species and then scaled these values with the mean and standard deviation to get a body condition measure that was comparable across the two species. We did not have tarsus measurement from one great tit (in heterospecific treatment) and this individual was therefore excluded from the models that included body condition index.

Differences in the number of aposematic prey attacked during the foraging trials were analysed using generalised linear models with a binomial error distribution (logit link function), with the number of aposematic and palatable prey attacked as a bound response variable. We first analysed birds' foraging choices in the first foraging trial after video playback. Explanatory variables in the model included an interaction between information treatment and species, and individuals' age and body condition index as covariates. We then analysed how birds improved across four foraging trials. The number of aposematic and palatable prey attacked in each trial was used as a bound response variable and this was explained by information treatment, species and trial number that was included as a continuous variable (trials 1-4). We started the model selection with the model that included a three-way interaction between the explanatory variables and selected the best-fitting model based on significance of the terms in the model (Table 1). All models included age and body condition index as covariates and bird identity as a random effect. The analyses were conducted in R version 3.3.1 (R Core Team, 2016), using *lme4* (Bates *et al*., 2015) and *survival* packages (Therneau, 2015).

RESULTS

First foraging trial

We found that social information affected how both blue tits and great tits responded to the prey during their initial encounter. While social information treatment did not influence which prey item great tits (chi-square test: $\chi^2 = 0.892$, df = 2, $p = 0.64$) or blue tits (chi-square test: $\chi^2 = 0.829$, df = 2, $p = 0.66$) attacked first, it reduced the overall predation risk for aposematic prey during the first trial (Fig. 2). We found that birds consumed fewer aposematic prey after receiving either conspecific or heterospecific information (Table 1). This decrease was biologically important, as it reduced relative predation risk for aposematic prey below 1.0 (Fig. 2), altering the relative fitness of aposematic and cryptic prey phenotypes. There was no difference between the two social information treatments (compared to conspecific information, the effect of heterospecific information: estimate = 0.142 ± 0.149, Z = 0.956, $p = 0.34$), or in how species used information (compared to blue tit control group, the effect of conspecific information * species: estimate = 0.445 ± 0.288, Z = 1.543, $p = 0.12$; the effect of heterospecific information * species: estimate = 0.471 ± 0.288, Z = 1.633, $p = 0.10$). Furthermore, the number of aposematic prey attacked in the first trial did not differ between the species, and nor was it affected by either individuals' age or body condition (Table 1). Most birds attacked the first prey item in the experiment quickly (median = 44 s, range = 4–3286 s), however 7 birds were considerably slower than others and took longer than 5 min to begin the experiment. The latency to attack the first prey was not explained by conspecific (compared to control group: estimate = 0.158 ± 0.311, Z = 0.506, $p = 0.61$) or heterospecific information (compared to control group: estimate = 0.376 ± 0.306, Z = 1.228, $p = 0.22$), but we found that blue tits tended to attack the first prey faster than great tits (the effect of species (great tit): estimate = -0.411 ± 0.244, Z = -1.687, $p = 0.09$; see Table 1 in Appendix 3 for the full model).

Table 1. Generalised linear model explaining the number of aposematic prey that birds (n = 74) attacked in the first trial (first 16 prey items). Intercept gives the estimate (logit) for the aposematic prey that adult blue tits attacked when they did not receive social information (control group).

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	0.149	0.117	1.275	0.20
Conspecific information	-0.460	0.145	-3.165	0.002
Heterospecific information	-0.318	0.144	-2.213	0.03
Species (great tit)	0.002	0.120	0.014	0.99
Age (juvenile)	0.012	0.123	0.095	0.92
Body condition	-0.001	0.060	-0.017	0.99

Learning across trials

Both blue tits and great tits showed increased avoidance of the aposematic prey over the course of the experiment (effect of trial number: estimate = -0.542 ± 0.032, Z = -17.084, *p* < 0.001; Fig. 2). However, while there were no differences in learning rate between the species according to information treatment (Table 2), blue tits and great tits responded to the source of social information differently overall (compared to blue tit control group, the effect of conspecific information * species: estimate = 0.509 ± 0.234, Z = 2.177, *p* = 0.03). To investigate these differences further, we next ran separate models for each species.

In blue tits, both conspecific and heterospecific information about prey unpalatability reduced predation risk for aposematic prey (Table 3a; Fig. 2a). This pattern was similar in great tits, although the effect of social information was not significant at alpha level 0.05 (Table 3b; Fig. 2b). However, 7 individuals had a very high initial wariness to attack novel prey (latency to start the experiment > 5 min). Five of these birds were great tits (2 in conspecific information and 3 in control treatment), and the effect of social information was stronger when these outliers were excluded from the analysis (effect of conspecific information: estimate = -0.358 ± 0.186, Z = -1.923, *p* = 0.05; effect of heterospecific information: estimate = -0.355 ± 0.181, Z = -1.960, *p* = 0.05). In blue tits, social information from conspecifics reduced predation on aposematic prey even more than social information from heterospecifics (compared to conspecific information, the effect of heterospecific information: estimate = 0.322 ± 0.159, Z = 2.023, *p* = 0.04; Fig. 2a). We did not, however, detect this difference in source of social information in great tits (estimate = 0.035 ± 0.174, Z = 0.202, *p* = 0.84; Fig. 2b). Finally, we found that age and body condition influenced great tits' foraging choices across the experimental trials, with adults and birds in a poor body condition attacking more aposematic prey (Table 3b), whereas we found no evidence that age or body condition influenced the blue tits' tendency to attack aposematic prey (Table 3a).

Table 2. Comparison of GLMMs explaining the number of aposematic prey attacked during the four foraging trials. Abbreviations of the explanatory variables are: S = species (blue tit/great tit), I = information treatment (conspecific/heterospecific/control), T = trial number (1-4), C = body condition, A = age, ID = bird identity. We started model selection with a model that included a three-way interaction between species, information treatment and trial number, and removed the interaction terms based on their significance.

Model	Model df	AIC	χ2	df	*P*
~ S * I * T + C + A + 1|ID	15	1188.4			
~ S * I + I * T + S * T + C + A + 1|ID	13	1185.5	1.040	2	0.59
~ S * I + I * T + C + A + 1|ID	12	1184.8	1.302	1	0.25
~ S * I + C + A + 1|ID	10	1183.6	2.832	2	0.24

Table 3. Generalised linear mixed effects models explaining the number of aposematic prey that (a) blue tits (n = 36) and (b) great tits (n = 36) attacked during the experiment (across 4 foraging trials). Intercept gives the estimate (logit) for the aposematic prey that adult birds attacked in the first trial when they did not receive social information (control group).

A) BLUE TITS

Terms in the model	Estimate	SE	Z	*P*
Intercept	0.305	0.117	2.600	0.009
Conspecific information	-0.926	0.155	-5.982	< 0.001
Heterospecific information	-0.603	0.145	-4.169	< 0.001
Trial number	-0.573	0.046	-12.542	< 0.001
Age (juvenile)	-0.005	0.135	-0.038	0.97
Body condition	-0.035	0.061	-0.574	0.57

B) GREAT TITS

Terms in the model	Estimate	SE	Z	*P*
Intercept	0.372	0.166	2.240	0.03
Conspecific information	-0.311	0.169	-1.836	0.07
Heterospecific information	-0.276	0.170	-1.621	0.11
Trial number	-0.513	0.044	-11.653	< 0.001
Age (juvenile)	0.388	0.139	-2.790	0.005
Sex (male)	-0.042	0.140	-0.302	0.76
Body condition	-0.170	0.072	-2.374	0.02

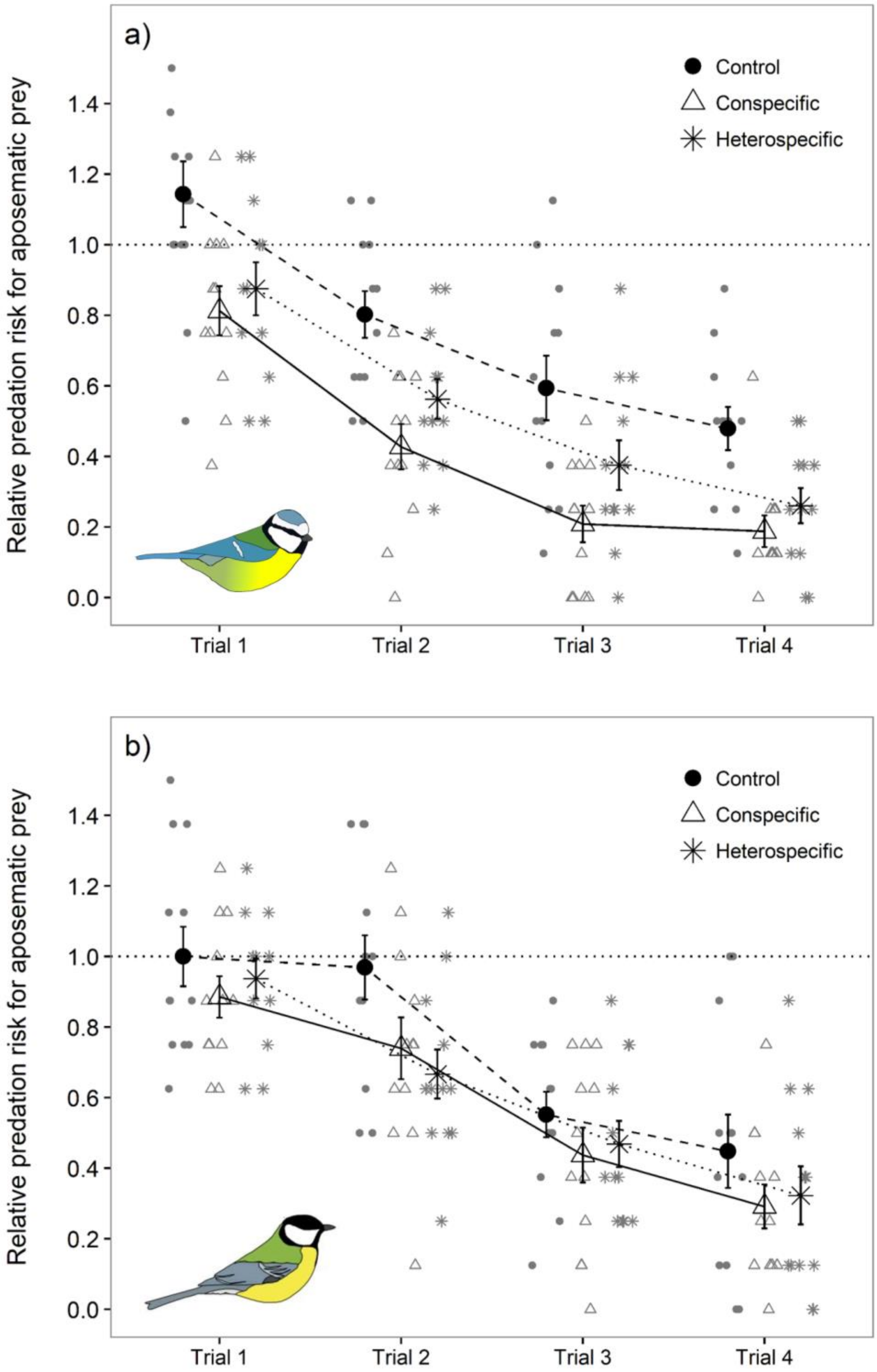


Figure 2. Relative predation risk (mean ± s.e.) for aposematic prey (number of aposematic prey attacked/ number expected by random chance) with (a) blue tit and (b) great tit predators. The graph shows the decrease in predation risk over four trials that were conducted over two consecutive days (2 trials/day). Each species had three treatment groups that (i) did not receive any social information (circles + dashed lines), (ii) received social information about aposematic prey from a conspecific (triangles + solid line), or (iii) received social information about aposematic prey from a heterospecific (stars + dotted line). Smaller symbols indicate individual variation within the treatment.

DISCUSSION

Social avoidance learning among predators can be an important force in facilitating and maintaining the evolution of prey signals (Mason & Reidinger, 1982; Johnston *et al*., 1998; Landová *et al*., 2017; Thorogood *et al*., 2018). However, experiments comparing ecologically similar predator species that have potential to learn from one another's foraging behaviour are scarce (e.g. Sasvári, 1979; Mason *et al*., 1984; Lefebvre *et al*., 1997; May & Reboreda, 2005). Here we combine these in one experiment to test the effects of conspecific and heterospecific information on avoidance learning of two predator species. We found that both blue tits and great tits used social information about prey unpalatability and that this reduced predation pressure on novel aposematic prey. Importantly, we also showed that both species could learn by observing each other. Although we expected that blue tits may not use social information as much as great tits (Sasvári, 1979; Aplin *et al*., 2013; Hämäläinen *et al*., 2017), surprisingly we found the opposite. Blue tits consumed fewer aposematic prey after observing a conspecific or a heterospecific demonstrator attacking the same prey signal. The trend was similar in great tits, although the effect was less clear than in our previous studies with a similar set-up (Hämäläinen *et al*., 2019a), or conducted at a larger scale where foraging costs may have differed (Thorogood *et al*., 2018). Our study suggests that social transmission about novel prey signals can occur across and among predator species and it could therefore have potent effects on prey evolution.

Social learning theories predict that individuals should value social information more when the cost to obtain personal information is high (Laland, 2004; Kendal *et al*., 2005). Therefore, social information about unpalatable food is likely to be important to predators if it prevents them ingesting potentially toxic food, and it might even be more valuable than information gathered from observing palatable foraging experiences. This could explain why we found strong evidence of blue tits learning by observing others in this experiment, in contrast to previous studies that focused on solving a foraging task (Sasvári, 1979; Aplin *et al*., 2013), or using social information in a simple multiple-choice foraging test (Hämäläinen *et al*., 2017; Hämäläinen *et al*., 2019b). In our current experiment birds encountered a more complex foraging environment where they were required to attack many novel prey and the higher energy and time investment, together with the risk of consuming prey with unknown toxin quantity might have increased the relative costs of gathering personal information (Skelhorn, Halpin & Rowe, 2016). Furthermore, our experiment demonstrates that blue tits can learn by watching video playback of a demonstrator. This is in contrast to our earlier work that suggested blue tits do not necessarily use the information provided, even though they paid more attention to video playback of a conspecific consuming aversive prey, compared to a positive foraging event (Hämäläinen *et al*., 2017). This indicates that social information use is context-dependent, and the failure to find clear evidence of the efficacy of videos in our previous studies resulted from different methods, such as simpler foraging tasks (Hämäläinen *et al*., 2017; Hämäläinen *et al*., 2019b), which highlights the importance of standardised experiments to compare information use across species (Shaw & Schmelz, 2017).

Social information use among predators might be even more widespread if learning occurs across species boundaries. Ecologically similar heterospecifics are suggested to provide a valuable source of social information and heterospecific information use has been now demonstrated in many different contexts (Seppänen *et al*., 2007). For example, Carib grackles copy the foraging techniques from both conspecific and heterospecific (Zenaida dove) demonstrators (Lefebvre *et al*., 1997), and shiny cowbirds learn a novel foraging task after observing either a conspecific or a heterospecific (a screaming cowbird; May & Reboreda, 2005). Similarly, predators might gather social information about prey defences by observing heterospecifics. This could be common in parid tits that share similar habitats and form mixed-species foraging flocks (Ekman, 1989). Predators might also differ in their tendency to sample aposematic prey (Exnerová *et al*., 2003; 2007). For example, previous studies suggest that blue tits are more hesitant to attack novel prey than great tits (Exnerová *et al*., 2007; Adamová-Ježová *et al*., 2016), and social information from heterospecifics might therefore be an important source of information for the more neophobic species. Our study supports this idea, as we found that blue tits sampled fewer aposematic prey after observing a negative foraging experience of a great tit demonstrator. However, blue tits still learned more effectively from conspecifics. This is similar to a previous study that found great tits learning a novel foraging skill better from conspecifics, compared to heterospecifics (Sasvári, 1979), and might be explained by birds paying more attention to individuals of their own species. Surprisingly, we did not find this difference in great tits that learned equally well from both blue tit and great tit demonstrators, which suggests that predator species may differ in how they rely on different social information sources.

Previous studies have shown how social avoidance learning can help facilitate the initial evolution of aposematic prey (Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a). Our finding that species can also learn from observing each other further supports this hypothesis as it increases both the potential audience and the availability of demonstrators. As in previous studies (Thorogood *et al*., 2018; Hämäläinen *et al*., 2019a), we also found that both blue and great tits varied in the strength of response to social information, with some individuals sampling more aposematic prey than others. This variation among predators has important potential consequences. For example, when some individuals continue to try new prey for longer, this provides additional opportunities for others to learn, including naïve immigrants and juveniles (Thorogood *et al*., 2018). Furthermore, this variation among predators would create varying selection pressures for warning signals in space and time (Endler & Mappes, 2004; Thorogood *et al*., 2018). For example, more conspicuous warning signals might be favoured when predators are more likely to learn about aposematic prey socially, and variation in social information use among predators could therefore help to maintain signal polymorphisms in the face of frequency-dependent selection (Nokelainen *et al*., 2014), as well as influence the cost of signal conspicuousness (Valkonen *et al*., 2012).

Overall, our study shows that social avoidance learning occurs in multiple predator species and also across species boundaries. However, we also demonstrate that predators are heterogeneous in how they use information. Social avoidance learning is yet to be tested in more than a handful of (avian) predator species (Mason & Reidinger, 1982; Johnston *et al*., 1998; Landová *et al*., 2017; Thorogood *et al*., 2018), so more research is needed to assess the effects of this variation on information use. In addition to birds, previous studies have shown that primates can learn about unpalatable food socially (Snowdon & Boe, 2003; Van de Waal, Borgeaud, Whiten, 2013), and it would be important to extend this research on other predator taxa. Furthermore, we do not know how predators learn about aposematic prey in the wild. Even though studies with birds in captivity have demonstrated that predators learn to avoid unpalatable prey faster after receiving social information (Mason & Reidinger, 1982; Johnston *et al*., 1998; Landová *et al*., 2017; Thorogood *et al.,* 2018), the situation is likely to be more complicated in the wild where predators can encounter many different prey types and have opportunities to gather social information from both conspecifics and heterospecifics. Field studies in different predator communities are therefore required to increase our understanding of social transmission in predator populations and its' effects on predator-prey coevolution.

CHAPTER 6

Social transmission of information about aposematic prey and palatable mimics in a wild predator community

Data collection for this chapter was assisted by Marianne Teichmann, Verity Bridger and Victoria Franks. Data analysis was done in collaboration with William Hoppitt.

Aposematic prey advertise their defences with warning signals, which leaves them vulnerable to attack by naïve predators. This predation cost is highest during the time period when juvenile birds have fledged, and explaining how warning signals are maintained in the face of repeated outbreaks of naïve predators remains a major puzzle in evolutionary biology. Nevertheless, this predation risk quickly diminishes and one explanation for this rapid learning could be if avoidance spreads via social transmission, with birds learning from observing the feeding attempts of other naïve individuals and/or by observing the avoidance of educated predators. On the other hand, social information use could *increase* predation on warningly coloured prey if naïve and/or educated birds learn by observing others consume palatable prey species that otherwise rely on mimicking aposematic models. However, neither hypothesis has yet been tested in the wild. Here, we investigate how great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) use social information about prey palatability using automated monitoring of social interactions and foraging choices. Our aim was to test 1) how quickly birds can learn to avoid novel unpalatable food and whether this is influenced by the expected number of observations of positive and/or negative foraging experiences of others, and 2) how quickly birds can reverse a learned aversion, particularly if this is influenced by the observation of others consuming previously unpalatable food ('mimics'). We compiled a social network for the predator community and presented birds with pairs of novel palatable and unpalatable foods that were visually distinct (coloured almonds). Across three different replicate colour pairs, we found that the expected number of observed unpalatable feeding events (as predicted from the social network) reduced birds' likelihood to choose that colour, and that this effect was similar regardless of whether birds observed conspecifics or heterospecifics. Birds relied more on social information from adults than from juveniles, and social transmission from adults was also important during reversal learning when both colours became palatable, with birds being more likely to sample previously unpalatable prey after observing adults feeding on them. Our results demonstrate that predators use social information about prey profitability in the wild and

social interactions among predators can have important consequences for the evolution and maintenance of prey defences.

INTRODUCTION

Explaining the origin and maintenance of aposematism has remained an enduring question in evolutionary biology. Aposematic animals signal their unprofitability with conspicuous warning signals, which predators learn to avoid (Poulton, 1890; Ruxton *et al.*, 2018). Conspicuous aposematic prey, however, are an easy target for naïve predators who have yet to associate the warning signal with unprofitability (Alatalo & Mappes, 1996; Mappes, Marples & Endler, 2005). This creates a problem for the evolution of novel aposematic prey, but also for the maintenance of existing warning signals – how can aposematic prey survive repeated outbreaks of naïve individuals in each predator generation? Initial wariness to attack novel (Marples, Kelly & Thomas, 2005) or warningly coloured prey (Lindström, Alatalo & Mappes, 1999b) might provide one solution to this puzzle, but juvenile fledging time of passerine birds is still a particularly risky period for conspicuous prey (Mappes *et al.*, 2014). This disadvantage of warning colouration, however, declines rapidly (Mappes *et al.*, 2014), which suggests that juvenile birds learn to avoid aposematic prey quickly, but this has not been directly tested with wild predator populations because following individual predators in the wild is logistically difficult. In fact, even though a number of experiments have investigated predation risk for artificial prey in the wild (e.g. Speed *et al.*, 2000; Valkonen *et al.*, 2012; Mappes *et al.*, 2014; Nokelainen *et al.*, 2014), all studies testing predator avoidance learning at an individual level have been conducted in captive environments (reviewed in Skelhorn, Halpin & Rowe, 2016). However, investigating how wild predators acquire information about novel unpalatable prey is important if we are to better understand the selective pressures operating on prey defences and signaling.

One explanation for the maintenance of warning signals might be social transmission of avoidance in the predator population (Thorogood, Kokko & Mappes, 2018). Indeed, there is now good evidence that avian predators can acquire avoidance to aposematic prey faster after observing other predators rejecting the same prey (Landová *et al.*, 2017), or showing an aversive response after attacking it (Mason & Reidinger, 1982; Mason, Arzt & Reidinger, 1984; Johnston, Burne & Rose, 1998; Thorogood *et al.*, 2018; Hämäläinen *et al.*, 2019a). If predators also use social information about prey defences in the wild, this could reduce the predation cost for conspicuous prey from naïve predators and facilitate the evolution and maintenance of aposematism (Thorogood *et al.*, 2018). However, the only evidence of social transmission of avoidance in the wild comes from a study with vervet monkeys (van de Waal, Borgeaud & Whiten, 2013), which found that naïve infants copied food preferences from mothers that had learned to avoid unpalatable food, and that migrating males switched their food preferences to the new local norm. This suggests that aposematic prey might benefit from social transmission of information if naïve individuals copy the foraging behaviour of educated predators, and if individuals prefer the same food as the majority of the population (conformity; van de Waal *et al.*, 2013; Aplin *et al.*, 2015b). The benefit of social information is, however, likely to depend on the structure of the predator community, with some predator species being less neophobic (Exnerová *et al.*, 2003; 2007; Adamová-Ježová *et al.*, 2016) or more resistant to prey toxins (Fink & Brower, 1981; Brodie & Brodie, 1990), and therefore attacking aposematic prey at higher rates than others. This variation among predator species might benefit more-risk aversive predators, as they could use heterospecific information to learn about prey defences (Mason *et al.*, 1984; Hämäläinen *et al.,* in review), but this has not been tested in the wild. Furthermore, van de Waal *et al*. (2013) focused on social transmission when the majority of the population was already trained to avoid unpalatable food, but they did not investigate social information use when novel food was introduced for the first time. Therefore, we do not know how predators use social information when all individuals are naïve, which could help us to understand the initial evolution of aposematic prey, as well as the maintenance of warning signals when a large proportion of predators are unexperienced (e.g. juveniles).

Social transmission of information about prey profitability might also influence the frequency-dependent model-mimic dynamics in prey population (Alcock, 1969). Batesian mimics gain protection from predators by resembling the defended model species (Bates, 1862), and there might also be within species variation in the strength of the defence, with automimics benefiting from the warning signal without producing chemical defences (Brower, Brower & Corvino, 1967). The presence of palatable mimics is costly to the defended models, as they dilute the protection from predators (Lindström, Alatalo & Mappes, 1997; Gamberale-Stille & Guilford, 2004; but see Rowland *et al.,* 2007). Social information about undefended mimics might increase predators' likelihood to sample previously unpalatable prey (Alcock, 1969) and further drive these frequency-dependent mimicry dynamics (Mappes & Lindström, 2012; Thorogood & Davies, 2012). However, experiments investigating the effect of social information on reversal learning about previously unpalatable food are scarce and have provided mixed results (Alcock, 1969; Fryday & Greig-Smith, 1994; Vale *et al.*, 2017; Hämäläinen *et al.*, 2019a). This indicates that predators' responses to social information about mimics may differ among predator species and depend on the foraging context, such as predators' personal experience with the defended models. Furthermore, a predator's willingness to sample mimics is likely to be influenced by many additional factors, including toxicity of the model (Lindström *et al.*, 1997; Skelhorn & Rowe, 2006), abundance of mimics (Sherratt, 2011; Kikuchi & Sherratt, 2015) and alternative prey (Kokko, Mappes & Lindström, 2003; Lindström *et al.*, 2004), and a predator's physiological state (Sherratt, 2003; Barnett, Bateson & Rowe, 2007; Barnett *et al.*, 2012; Skelhorn *et al.*, 2016).

Although recent technological advances make it now possible to follow individual predators in the wild (e.g. Roth & Lima, 2007), predator avoidance or reversal learning at an individual level has not been tested with wild predator populations. Furthermore, we do not know how social transmission of information about aposematic prey and their mimics spreads in the wild when individuals have opportunities to observe both conspecifics and heterospecifics, and learn from both positive and negative feeding events of others. Radio frequency identification (RFID) tags are now widely used when studying social interactions in wild bird populations (e.g. Aplin *et al*., 2012; Aplin *et al*., 2015b; Jones *et al*., 2017) and by fitting feeders with RFID antennas, it is possible to collect data remotely on individuals' foraging choices. Records of social interactions at the feeders can be further used for constructing social networks (Farine & Whitehead, 2015), and previous studies have shown that information about the location of food (Aplin *et al.*, 2012; Farine *et al.*, 2015) and novel foraging skills (Aplin *et al.*, 2015b) can spread through these networks. All these studies have, however, focused on learning from positive foraging experiences of others, and our aim here is to investigate how social information about prey unpalatability spreads in a wild bird population.

We designed a field experiment where we investigated avoidance learning and social information use in a wild blue tit and great tit population during the summer when juveniles were abundant and aposematic prey is predicted to suffer high predation (Mappes *et al.*, 2014). Our aim was to test 1) how fast birds learn to discriminate novel palatable and unpalatable food and whether they use positive and/or negative social information during this learning process, and 2) whether educated birds reverse their learned avoidance towards previously unpalatable food ('models') and if this is influenced by the observation of others consuming similarly looking palatable food ('mimics'). We presented a population of RFID tagged great tits and blue tits with novel palatable and unpalatable food (almond flakes of different colours) at bird feeders that had RFID antennas that enabled us to record each individual's foraging choices. This allowed us to investigate if individuals' foraging choices were influenced by the observation of positive or negative feeding events of others (expected number of observations calculated from the social network), or whether they were driven by birds' personal experience (previous visits to the feeders). We replicated the avoidance learning experiment three times during the summer, each time using different colour pairs to indicate prey palatability. With one of the colour pairs, we also tested reversal learning by presenting educated birds with palatable almonds of the same colour that they had previously learned to avoid. We could then investigate how fast educated birds reversed their acquired avoidance and whether this was influenced by social information from others.

METHODS

Study site

The experiment was conducted at Madingley Wood, Cambridge, UK (0◦3.2´E, 52◦12.9´N) during summer 2018. Madingley Wood is an established study site with an ongoing long-term study of blue tit and great tit populations. During the autumn and winter birds are caught from feeding stations using mist nets and they are fitted with British Trust of Ornithology (BTO) ID rings. Since 2012, blue tits and great tits have been fitted with RFID tags, which enables collecting data remotely about their foraging behaviour and social relationships. The study site has 90 nest boxes that are monitored annually during the breeding season. In 2018 chicks fledged successfully from 45 nest boxes, and all nestlings (n = 325) were ringed and fitted with RFID tags when they were approximately 10 days old. Because new juvenile flocks were arriving to our study site throughout the summer, we also conducted several mist netting sessions in July and August to maintain a high proportion of blue tits and great tits ringed and RFID tagged for the experiments.

Prey items

We investigated birds' foraging choices by offering them almond flakes at bird feeders that were distributed within the wood. In the learning experiments almond flakes were dyed with non-toxic food dye (Classikool Concentrated Droplet Food Colouring). We used three different colour pairs: green ('Leaf Green') and red ('Bright Red'), purple ('Lavender Purple') and blue ('Royal Blue'), and orange ('Satsuma Orange') and yellow ('Dandelion Yellow'). We decided to use green palatable and red unpalatable almonds in our first avoidance learning experiment, based on our pilot tests that indicated that birds had a slight preference for red almonds in captive experiments, but no preferences in the wild (see Appendix 4). The preference for other colours was not tested prior to the experiment. We chose the colour pairs that were unlikely to get generalised to green and red (to prevent any initial biases), and that had similar contrast ratios as green and red, based on their RGB values (measured from photographs). Almond flakes were dyed by soaking them for approximately 20 minutes in a solution of 900 ml of water and 30 ml of food dye, and then left air-drying for 48 hours. In the avoidance learning experiments, we made half of the almond flakes unpalatable by soaking them for one hour in 67 % solution of chloroquine, following previously established methods from avoidance learning studies with birds in captivity (e.g. Lindström *et al.*, 2001a; Thorogood *et al.*, 2018). The food dye was added to the solution during the last 20 minutes before drying.

Experimental procedure

Recording social associations

Before starting the experiments with coloured almonds, we collected data on individuals' social associations at the feeders using plain 'control' almonds (not coloured and palatable). We introduced the feeders in the beginning of June when the nestlings had fledged and were starting to forage independently. We had three different feeding stations distributed to the wood (approximately 170 m from each other) and each had two feeders, positioned approximately 1.5 meters apart. We monitored the visits at the feeders using RFID antennas and data loggers (Francis Scientific Instruments, Ltd) that scanned birds' unique RFID tag codes when they landed on a feeder. The feeders were surrounded with metal cages to exclude larger birds. We placed plastic buckets under the feeders to collect spilled almonds and minimise birds' opportunities to forage from the ground instead of landing on the antenna. We started the first experiment with coloured almonds in the beginning of July and conducted four different learning experiments during the summer (Fig. 1). Between the experiments, we always presented birds with plain control almonds and recorded their visits at the feeders, and the data of the feeding records outside the experiments was used for constructing a social network of the bird population. Because individuals were likely to vary in their hesitation to visit novel coloured almonds, we assumed that this 'control' data (visits to familiar plain almonds) would give us the most accurate measure of foraging associations in the population.

Learning experiments with coloured almonds

We conducted three avoidance learning experiments with different colour pairs throughout the summer (unpalatable vs. palatable): red vs. green, blue vs. purple, and yellow vs. orange (Fig. 1). In addition, we conducted a reversal learning experiment with the blue/purple colour pair by making both colours palatable after birds had acquired avoidance to blue almonds. Each experiment followed a similar protocol, in which birds were presented with coloured almonds at the same three feeding stations where they were previously offered plain almonds. Each feeding station had two feeders, with one of them containing of palatable almonds and the other one differently coloured unpalatable almonds (except in the reversal learning test in which both colours were palatable). We switched the side of the feeders every day to make sure that birds learned to associate palatability with an almond colour and not a feeder position. The feeders were filled at least once a day (or more often if necessary) to make sure that birds always had access to both colours. We continued each avoidance learning experiment until > 90 % of all recorded visits were to the feeder with palatable almonds, indicating that most birds in the population had learned to discriminate the colours. This took 7 days in the red/green experiment and 8 days in the other two colour pairs (blue/purple and yellow/orange). The reversal learning experiment was finished after 9 days when > 50 % of the visits were to the previously unpalatable colour (blue), indicating that most birds had reversed their learned avoidance towards it.

During the learning experiments, each day we recorded videos from all three feeding stations (using Go Pro Hero Action Camera and Canon Legria HF R66 Camcorder). From the videos, we estimated the proportion of blue tits and great tits that did not have RFID tags (and were therefore not recorded when visiting the feeders). We realised that the number of new individuals was very high (approximately 50 % of all visiting birds) when we started the experiment with the first colour pair (red/green). We therefore stopped the experiment after two days and caught birds from the feeding stations with mist nets to fit RFID tags to new individuals. To maintain a high number of individuals RFID tagged for the other colour pairs, we conducted a mist netting session a day before starting each experiment, as well as 4-5 days after it. We always switched the feeders back to containing of plain almonds during mist netting sessions to ensure that this would not interfere with the learning experiments. Apart from the first two days of the red/green experiment, the RFID tag coverage was on average 89 % throughout the experiments (varying between 80 and 95 %, see Appendix 4 for details).

Statistical analyses

We first analysed how birds' foraging choices changed during the learning experiments using generalised linear mixed effects models with a binomial error distribution. The number of times an individual visited each feeder on each day of the experiment was used as a bound response variable, and this was explained by species (blue tit/great tit), individuals' age (juvenile/adult) and day of the experiment (continuous variable), as well as bird identity as a random effect. When analysing avoidance learning, initial exploration of data suggested that results were similar across all three experiments, so we combined them in the same model and included colour pair (red/green, blue/purple, yellow/orange) as a random effect. To investigate whether learning curves differed between the species or age groups, the day of the experiment was included as a second order polynomial term, and we started model selections with models that included a three-way interaction between species, age and day (polynomial). Best-fitting models were selected based on Akaike's information criterion (see Appendix 4 for model selections).

To investigate if birds used social information in their foraging choices, we first constructed a social network of the bird population based on the social association at the feeders outside the learning experiments (i.e. when birds were presented with plain almonds). We used a Gaussian mixture model to detect the clusters of visits ('gathering events') at the feeders (Psorakis *et al.*, 2012), and then calculated association strengths between individuals based on how often they were observed in the same group (gambit of the group approach; Franks, Ruxton and James, 2010). These associations estimate the probability that two individuals are in the same group at a given time (Cairns and Schwager, 1987). If birds socially learned to avoid the unpalatable food and/or prefer the palatable food by observing the choices of others, we would expect avoidance of the unpalatable option (relative to the palatable option) to follow the connections of the association network, since this reflects opportunities for members of each dyad to observe one another. Similar logic led to network-based diffusion analysis (NBDA; Franz & Nunn, 2009), a statistical method for detecting the spread of novel behaviour by social transmission. Here, we are unable to apply NBDA, since we are not interested in the first time a target behaviour is performed (with the exception of reversal learning - see below), but rather whether birds socially learn to avoid performing a particular behaviour. Therefore, here we devise and apply a statistical procedure to test for social aversion learning under the assumption it follows an association network. We reasoned that the probability that one individual A, observes a specific feeding event by another individual B, is proportional to the network connection between them (probability they are in the same feeding group at a given time). Therefore, in each avoidance learning experiment (i.e. different colour pair), we calculated the expected number of negative feeding events observed, prior to each choice (occurring at time t) as

$$O_{-,i}(t) = \sum_j N_{-,j}(t) a_{ij},$$

where $N_{-,j}(t)$ is the number of times *j* had visited unpalatable almonds prior to time *t*, and summation is across all birds in the network, and likewise for the expected number of positive feeding events:

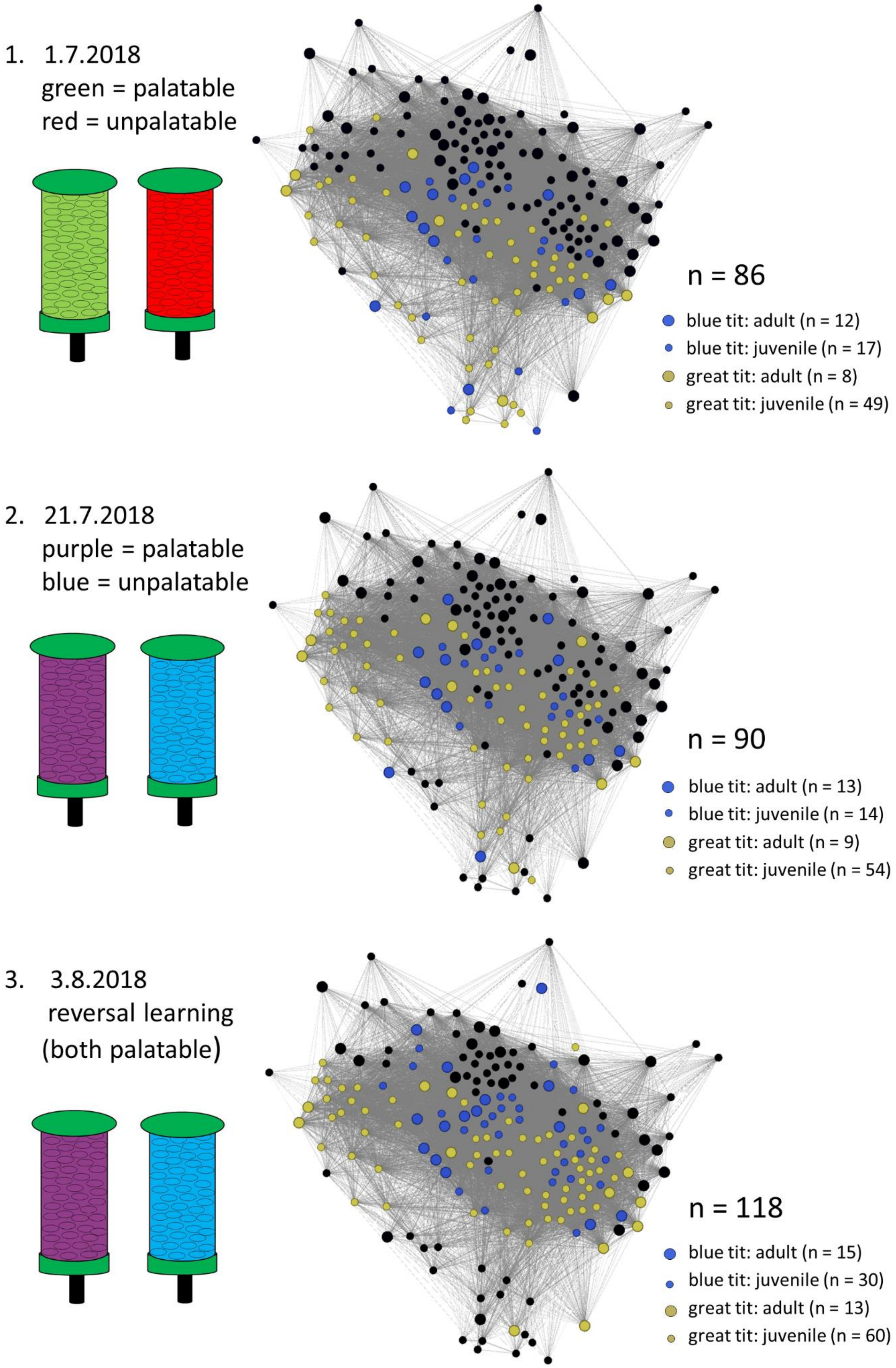
$$O_{+,i}(t) = \sum_j N_{+,j}(t) a_{ij},$$

where $N_{+,j}(t)$ is the number of times *j* had visited palatable almonds prior to time *t*. Strictly speaking, $O_{-,i}(t)$ and $O_{+,i}(t)$ are upper limits on the expected number of observations, assuming that birds observe all feeding events in the groups in which they are present, whereas only an unknown proportion of such events (p_o) will be observed. Therefore, the real expected number of negative and positive observations would be $p_oO_{-,i}(t)$ and $p_oO_{+,i}(t)$ respectively. This affects the interpretation of effect sizes but not the underlying logic of our approach.

We analysed whether the expected observations of positive and/or negative feeding events of others influenced the foraging choices in the avoidance learning experiments using generalised linear mixed effects models with a binomial error distribution. We used each choice (i.e. visit to a feeder) as a binary response variable (1 = unpalatable chosen, 0 = palatable chosen). Explanatory variables in the model included the number of times a choosing individual had visited palatable (positive personal information) and unpalatable feeder (negative personal information) before its current choice, and the expected number of observed positive (positive social information) and negative feeding events (negative social information) calculated from the network. Bird identity was included as a random effect. We also investigated how birds used different sources of social information by testing whether individuals were more likely to learn socially by observing conspecifics than heterospecifics. This was done by splitting the expected number of observed positive and negative feeding events to observations of conspecifics and heterospecifics, and including these in the model as separate explanatory variables. To investigate whether observation of adults had a stronger effect on foraging choices than observation of juveniles, we further split the observed feeding events to observations of adults and juveniles.

Whilst the model described above is formulated under the assumption that the network determines opportunities for social learning, a positive result for one or both of the social effects does not necessarily constitute strong evidence of social effects following the network. A social effect that operates homogeneously among all birds might also be detected by the model (i.e. a model with network-based effects is likely to explain homogeneous social learning better than a model with no social effects at all). However, a statistical effect consistent with homogeneous social learning is somewhat less convincing than an effect following the network, since it might be a spurious result of another confounding variable that causes a reduction in preference for the aversive option over time. Therefore, we require a way to test whether putative social effects follow the network. When using an NBDA, researchers can compare a network model with one in which the network has homogeneous connections among all individuals (Hoppitt and Laland, 2013), but we found this to be unreliable for the model described above. Instead, we used a simulation approach to generate a null distribution for the null hypothesis of homogeneous social effects, taking the size of the social effects from the fitted models. We ran 1000 simulations for all social effects that were found to be significant in each avoidance learning model (each colour pair). The total number of expected observations was kept equal, but we homogenised the observation effect across all birds (i.e. all birds had the same probability of observing the feeding event). The model was fitted to the simulated data each time to extract the Z value of the social effect that we were interested. The distribution of these values was then used as a null distribution to test whether our observed social effect differed from the effects that did not follow the social network.

To investigate social information use during reversal learning, we used the order of acquisition diffusion analysis (OADA), a variant of NBDA (Franz & Nunn, 2009), which explores the order in which individuals acquire a behavioural trait (Hoppitt, Boogert & Laland, 2010; Hoppitt & Laland, 2011). The rate of social transmission between two individuals is assumed to be linearly proportional to their network connection, and the spread of trait acquisition is therefore predicted to follow the network patterns if individuals are using social information. We used NBDA to investigate whether the order of individuals' first visit to the previously unpalatable blue almonds ('mimics') followed the network. We fitted several different models that included (i) only asocial learning, (ii) social transmission of information following a homogeneous network (equal associations among all individuals), or (iii) social transmission of information following our observed network. Models that included social transmission were further divided to models with equal or different transmission rate from adults and juveniles, and from conspecifics and heterospecifics by constructing separate networks for each adult/juvenile and conspecific/heterospecific combination. To investigate whether asocial or social learning rates differed between blue tits and great tits, we included species as an individual-level variable. We then compared different social transmission models that assumed that species differed in both asocial and social learning rates, only in asocial or only in social learning rates, or that they did not differ in either. The best-supported model was selected using a model-averaging approach with Akaike's information criterion corrected for small sample sizes. All analyses were conducted with the software R.3.6.0 (R Core Team, 2016), using *lme4* (Bates *et al.*, 2015), *NBDA* (Hoppitt *et al.*, 2019) and *asnipe* (Farine, 2013) packages.



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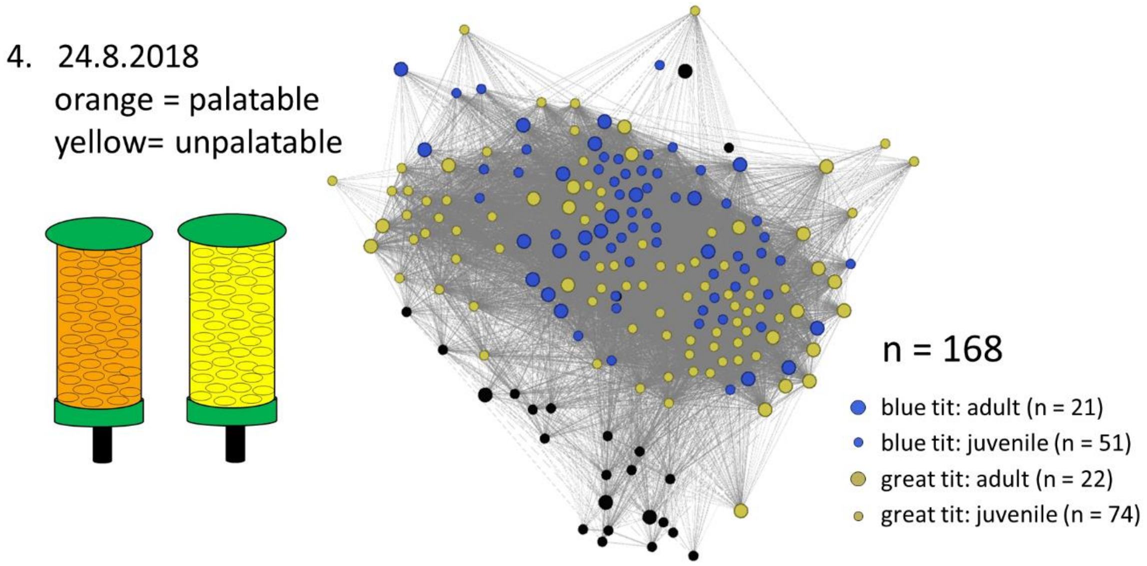


Figure 1. Summary of the different learning experiments and the social network of birds (n = 191) that visited the coloured almonds. (1) We started the first avoidance learning experiment in the beginning of July by presenting birds green and red almond flakes. (2) We then replicated this with purple and blue almonds, and (3) after birds had acquired avoidance to blue almonds, both colours were switched to be palatable to investigate reversal learning. (4) Finally, we conducted one more avoidance learning test in the end of August using orange and yellow almonds. Plain (control) almonds were presented always between the experiments to record social associations at the feeders, and social network of the bird population was constructed based on this data. Nodes in the networks represent blue tit (big blue circles = adults, small blue circles = juveniles) and great tit individuals (big yellow circles = adults, small yellow circles = juveniles), and lines (edges) their associations in the network. The number of birds visiting the feeders varied among the experiments and increased throughout the summer. In each experiment, blue and yellow symbols represent individuals that visited the feeders during the experiment, and black symbols are individuals that were not recorded visiting that colour pair.

RESULTS

Foraging choices in avoidance learning experiments

A total of 191 individuals (blue tits: n = 79, great tits: n = 112) visited the feeders during the experiments. This number increased throughout the summer, with the highest number of individuals recorded in the last avoidance learning experiment (yellow/orange; n = 168; Fig. 1). Approximately 75 % of individuals in each experiment were juveniles and 25 % adults, and great tits were more common than blue tits (Fig. 1). We found that in each experiment birds learned to discriminate palatable and unpalatable almonds within 8 days, by which time predation risk for unpalatable prey decreased below 0.1 (Fig. 2a). When investigating the first choice of each bird that visited the feeders on the first day of the experiment, we found that birds had a slight preference for green almonds in the red/green experiment (25 birds visited green and 13 red as their first choice; binomial test = 25/38, $p = 0.07$), but no initial preferences in blue/purple (25 birds visited purple and 36 blue as their first choice; binomial test = 25/61, $p = 0.20$) or yellow/orange experiments (63 birds visited orange and 69 yellow as their first choice; binomial test = 63/132, $p = 0.66$). There were no species-level differences in learning or in the total consumption of unpalatable almonds (Fig. 2a; see Table 1 in Appendix 4). However, an individual's age had a significant effect on the learning rate (day (polynomial) * age (juvenile): estimate = -22.981 ± 2.947, Z = -7.798, $p < 0.001$), with adults decreasing their consumption of unpalatable almonds at a faster rate than juveniles (Fig. 2a). The variance estimate for bird identity was relatively high (variance = 0.807), but the colour pair (red/green, blue/purple, yellow/orange) had a small effect on the foraging choices (variance = 0.012).

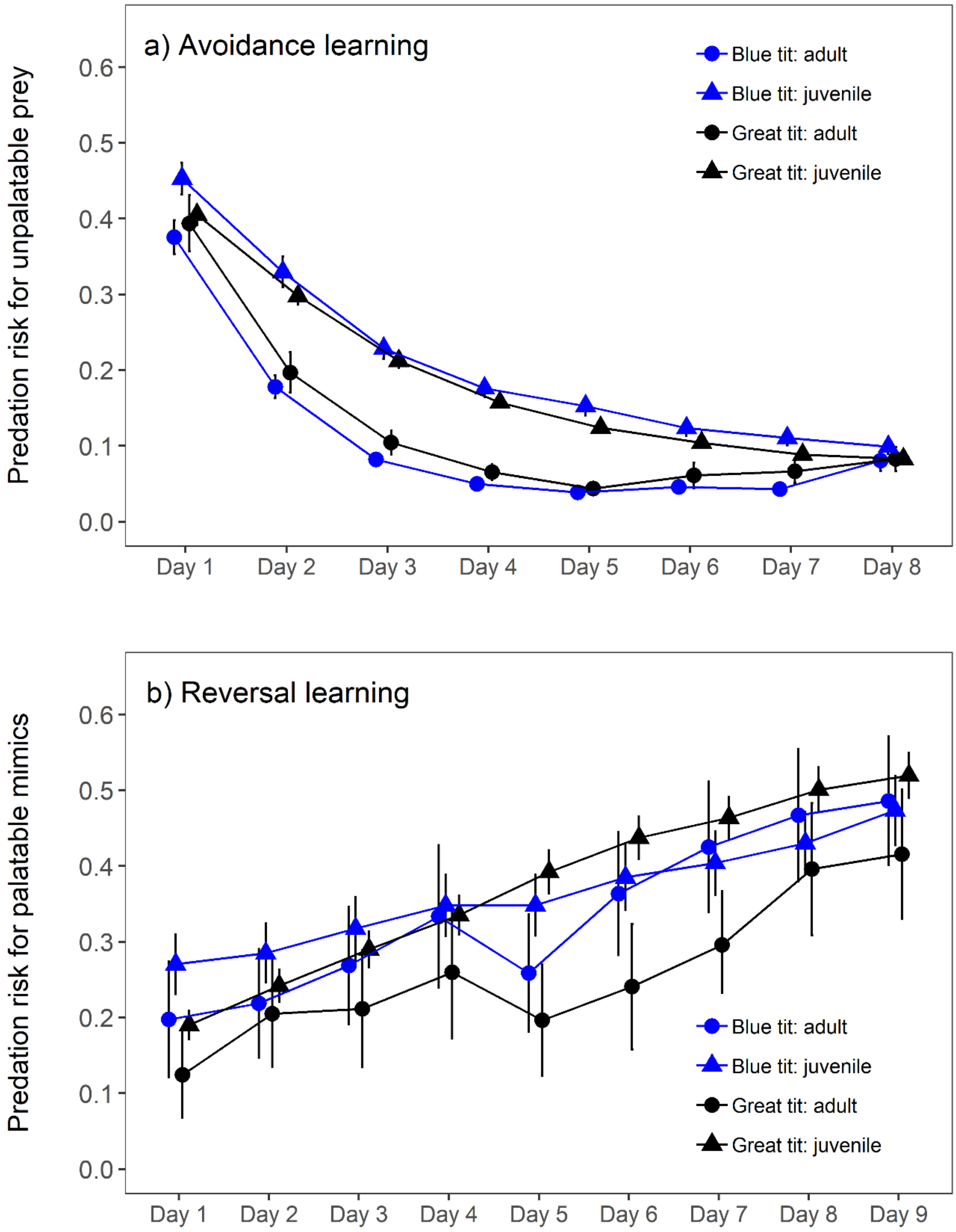


Figure 2. Predation risk for (a) unpalatable prey in the avoidance learning experiments and (b) for palatable mimics in the reversal learning experiment. Graphs show the mean (± s.e.) predation risk across the days of the experiment, i.e. the number of times an individual visited the feeder with (a) unpalatable colour or (b) palatable mimics divided by individuals' all visits on that day. All three avoidance learning experiments (red/green, blue/purple and yellow/orange) are combined in graph (a). Circles indicate the foraging choices of adults (blue: blue tits, black: great tits) and triangles show the choices of juveniles (blue: blue tits, black: great tits). The plotted data were derived from the generalised linear mixed effects models.

Social information use during avoidance learning

We found evidence of a social effect on birds' foraging choices, consistent with social learning resulting from observations of others consuming unpalatable almonds. An increasing number of expected observations of negative feeding events (as predicted by the network) made individuals less likely to choose the unpalatable colour, and this effect was consistent across all experiments (Table 1). The effect was similar when birds observed conspecifics and heterospecifics, and we therefore pooled the observed negative feeding events in the final models (see Appendix 4 for model selections). We also found that social effects of negative feeding events followed our observed network (Table 1), which means that the estimates from our network were a better predictor than estimates from a network where the observation effect was homogenised across all birds. This was consistent across the experiments, although the effect was not significant at alpha level of 0.05 in the blue/purple experiment (Table 1). When observing positive feeding events, the observation of conspecifics and heterospecifics had a different effect on birds' foraging choices, however, these effects were not consistent across the experiments (Table 1). In general, observing conspecifics eating palatable almonds made birds more likely to choose the same palatable colour, but this effect was statistically significant only in the yellow/orange experiment. In contrast, observing positive foraging events of heterospecifics made birds more likely to choose the opposite (unpalatable) feeder. However, this effect was not observed in the blue/purple experiment, and we also did not find evidence that it followed the network in the red/green experiment (Table 1).

We next investigated differences in social transmission of information from adults and juveniles. In general, an observation of a negative or a positive feeding event of an adult had a stronger effect on birds' foraging choices compared to an observation of a juvenile (Table 2, see Appendix 4 for the full models). This difference was clearest in the yellow/orange experiment, with birds reducing their likelihood to choose unpalatable (yellow) almonds only after seeing negative feeding events of adults but not juveniles (Fig. 3, Table 2). Similarly, an observation of adults consuming palatable (orange) almonds had a stronger effect on foraging choices compared to an observation of juveniles (Table 2), and the same difference in the observations of positive and negative feeding events of adults and juveniles was found in the red/green experiment (Table 2). The coefficients for the observations of adults were larger than for the observations of juveniles also in the blue/purple experiment (Table 2, see Appendix 4). However, although the results are not inconsistent with the other two colour pairs, because of large standard errors, we cannot make strong conclusions about the relative effects of the observations of adults and juveniles in this experiment.

Table 1. Summary of the social effects in three avoidance learning experiments. All observations of negative foraging experiences were pooled in the same social effect, but observations of positive foraging experiences were split between conspecifics and heterospecifics.

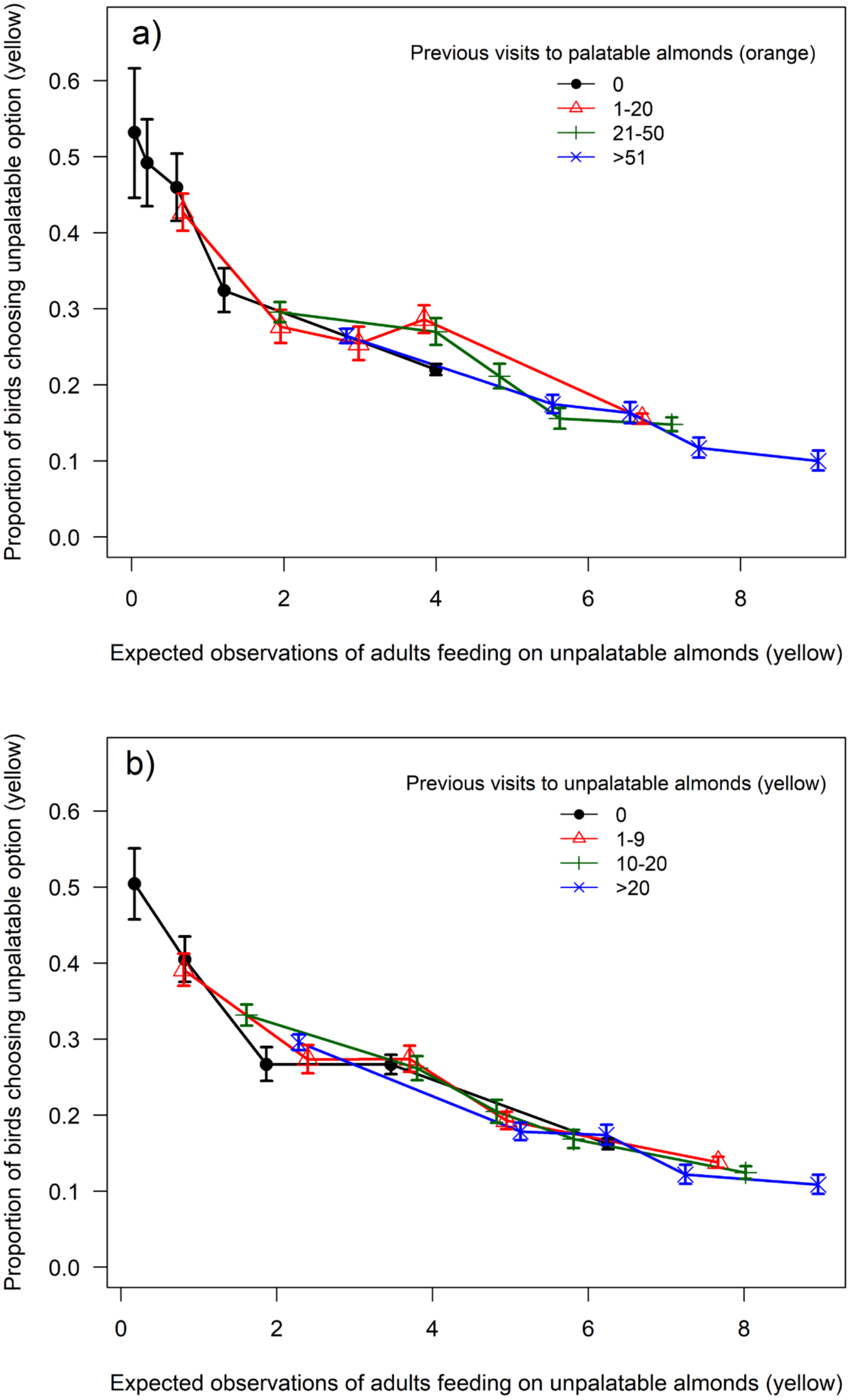
Social effect	**Estimate per expected observation on log odds scale (SE)** **Multiplicative effect on odds of choosing aversive [95% CI]** ***p*-value (simulation *p*-value*)**		
	Red/Green	***Blue/Purple***	***Yellow/Orange***
Observing a negative feeding experience	-0.015 (0.005) *x0.985 [0.976, 0.994]* $p < 0.001$ ($p_s = 0.04$)	-0.042 (0.014) *x0.959 [0.933,0.986]* $p = 0.004$ ($p_s = 0.09$)	-0.006 (0.002) *x0.994 [0.990, 0.997]* $p < 0.001$ ($p_s = 0.02$)
Observing a positive feeding experience of a conspecific	-0.010 (0.006) *x0.990 [0.978, 1.002]* $p = 0.11$	-0.004 (0.003) *x0.996 [0.989, 1.003]* $p = 0.26$	-0.008 (0.001) x*0.992 [0.990, 0.994]* $p < 0.001$ ($p_s = 0.002$)
Observing a positive feeding experience of a heterospecific	0.032 (0.007) *x1.033 [1.018, 1.047]* $p < 0.001$ ($p_s = 0.17$)	-0.002 (0.004) *x0.998 [0.989, 1.007]* $p = 0.66$	0.003 (0.001) *x1.003 [1.001, 1.005]* $p = 0.006$ ($p_s = 0.001$)

* The simulation *p*-value (p_s) tests whether the putative social effect follows the social network as opposed to operating homogeneously among the birds. This is provided only in cases where there was a significant ($p < 0.05$) social effect. Significant social effects found to follow the network ($p < 0.05$, $p_s < 0.05$) are shaded dark grey and otherwise ($p < 0.05$, $p_s > 0.05$) shaded light grey.

Table 2. Summary of differences in the effects of observing adults and juveniles in the three avoidance learning experiments. See Appendix 4 for the full models.

Social effect	**Estimate per expected observation on log odds scale (SE) for transmission from juveniles and adults** ***p*-value for difference between adults and juveniles**		
	Red/Green	***Blue/Purple***	***Yellow/Orange***
Observing a negative feeding experience	Juveniles: -0.061 (0.028) Adults: -1.287 (0.603) *p* = 0.046	Juveniles: -0.048 (0.023) Adults: -0.087 (0.273) *p* = 0.90	Juveniles: 0.005 (0.004) Adults: -0.239 (0.043) *p* < 0.001
Observing a positive feeding experience of a conspecific	Juveniles: 0.003 (0.009) Adults: -0.111 (0.046) *p* = 0.02	Juveniles: 0.000 (0.006) Adults: -0.042 (0.029) *p* = 0.20	Juveniles: -0.004 (0.001) Adults: -0.039 (0.007) *p* < 0.001
Observing a positive feeding experience of a heterospecific	Juveniles: 0.041 (0.008) Adults: -0.058 (0.091) *p* = 0.29	Juveniles: 0.005 (0.007) Adults: -0.025 (0.042) *p* = 0.50	Juveniles: 0.011 (0.002) Adults: -0.042 (0.008) *p* < 0.001
	AIC difference of adding age specific transmission		
	-25.48	+ 3.35	-124.96

* Significant difference in social effects between adults and juveniles ($p < 0.05$) are shaded dark grey.



(Figure caption on following page)

Figure 3. Proportion of individuals choosing the unpalatable (yellow) option in the yellow/orange experiment decreased when birds (n = 168) observed adults feeding on unpalatable almonds, and this was not explained by birds' personal experience of (a) palatable or (b) unpalatable almonds. In each graph, the data is divided into quartiles based on how many times birds had personally sampled (a) palatable or (b) unpalatable almonds before their current choice (represented by different symbols and colours). Within these 'personal experience categories', the data is further split to quartiles based on the expected number of observed unpalatable feeding events of adults (including the minimum value, i.e. five points for each personal experience category). Symbols show the mean and 95 % CI for the proportion of birds choosing the unpalatable option. If birds used only personal information, we would expect to see differences between each personal experience category and no decreasing trend when birds had not personally visited feeders (circles + black line). See Appendix 4 for the same graphs for other colour pairs.

Reversal learning

Birds reversed their learned avoidance towards previously unpalatable (blue) almonds quickly: in 9 days birds visited feeders with blue almonds equally often than the other option (purple; Fig. 2b). Change in the consumption across days (day (polynomial) * species (great tit): estimate = -2.999 ± 1.256, Z = -2.388, p = 0.02), as well as overall learning rate (day (linear) * species (great tit): estimate = 9.077 ± 1.314, Z = 6.908, $p < 0.001$) differed between great tits and blue tits, with great tits being more hesitant in sampling blue almonds in the beginning of the experiment (Fig. 2b). Furthermore, adults and juveniles differed in how fast they reversed their avoidance (day (linear) * age (juvenile): estimate = -0.128 ± 0.028, Z = -4.648, $p < 0.001$), with adults showing greater hesitation to sample previously unpalatable colour (Fig. 2b). Adults also reduced the consumption of blue almonds on Day 5 when coloured almonds were introduced again after a 2-day break for mist netting (see Methods), whereas this break did not increase wariness in juveniles (Fig. 2b). Because the number of individuals that visited the feeders during reversal learning experiment was higher than the number of birds that were recorded during avoidance learning (blue/purple; Fig. 1), some individuals might not have acquired avoidance to blue almonds before reversal learning. We therefore conducted the same analysis excluding individuals that had not visited the feeders during blue/purple avoidance learning experiment (n = 18) or that had been ringed after it (n =18), but this did no influence our results, with the differences between age and species groups remaining significant.

We found strong evidence that birds used social information in their decision to sample blue almonds for the first time, with the best-fit NBDA models including social transmission following our observed network (Table 3). We also found complete support for social transmission following our network when we compared Akaike weights of different social transmission models, with less than 1 % support for the models with only asocial learning or social transmission following the homogeneous network. The best-supported (Akaike weight = 64 %) models included social transmission following our observed network with equal transmission rates from conspecifics and heterospecifics, but different learning rates from adults and juveniles. There was no strong evidence for different asocial learning rates between the two species: blue tits were estimated to be slightly faster at sampling blue almonds than great tits (estimated effect of species (blue tit) = 1.48x faster), but also opposite effect was possible (95 % CI: 0.83–2.61). Similarly, we did not find strong support for differences in social learning: great tits were estimated to have a faster social learning rate than blue tits (estimated effect of species (great tit) = 2.10x faster), but also equal learning rates were possible (95 % CI: 0.99–4.41).

The best-fit model included social transmission following our observed network with different learning rates from adults and juveniles, and different asocial and social learning rates between the species, but no differences in conspecific and heterospecific information use (Table 3). The estimated social transmission parameters in this model were 10.83 (95 % CI: 1.60–67.26) from adults and 0 (95 % CI: 0–1.75) from juveniles, suggesting that an observation of adults feeding on blue almonds had a stronger effect on observers' decisions to sample the same colour than an observation of juveniles (95 % CI for the difference in social transmission rates from adults and juveniles: 1.60–67.26). These social transmission rates correspond to approximately 67 % (95 % CI: 52–80) of visits being influenced by the observation of adults (excluding the first bird sampling the blue almonds, i.e. 'innovator') and 0 % (95 % CI: 0–35) being influenced by the observation of juveniles. Finally, we further investigated potential differences in social transmission between conspecifics and heterospecifics. Because social transmission happened mainly by observing adults, we investigated this by fitting a model in which we assumed social transmission only from adults, and which included different conspecific and heterospecific transmission rates, and different asocial and social learning rates between the two species. The estimated social transmission parameters were 14.47 (95 % CI: 2.02–98.52) between conspecifics and 6.84 (95 % CI: 0.78–53.29) between heterospecifics, suggesting that there was social transmission both within and between the species. There was no clear evidence of differences in the strength of social transmission between conspecifics and heterospecifics, with potential differences possible in either direction (95 % CI for the difference in social transmission rates from conspecifics and heterospecifics: -17.79–65.86).

Table 3. Summary of the best supported models with social transmission following the observed (models with ∆AIC < 2) or homogeneous network, or with asocial learning only.

Model: Equal/different asocial and social learning rates between the species	**Transmission rate from adults vs. juveniles**	**Transmission rate from conspecifics vs. hetero-specifics**	**AICc**	**∆AICc**	**Social transmission parameter (s)**
Social transmission following the observed network					
Different asocial and social learning rates	different	same	851.2	0	10.83 (adults) 0 (juveniles)
Equal asocial and different social learning rates	different	same	852.2	+1.0	23.06 (adults) 0 (juveniles)
Social transmission following a homogeneous network					
Equal asocial and social learning rates	same	different	886.4	+35.2	0.10 (CS*) 0.03 (HS*)
Only asocial learning					
Equal asocial learning rate	NA	NA	883.3	+32.1	constrained to 0

* CS = social transmission rate from conspecifics, HS = from heterospecifics

DISCUSSION

In this experiment, we coupled a novel experimental design in the field with methodological advances in statistical analysis to test if social information plays a key role in reducing the predation risk faced by aposematic prey. We found that blue tits and great tits quickly acquired avoidance to novel unpalatable food in the wild, and this was influenced by social information from other individuals. Although we tested avoidance learning only in one predator population, we replicated the experiment three times using differently coloured prey items, and found consistent results that observing others consuming unpalatable almonds reduced birds' likelihood to choose the same prey type. This 'social avoidance learning' has been previously demonstrated only in controlled captive conditions (Mason & Reidinger, 1982; Mason *et al.*, 1984; Johnston *et al.*, 1998; Landová *et al.*, 2017; Thorogood *et al.*, 2018; Hämäläinen *et al.*, 2019a), and our study provides the first evidence that avian predators use social information about prey quality in the wild. Birds learned equally well by observing negative foraging experiences of conspecifics and heterospecifics, but an observation of adults had a stronger effect on birds' foraging choices than an observation of juveniles. When palatable mimics were introduced to the prey population, we similarly found that individuals used social information from adults, with birds being more likely to sample mimics after observing adults eating them. Our results demonstrate that social transmission of information about prey quality can reduce predation on aposematic prey in the wild, which can help us to explain a long-standing question of the evolution and maintenance of warning signals. However, social interactions among predators have also potential to increase predation on palatable mimics and influence model-mimic dynamics in the prey population.

Aposematic prey are assumed to suffer high predation when naïve juveniles are abundant (Mappes *et al.*, 2014), and our results suggest that social information from adults could reduce this predation cost by facilitating rapid avoidance learning. We found that juveniles were more likely to use social information about prey quality from adults than from other juveniles. This is in line with predictions that individuals often rely more on social information from older and more experienced individuals (Laland, 2004; Galef & Laland, 2005), however, this has rarely been demonstrated (but see Farine, Spencer & Boogert, 2015). In our experiment all individuals were naïve to different prey types, therefore juveniles had opportunities to observe the negative feeding events of other juveniles as well as adults. This situation might be different to the real world, where adults may have already encountered aposematic prey: although experienced predators still continue to attack defended prey based on nutrient-toxin trade-offs (Barnett *et al.*, 2007; Barnett *et al.*, 2012; Skelhorn *et al.*, 2016), the opportunities to obtain social information by observing the negative feeding events of adults are likely to be reduced. Nevertheless, our results suggest that even though juveniles might rely more on social information from older individuals, they can also learn about unpalatable prey by observing the negative feeding experiences of other juveniles, and this 'horizontal transmission' of information might be more important if social information from adults is not available.

In addition to learning by observing the negative foraging experiences of others (Mason & Reidinger, 1982; Mason *et al.*, 1984; Johnston *et al.*, 1998; Thorogood *et al.*, 2018; Hämäläinen *et al.*, 2019a), predators may gather information about prey quality by observing avoidance behaviour (Landová *et al.*, 2017), or positive feeding events (Mason & Reidinger, 1981; Fryday

& Greig-Smith, 1994; Benskin *et al.*, 2002; Sherwin, Heyes & Nicol, 2002). We found that observing other individuals eating unpalatable prey resulted in birds being less likely to choose the same prey, and this was apparent in all three experiments. The effects of observing positive feeding events, however, were weaker and less consistent (see Table 1). This suggests that witnessing a strong response to unpalatable prey (e.g. vigorous beak wiping and head shaking) provides observers more salient social information than positive information about prey palatability. Indeed, we have previously found that blue tits pay more attention to negative than positive feeding experiences of others (Hämäläinen *et al.*, 2017). Ignoring social information about prey unpalatability might also be more costly to predators because of the risk of consuming highly toxic prey. However, our experimental set-up with highly aggregated prey might have created competition at the feeders, which could provide another explanation for the inconsistent results of positive social information use, as birds might have chosen the more available feeder even after observing others feeding on palatable almonds of the opposite colour. Our finding of birds relying more on conspecific than heterospecific information about positive feeding events supports this idea, and especially smaller blue tits might have avoided the feeder that was occupied by great tits. It is therefore possible that positive social information might have a bigger impact on foraging choices when prey are less aggregated and the immediate competition is reduced.

Prey aggregation in our experiment provided individuals many opportunities to observe other predators. While this could have overinflated the strength of our results, aggregation has been suggested to increase the survival of aposematic prey by enhancing avoidance learning and diluting the mortality cost if predators leave the aggregation after sampling one individual (Alatalo & Mappes, 1996; Mappes & Alatalo, 1997; Lindström *et al.*, 2001b; Riipi *et al.*, 2001), as well as increasing initial wariness to attack warningly coloured prey (Gamberale & Tullberg, 1998; Rowland, Ruxton & Skelhorn, 2013). Our experiment suggests that aposematic prey might also benefit from aggregation by attracting the attention of many predators and increasing the likelihood that the negative foraging experience is witnessed by others. Aggregation among aposematic species is, however, relatively scarce (Ruxton & Sherratt, 2006), and further work is needed to investigate how predators use social information about prey defences in the wild when prey are less gregarious. Previous studies with birds in captivity have demonstrated that a single observation of others attacking aposematic prey can influence predators' foraging decisions (Thorogood *et al.*, 2018; Hämäläinen *et al.*, 2019a), which suggests that social transmission of information could be important even when predators do not witness multiple predation events. In fact, the magnitude of social effects might be even higher than estimated in our experiment because our models included upper limits of the expected number of observations (see Methods). In reality, birds were likely to observe only a proportion of these feeding events and the effect of one observation might therefore have a bigger impact on birds' foraging choices than the coefficients in our models predict. To get a more accurate estimate of the effect social information, future studies should aim to quantify the real number of observed feeding events, although this is logistically challenging.

Our experiment indicates that palatable mimics lose protection rapidly when they do not co-occur with their defended models, and social transmission of information can further accelerate this reversal learning. This is in contrast to our previous experiment with great tits in captivity, in which birds did not reverse their learned avoidance after receiving social information about mimics (Hämäläinen *et al.*, 2019a). Similarly, other studies have found that animals often rely on their recent personal experience when personal and social information conflict (Fryday & Greig-Smith, 1994; van Bergen, Coolen & Laland, 2004). However, these experiments are often conducted over short time scales. For example, in our previous experiment birds' foraging choices were tested in only two foraging trials that were conducted shortly after birds had personally experienced defended prey (Hämäläinen *et al.*, 2019a), whereas our current experiment was conducted over a longer time period. Predators' willingness to attack palatable mimics can also be influenced by the abundance of alternative prey (Kokko *et al.*, 2003; Lindström *et al.*, 2004), and birds in the field might have been more willing to rely on social information and sample previously unpalatable prey because of higher competition at the palatable feeder. The effect of social information might be particularly important when predator populations are dynamic and new naïve individuals enter the population, as individuals without personal experience of defended prey might be more likely to sample mimics and at the same time provide social information of their palatability to others. However, educated predators might also differ in their likelihood to attack mimics, depending on their current toxin load (Skelhorn & Rowe, 2007), nutritional state (Barnett *et al.*, 2007; Barnett *et al.*, 2012), and the degree of dietary conservatism (Marples & Mappes, 2011), and some predator species might be more likely to attack defended prey than others (Exnerová *et al.*, 2003; Endler & Mappes, 2004). Similar to previous studies in captivity (Mason *et al.*, 1984; Hämäläinen *et al.*, in review), we found that individuals gained information about unpalatable prey and their mimics by observing both conspecifics and heterospecifics. Predators are therefore likely to have many opportunities to gather social information about palatable mimics, and our results suggest that this can accelerate predation on mimics, at least when their defended models are not present.

Social transmission of information in wild bird populations is now well documented (e.g. Aplin *et al.*, 2015b; Farine *et al.*, 2015; Jones *et al.*, 2017), however, our study provides the first evidence that avian predators use social information in the wild to learn about prey defences. This can help us to understand how conspicuous aposematic prey survive when a new generation of naïve juveniles enter the predator population. The fledging period of passerine birds increases predation pressure on aposematic prey (Mappes *et al.*, 2014), but juveniles learn about prey signals rapidly, and our study indicates that this fast learning can be explained by social transmission of information about prey unpalatability. We found that juveniles learned more effectively by observing negative feeding events of adults, however, these opportunities for social learning might be reduced when adults are experienced. Instead of learning what to avoid, juveniles might therefore learn about favourable prey types by observing the successful foraging behaviour of adults. Furthermore, juveniles might acquire social information about prey quality from their parents before starting to forage independently. Indeed, cross-fostered blue tits and great tits differ in their prey choices, compared to individuals that are raised by the parents of their own species, which suggests that food preferences are learned from parents (Slagsvold & Wiebe, 2011). We started our experiment after juveniles were foraging independently, and also adults were naïve to unpalatable prey. Further work is therefore required to understand the early-life effects of social information from parents to offspring, and how this influences selective pressures for prey defences.

CHAPTER 7: General discussion

In my thesis I have investigated how social information use by predators can influence selection pressures for prey defences. Most previous work has assumed that predators need to personally sample aposematic prey to gather information about their defences, which makes the evolution and maintenance of aposematism paradoxical. Here I have used an information ecology approach to show that social transmission of avoidance can reduce the initial predation risk for aposematic prey and help to resolve this puzzle. I found that both blue tits and great tits used social information when learning about prey defences in a captive environment and in the wild. However, this seemed to be context-dependent, with individuals varying in their information use, and blue tits ignoring social information when the foraging task was simple. I further investigated the effects of social transmission of information on model-mimic dynamics in the prey population. Predation risk for mimics was not increased after a single observation of a conspecific consuming a mimic when alternative prey was abundant and predators had recent experience of the defended model. However, social information facilitated learning about mimics in the wild where individuals had opportunities to observe multiple predation events. Together, my results indicate that social transmission of information can shape selection for prey defences by both facilitating predator avoidance learning, as well as informing predators about palatable mimics, but the importance of these effects is likely to vary among different predator-prey communities. Here I discuss how an information ecology approach can help us to understand predator-prey coevolution and address potential areas for future research.

HOW DO PREDATORS VALUE DIFFERENT SOURCES OF INFORMATION?

Predators are predicted to gather as much information about prey quality as possible to make strategic foraging decisions (Dall *et al.*, 2005; Skelhorn, Halpin & Rowe, 2016). However, in their recent review, Skelhorn *et al*. (2016) discuss 'what surprisingly little we know about what predators learn about aposematic prey and how they use that information when foraging'. Many theoretical models have investigated the costs and benefits of gathering information about novel prey (Kokko, Mappes & Lindström, 2003; Sherratt, 2003; 2011; Kikuchi & Sherratt, 2015), but these have only considered how predators make adaptive decisions to acquire personal information about prey quality. For example, Skelhorn *et al*. (2016) suggest that predators' motivation to gather personal information about novel prey may vary depending on their physiological state. Similarly, predators' current state might influence their likelihood to use other sources of information, and in Chapter 2, I investigated this by testing whether previous experience of toxins influences how great tits use social information about novel aposematic prey (Hämäläinen *et al*., 2019a).

Social learning theories predict that individuals should rely more on social information when personal learning is costly (Laland, 2004; Kendal *et al.*, 2005) and this selective information use has been demonstrated in many experimental studies (Templeton & Giraldeau, 1996; Kendal, Coolen & Laland, 2004; Webster & Laland, 2008; Baracchi *et al.*, 2018). I predicted that the cost to sample novel prey would be higher when predators had consumed toxins (i.e. their 'toxin load' was high), which would increase the value of social information from other individuals. Furthermore, previous experience of toxins might alert individuals about the presence of defended prey in the environment (Rowe & Skelhorn, 2005; Skelhorn, Griksaitis & Rowe, 2008) and therefore increase their attention to social information. However, against my prediction, I found no evidence that previous consumption of toxins influenced how great tits used social information. Instead, social information had a similar effect in both toxin load treatments, with socially educated birds sampling fewer aposematic during avoidance learning compared to the control birds. This suggests that the cost to sample novel prey with unknown toxin quality and quantity is risky even when predators' current toxin load is low, and social information about prey profitability might therefore be valuable to naïve predators in all encounters with novel prey.

In addition to gathering information about novel prey, predators can update their existing knowledge about prey defences (Skelhorn *et al*., 2016). For example, encountering a palatable mimic might change predators' evaluation of prey quality and increase their willingness to gather more information by sampling the same prey type again. However, sampling mimics personally can be costly (Kikuchi & Sherratt, 2015), and social information about the presence of mimics might therefore be important in influencing predators' decisions to attack them (Alcock, 1969). In Chapter 2, I tested this by providing educated great tits with social information about palatable mimics before investigating their foraging choices (Hämäläinen *et al*., 2019a). However, I did not find evidence that receiving social information increased birds' willingness to sample mimics, which suggests that recent personal experience might override social information, similar to previous studies (Fryday & Greig-Smith, 1994; van Bergen, Coolen & Laland, 2004). It is also possible that the high cost of consuming toxins makes negative information about prey defences more valuable than positive information about prey profitability. For example, predators with previous positive experience of palatable prey (e.g. previous encounters with mimics) might still rely on conflicting social information about their unpalatability, and this requires further investigation.

Predators' likelihood to sample mimics might also depend on many other factors, such as the abundance of the mimics (Kikuchi & Sherratt, 2015), abundance of alternative prey (Kokko *et al*., 2003; Lindström *et al.*, 2004) and the model's level of defence (Lindström, Alatalo & Mappes, 1997; Skelhorn & Rowe, 2006). Birds' hesitation to attack mimics in my captive experiment (Chapter 2; Hämäläinen *et al*., 2019a) might therefore be explained by the low costs of continuing to attack only familiar palatable prey, as well as birds' recent personal experience of the defended models. Indeed, in my field experiment (Chapter 6), I found an opposite result with birds reversing their avoidance towards the models, and this reversal learning was facilitated by social transmission of information in the bird population. Although the familiar palatable prey was always available in the field, competition at the palatable feeder might have increased birds' willingness to sample the abundant (previously unpalatable) alternative prey. Together, my results suggest that the effects of social information on model-mimic dynamics are context-dependent: social information might not influence predation on mimics on a short time scale when alternative prey is abundant and predators have recently encountered aposematic models, but it might accelerate learning about mimics over longer time period, especially if mimics are abundant and predators have multiple opportunities to observe others feeding on them. However, I investigated social learning about mimics when mimics did not co-occur with their models, and it would be important to test how predators combine different information sources when both prey types co-exist and predators can gather both positive (seeing others consuming mimics) and negative social information (seeing others consuming models) of their palatability. Furthermore, I tested how predators learn about perfect mimics, but less accurate mimicry is common in nature (Penney *et al.*, 2012; Kikuchi & Pfennig, 2013), and more work is needed to test whether predators are more likely to rely on social information when models and mimics are easier to discriminate.

DOES THE PREY COMMUNITY INFLUENCE HOW PREDATORS USE SOCIAL INFORMATION?

The abundance of alternative prey might be important in influencing a predator's decision to gather and use information about palatable mimics (Kokko *et al*., 2003; Lindström *et al.*, 2004), and the prey community's composition might similarly influence learning about aposematic prey (Ihalainen *et al.*, 2012). In my thesis, I investigated social information use in simple prey communities with only one palatable and one aposematic prey. However, the cost to learn about aposematic prey is likely to be higher when the prey community is complex and signals are more variable (Ihalainen *et al.*, 2012), which could make social information even more useful (Laland, 2004; Kendal *et al.*, 2005). Further work is also needed to understand how predators generalise social information about prey unpalatability if the prey community consists of several aposematic species, including similar-looking Müllerian mimics (Müller, 1879). Skelhorn (2011) found that an observation of an aversive response of others can create general foraging biases away from warningly coloured (red and yellow) prey, which suggests that witnessing a negative foraging experience of others can increase wariness to attack any prey with typical aposematic colouration. In addition to facilitating learning about a specific prey type, social information might therefore reduce predation on aposematic prey by increasing neophobia towards any conspicuous prey. Furthermore, social information might make birds more cautious when approaching and handling novel prey, and this 'go-slow' behaviour could increase the survival of aposematic prey (Guilford, 1994), but this idea remains untested.

The abundance and distribution of different prey types is also likely to influence how predators gather and use social information. Gregariousness is often suggested to be beneficial for aposematic prey: even though it increases detection of prey, this cost can be compensated by faster avoidance learning and the dilution effect if predators desert the aggregation after detecting prey defences (Alatalo & Mappes, 1996; Mappes & Alatalo, 1997; Riipi *et al.*, 2001). Furthermore, predators might have higher initial wariness to attack warningly coloured prey that is aggregated (Gamberale & Tullberg, 1996; 1998; Rowland, Ruxton & Skelhorn, 2013). Aposematic prey might benefit from aggregation also if it increases social transmission of information in the predator community by attracting more observers to witness the negative foraging experience. Indeed, I found strong evidence of social information use in my field experiment (Chapter 6), in which prey were aggregated in the feeding stations, providing individuals many opportunities to observe foraging behaviour of others. Observers might also gather more accurate information about prey appearance by observing others feeding on aggregated prey, as this could provide stronger visual signals. How predators use social information in the wild when prey is less gregarious, however, needs more investigation.

Previous work (Thorogood *et al*., 2018) and the results from my experiments (Chapters 2 and 5; Hämäläinen *et al*., 2019a) suggest that a single observation of a negative feeding experience of others is sufficient to facilitate avoidance learning. Therefore, socially foraging predators are likely to gather social information about prey quality even when aposematic prey is less aggregated.

HOW DO PREDATORS VARY IN THEIR INFORMATION USE?

Selective pressures for warning signals depend on the predator community composition, with predators varying in their response to defended prey (Endler & Mappes, 2004). Social information about prey defences is likely to be important when predators are social foragers, such as blue tits and great tits that form foraging flocks (Ekman, 1989), whereas solitary predators might have fewer opportunities for social learning. However, even ecologically similar species might differ in their information use. In Chapters 3 and 4, I found that blue tits did not use social information about prey palatability or location when they were presented with a multiple-choice foraging task (Hämäläinen *et al.*, 2017; Hämäläinen *et al.*, 2019b). Together with previous studies (Sasvári, 1979; 1985; Aplin, Sheldon & Morand-Ferron, 2013), this indicates that blue tits are less likely to rely on social information compared to great tits that have been found to copy a demonstrator also in simple preference tests (Marchetti & Drent, 2000; Thorogood *et al*., 2018; Smit & van Oers, 2019). Nevertheless, in Chapter 5, I found that blue tits used conspecific and heterospecific information about aposematic prey when novel prey items were encountered in the more complex 'novel world' environment (Alatalo & Mappes, 1996). It is possible that birds valued social information more in this experiment because of an increased cost to sample prey. Because of the smaller body size, the physiological cost of consuming toxic prey might be even higher for blue tits compared to larger great tits, which might explain why blue tits are often found to be more neophobic towards novel prey (Exnerová *et al.*, 2007; Adamová-Ježová *et al.*, 2016). Variation in the wariness to attack aposematic prey among predator species (Exnerová *et al.*, 2003) also means that more risk-aversive predators can gather information about prey quality from less neophobic species. Indeed, in Chapters 5 and 6, I found that birds used social information from both conspecifics and heterospecifics, which increases opportunities for social learning. However, social avoidance learning has so far been tested in relatively few species (e.g. Mason & Reidinger, 1982; Fryday & Greig-Smith, 1994; Johnston, Burne & Rose, 1998; Thorogood *et al*., 2018) and more studies are needed to understand how social transmission of information varies among predator communities and what effects it has for predator-prey coevolution.

In addition to between-species differences in information use, individuals within species may differ in how they use social information in their foraging choices. Throughout my thesis, I found evidence that individuals varied in their tendency to attack chemically defended prey. Some of this variation is likely to be influenced by the predator's state (Barnett, Bateson & Rowe, 2007; Sandre, Stevens & Mappes, 2010; Barnett *et al.*, 2012), and in Chapter 5, I indeed found that great tits attacked more aposematic prey when they were in poorer body condition. However, this was not observed with blue tits (Chapter 5) or in another experiment with great tits (Chapter 2), and I also did not find evidence that the predator's physiological state (toxin load) influenced social information use (Chapter 2; Hämäläinen *et al*., 2019a). Other possible explanations for the observed variation among birds include individual differences in personality or dietary wariness which could influence both willingness to attack aposematic prey (Exnerová *et al.*, 2010; Marples & Mappes, 2011), as well as social information use (Marchetti & Drent, 2000; Kurvers *et al.*, 2010; Smit & van Oers, 2019). For example, Exnerová *et al.* (2010) found that slow-exploring great tits were more hesitant to attack aposematic prey and acquired avoidance to them faster than fast-exploring birds, and Smit & van Oers (2019) demonstrated that slow-exploring birds relied more on social information compared to fast-explorers. I did not investigate exploration behaviour in my thesis, but it is likely that tested individuals varied in the degree of exploration, boldness and dietary wariness, and future studies should aim to investigate how these effects combine to influence selection pressures exerted on aposematic prey.

EVOLUTION OF APOSEMATISM AND THE MAINTENANCE OF WARNING SIGNALS

Explaining the existence of aposematism poses two problems: 1) how can novel conspicuous warning signals evolve when all predators are naïve (Alatalo & Mappes, 1996; Mappes, Marples & Endler, 2005), and 2) how can they be maintained in the prey population when a new generation of naïve individuals enters the predator community (Mappes *et al.*, 2014). In my thesis, I have demonstrated that social transmission of avoidance might help us to solve both of these puzzles. Captive 'novel world' experiments use prey with novel artificial symbols (Alatalo & Mappes, 1996), which ensures that birds are naïve to all prey types, and enables us to investigate the initial evolution of warning signals. Together with previous novel world experiments (Lindström *et al.*, 1999a; Thorogood *et al*., 2018), my findings in Chapters 2 and 5 demonstrate that initial predation risk for conspicuous aposematic prey is high when predators do not have prior social information about prey defences (Hämäläinen *et al*., 2019a). However, an observation of the negative feeding event of others reduces this relative predation risk below 0.5, which can increase the likelihood that aposematism reaches fixation in the prey population (Thorogood *et al*., 2018), indicating that social learning among predators might have an important role in the initial evolution of warning signals. Social effects might also work together with other possible mechanisms; for example, neophobia (Marples, Kelly & Thomas, 2005) and go-slow predation (Guilford, 1994) are suggested to facilitate the survival of aposematic prey, and social interactions among predators might further enhance these receiver biases. Similarly, the benefits of prey aggregation (Mappes & Alatalo, 1997; Riipi *et al.*, 2001) might be increased if aggregation facilitates social avoidance learning in the predator population.

Social information about prey defences can also help us to explain how aposematic prey survive when naïve juveniles enter the predator population. In Chapter 6, I investigated how juveniles learn about novel unpalatable prey, and found that observing a negative foraging experience of others reduced their likelihood to sample the same prey type. The effect was strongest when juveniles observed adults, which is in accordance to social learning theories that often predict that individuals should rely more on information from older and more experienced individuals (Laland, 2004; Galef & Laland, 2005). However, I also found evidence that juveniles used information from other juveniles (‘horizontal transmission of information’), and this might be even more important when adults are experienced and the opportunities to learn from them attacking aposematic prey are reduced. In addition, juveniles might learn about prey quality by observing adults refusing to attack aposematic prey (Landová *et al.*, 2017), or by gathering information from their positive feeding events (Mason & Reidinger, 1981; Fryday & Greig-Smith, 1994; Sherwin, Heyes & Nicol, 2002). Furthermore, prey preferences can be learned early in life from parents (Slagsvold & Wiebe, 2011), and further studies should aim to investigate this transmission of information from parents to offspring before juveniles start to forage independently.

CONCLUSION

It is now well established that animals use social information in many different contexts and across a wide range of taxa, however, we are just beginning to investigate the potential evolutionary consequences of social transmission (Whitehead *et al.*, 2019). Throughout my thesis, I have demonstrated that predators use social information in their foraging decisions, and that this can shape selective pressures for aposematic prey and their palatable mimics. My findings show that social information about prey defences can reduce predation on novel warningly coloured prey and help us to explain a long-standing question of how aposematic species can evolve when predators are naïve to warning signals. Furthermore, juveniles can quickly acquire avoidance to aposematic prey by observing others, which can increase the survival of warningly coloured prey when a new generation of predators enters the predator community. Social transmission of information among predators may also further complicate model-mimic dynamics by increasing predator attacks towards palatable mimics and their defended models. The importance of these effects is, however, likely to be vary among predator-prey communities, depending on both predator species, as well as on the abundance of different prey types. In addition to variation in other predators' characteristics (Endler & Mappes, 2004), differences in social information use can therefore introduce more heterogeneity in the selective pressures for prey defences. This highlights the importance of considering the 'information ecology of warning signals' if we are to understand the wide diversity of prey defences and warning signals in nature.

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Appendix 1

Supplementary material for Chapter 2:

Social information about novel aposematic prey is not influenced by a predator's previous experience with toxins

1. SUPPLEMENTARY METHODS

1.1 Prey symbol preference and visibility tests

Before the avoidance learning experiment, we investigated whether great tits had any initial preferences towards the cross and square symbols by testing the preference with 10 individuals that did not participate in the main experiment (2 female juveniles, 2 female adults, 2 male juveniles, 4 male adults). During the preference test, birds were simultaneously offered both prey items (cross and square) on a white feeding tray and their first choice was recorded. Both prey items were palatable and birds were allowed to eat both of them. This was repeated five times, alternating which symbol was on the left and which on the right side of the tray. We analysed birds' preferences towards the symbols using a generalised linear mixed model with a binomial error distribution, with the order in which prey items were consumed as a response variable, explained by prey symbol (square/cross) and bird identity as a random effect. Similar to previous studies (Lindström et al., 2001a), we found that the birds did not prefer either symbol during the five presentations (effect of square symbol: estimate = -0.646 ± 0.405, Z = -1.593, $p = 0.11$). In addition, during the first encounter (i.e. first symbol pair) both symbols were chosen first equally often (5 birds chose a cross and 5 birds a square as their first choice).

We next tested the visibility differences between the symbols, i.e. how easily birds would find them from the novel world background. We tested this with the same 10 individuals that were used for the preference test. During the preference test, birds had eaten five prey items of each type, so they were motivated to attack both symbols. We then presented them with five backgrounds (similar to those used in the main experiment) that contained 8 palatable prey items of each type (cross and square). Birds were allowed to take 20 prey (4 from each of 5 backgrounds that were replaced sequentially). We recorded how many squares and crosses each bird attacked and used a paired sample t-test to compare these numbers. We found that birds consumed significantly more squares compared to cryptic crosses (t = 6.946, df = 9, $p <$

0.001). On average, birds attacked 16.4 squares and 3.6 crosses, which indicates that squares were approximately four times more visible against the background compared to the crosses, which is similar to previous experiments in a large aviary (Lindström et al., 1999a; Ihalainen et al. 2007).

1.2 Pre-training of birds

Before the experiment, birds were trained in their home cages to consume artificial prey. Training was done step-wise by presenting birds with 1) small almond pieces, 2) one-sided prey items (almonds glued on top of the paper packet), 3) prey items with almonds visible from the paper packet, and 4) prey items with almonds completely hidden inside the paper packet (similar to the prey used in the experiment). During the training, we used brown paper packets, so that birds would not get information about the symbols. After birds had learned to open the paper packets, we presented them with one training background (A3 sized paper sheet) to ensure that they learned to detach the prey items that were glued to the background. The training backgrounds resembled those used in the main experiment but instead of cross symbols, we printed them with >? symbols and added 10 fake prey (piece of double-sided mounting tape) with the same signal. The background included three brown and three cryptic prey (with >? symbol) and birds were required to find and eat all of them before training was complete.

2. SUPPLEMENTARY TABLES

Table 1. Best-fit generalised linear model explaining the latency to attack the first prey item in the experiment and summary of model selection.

A) We analysed the latency to attack the first prey using a generalised linear model with a negative binomial error distribution. Explanatory variables in the best-fit model included an interaction between social information treatment (control/social information) and body condition index, and toxin load treatment (chloroquine/water) as a fixed effect. Intercept gives the estimate for the time it took for control (no social information) birds to attack the first prey item when their toxin load was not increased.

B) Best fit model was selected based on Akaike's information criterion corrected for small sample sizes. Abbreviations of the explanatory variables are: SI = social information, TL = toxin load, BC = body condition. Seven individuals did not select any prey items in 20 min and were excluded from the analysis (n = 50).

A) Latency to attack the first prey

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	24.412	5.742	4.251	< 0.001
Social information	-18.777	7.022	-2.674	0.007
Toxin load	-0.592	0.346	-1.710	0.09
Body condition	-1.061	0.308	-3.448	< 0.001
Social information * Body condition	1.024	0.378	2.708	0.007

B) Model selection

Alternative models	**∆AICc**
~ SI * BC	0.19
~ SI * BC + TL + Sex	2.52
~ SI * BC + TL + Age + Sex	5.27
~ TL * BC + SI + Age + Sex	10.22
~ SI * TL + BC + Age +Sex	10.42

Table 2. Best-fit generalised linear model explaining the number of aposematic prey attacked in the first trial (first 16 prey items).

A) We analysed the number of aposematic prey attacked using a generalised linear model with a poisson error distribution. Explanatory variables in the best-fit model included social information treatment (control/social information) and body condition index. Intercept gives the estimate for the number of aposematic prey that birds attacked when they did not receive social information. Birds (n = 57) were allowed to attack 16 prey items.

B) Best fit model was selected based on Akaike's information criterion corrected for small sample sizes. Abbreviations of the explanatory variables are: SI = social information, TL = toxin load, BC = body condition.

A) Number of aposematic prey attacked

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	3.093	0.935	3.308	< 0.001
Social information	-0.185	0.092	-2.009	0.045
Body condition	-0.046	0.050	-0.921	0.36

B) Model selection

Alternative models	**∆AICc**
~ SI + TL + BC	1.12
~ SI + TL + BC + Sex	2.34
~ SI	3.14
~ SI + TL + BC + Age + Sex	4.83
~ SI * TL + BC + Age + Sex	6.95
~ SI * BC + TL + Age + Sex	7.26
~ TL * BC + SI + Age + Sex	7.44

Table 3. Best-fit generalised linear model explaining the time to complete the first trial and summary of model selection.

A) We analysed the time to complete the first trial using a generalised linear model with a negative binomial error distribution. Explanatory variables in the best-fit model included an interaction between social information treatment (control/social information) and toxin load treatment (chloroquine/water), and age and body condition as covariates. Intercept gives the estimate for the time it took for adult control (no social information) birds to complete the first trial when their toxin load was not increased (n = 57).

B) Best fit model was selected based on Akaike's information criterion corrected for small sample sizes. Abbreviations of the explanatory variables are: SI = social information, TL = toxin load, BC = body condition.

A) Time to complete the first trial

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	5.748	1.545	3.721	< 0.001
Social information	0.222	0.217	1.026	0.31
Toxin load	0.599	0.219	2.734	0.006
Age (juvenile)	-0.370	0.156	-2.368	0.02
Body condition	-0.112	0.082	-1.362	0.17
Social information * Toxin load	-0.688	0.304	-2.263	0.02

B) Model selection

Alternative models	**∆AICc**
SI * TL + BC + Age + Sex	2.26
SI * TL + BC	2.75
SI * BC + TL + Age + Sex	6.04
TL * BC + SI + Age + Sex	6.05
SI * TL + Age	7.59
SI * TL	9.79

Table 4. Best-fit generalised linear model explaining the number of aposematic prey attacked during the avoidance learning experiment (across all 5 trials) and summary of model selection.

A) We analysed the number of aposematic prey attacked using a generalised linear model with a poisson error distribution. Explanatory variables in the best-fit model included social information treatment (control/social information), trial number (1-5) and body condition index as a covariate. In addition, bird identity (variance = 0.105) was included as a random effect. Intercept gives the estimate for the number of aposematic prey that birds attacked in the first trial when they did not receive social information. Birds (n = 57) were allowed to attack 16 prey items in each of the five trials.

B) Best fit model was selected based on Akaike's information criterion corrected for small sample sizes. Abbreviations of the explanatory variables are: SI = social information, TL = toxin load, BC = body condition.

A) Number of aposematic prey attacked

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	3.646	1.037	3.516	< 0.001
Social information	-0.341	0.103	-3.312	< 0.001
Trial number	-0.326	0.019	-16.723	< 0.001
Body condition	-0.070	0.056	-1.263	0.21

B) Model selection

Alternative models	**∆AICc**
~ SI + Trials + TL + BC	1.75
~ SI + Trials + TL + BC + Sex	3.12
~ SI * Trials + TL + BC + Age + Sex	4.48
~ SI + Trials + TL + BC + Age + Sex	4.99
~ TL * BC + SC + Trials + Age + Sex	5.19
~ SI * TL + BC + Trials + Age + Sex	6.79
~ SI * BC + TL + Trials + Age + Sex	6.95
~ TL * Trials + SI + BC + Age + Sex	6.98
~ SI + Trials	22.12

Table 5. Best-fit generalised linear model explaining the number of palatable mimics (prey with square symbol) attacked during the reversal learning test and summary of model selection.

A) We used the difference between the number of aposematic prey attacked in the last foraging trial and the number of palatable mimics attacked in the reversal learning test as a response variable, using a generalised linear model. Explanatory variables in the best-fit model included social information about aposematic prey before the avoidance learning test (control/social information) and social information about palatable mimics before the reversal learning test (control/social information), and body condition index as a covariate. Intercept gives the estimate for the number of palatable mimics that birds attacked in the reversal learning test when they did not receive social information about aposematic prey (first video presentation) or about palatable mimics (second video presentation). Birds (n = 46) were allowed to attack 32 prey items.

B) Best fit model was selected based on Akaike's information criterion corrected for small sample sizes. Abbreviations of the explanatory variables are: SI = social information about aposematic prey, SI2 = social information about palatable mimics, BC = body condition.

A) Number of palatable mimics attacked

Terms in the model	**Estimate**	**SE**	**t**	***P***
Intercept	0.520	8.698	0.060	0.95
Social information about palatable mimics	-0.042	0.917	-0.046	0.96
Social information about aposematic prey	0.055	0.920	0.060	0.95
Body condition	0.024	0.465	0.052	0.96

B) Model selection

Alternative models	**∆AICc**
~ SI + SI2	1.84
~ SI + SI2 + BC + Sex	2.01
~ SI + SI2 + BC + Age + Sex	4.42
~ SI * SI2 + BC + Age + Sex	6.94
~ SI * BC + SI2 + Age + Sex	7.08
~ SI2 * BC + SI + Age + Sex	7.21

Table 6. Best-fit generalised linear model explaining hesitation to sample palatable mimics (prey with square symbol) in the reversal learning test and summary of model selection.

A) We analysed the number of cryptic prey attacked before sampling the first aposematic prey using a generalised linear model with a poisson error distribution. Explanatory variables in the best-fit model included social information about aposematic prey before the avoidance learning experiment (control/social information) and social information about palatable mimics before the reversal learning test (control/social information), and body condition index and sex as covariates. Intercept gives the estimate for the number of palatable cryptic prey (prey with cross symbol) that females attacked before sampling the first mimic when they did not receive social information about aposematic prey (first video presentation) or about palatable mimics (second video presentation). Birds (n = 46) were allowed to attack 32 prey items.

B) Best fit model was selected based on Akaike's information criterion corrected for small sample sizes. Abbreviations of the explanatory variables are: SI = social information about aposematic prey, SI2 = social information about palatable mimics, BC = body condition.

A) Number of cryptic prey attacked before sampling the first palatable mimic

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	0.815	0.663	1.230	0.22
Social information about palatable mimics	-0.056	0.071	-0.782	0.43
Social information about aposematic prey	0.294	0.073	4.029	< 0.001
Body condition	0.112	0.036	3.157	0.002
Sex (male)	-0.232	0.072	-3.213	0.001

B) Model selection

Alternative models	**∆AICc**
~ SI2 * BC + SI + Age + Sex	2.19
~ SI + SI2 + BC + Age + Sex	2.39
~ SI * BC + SI2 + Age + Sex	4.22
~ SI * SI2 + BC + Age + Sex	4.58
~ SI + SI2 + BC	7.66
~ SI + SI2 + Sex	25.5
~ SI + SI2	28.6

Appendix 2

Supplementary material for Chapter 3:

Can video playback provide social information for foraging blue tits?

SUPPLEMENTARY TABLES

Table 1. GLMM explaining the time focal birds faced a screen during video playback. Intercept gives the estimate for the time birds (n = 16) faced a screen when they were shown a cup before a demonstrator in the first test, and video playback of aversive prey. Bird identity (variance = 0.674) and demonstrator video (variance = 1.417) were included as random effects.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	1.290	0.590	2.186	0.02
Cup after	- 0.392	0.181	-2.167	0.03
Demonstrator	0.366	0.169	2.162	0.03
Palatable prey	0.318	0.720	0.441	0.66
Second test	0.386	0.144	2.679	0.007
Association score	-28.099	12. 296	-2.285	0.02
Cup after * palatable prey	-0.570	0.269	-2.118	0.03
Demonstrator * palatable prey	-0.836	0.252	-3.320	< 0.001

Table 2. GLMM explaining the time focal birds were flying in a cage during video playback. Intercept gives the estimate for the time birds (n = 16) were flying when they were shown a cup before a demonstrator in the first test. Bird identity (variance = 0.908) and demonstrator video (variance = 0.987) were included as random effects.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-2.355	0.479	-4.913	< 0.001
Cup after	-0.032	0.154	-0.207	0.84
Demonstrator	-0.248	0.144	-1.729	0.16
Second test	0.114	0.158	0.718	0.47
Association score	14.913	13.957	1.069	0.29

Table 3. GLMM explaining the number of head turns focal birds performed during video playback. Intercept gives the estimate for the number of head turns when birds (n = 16) were shown a cup before a demonstrator in a first test, and video playback of aversive prey. Bird identity (variance = 0.081) and demonstrator video (variance = 0.158) were included as random effects.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	1.905	0.233	8.192	< 0.001
Cup after	0.306	0.146	2.103	0.03
Demonstrator	0.288	0.146	1.969	0.049
Palatable prey	0.015	0.278	0.055	0.96
Second test	0.188	0.141	1.337	0.18
Association score	-8.142	5.062	-1.608	0.11
Cup after * palatable prey	-0.543	0.199	-2.726	0.006
Demonstrator * palatable prey	-0.393	0.196	-2.002	0.045

Table 4. GLMM explaining the number of hops focal birds performed during video playback. Intercept gives the estimate for the number of hops when birds (n = 16) were shown a cup before a demonstrator in a first test. Bird identity (variance < 0.001) and demonstrator video (variance < 0.001) were included as random effects.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-1.870	0.619	-3.023	0.003
Cup after	1.015	0.586	1.732	0.08
Demonstrator	1.967	0.565	3.482	< 0.001
Second test	0.135	0.452	0.297	0.77
Association score	6.237	10.131	0.616	0.54

Table 5. GLMM explaining focal birds' (n = 22) first cup choice (same/different cup that a demonstrator fed from) after video playback.

Explanatory variables include information type and test order (baseline level includes video of aversive prey and first test). Bird identity (variance = 0.031) and demonstrator video (variance = 0.442) were included as random effects.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-0.343	0.697	-0.492	0.62
Palatable prey	0.372	0.814	0.457	0.65
Second test	0.829	0.745	1.113	0.27
Association score	-17.137	14.740	-1.163	0.25

Table 6. GLMM explaining the latency to choose a cup after video playback.

Intercept gives the estimate for the time (s) that it took for focal birds (n = 22) to choose a cup when their choice did not match a demonstrator's behaviour, and when they saw video playback of aversive prey in the first test. Bird identity (variance = 0.167) and demonstrator video (variance = 0.062) were included as random effects.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	4.661	0.273	17.075	< 0.001
Palatable prey	-0.024	0.262	-0.092	0.93
Second test	0.010	0.226	0.043	0.97
Matching demonstrator	-0.837	0.265	-3.154	0.002

Appendix 3

Supplementary material for Chapter 5:

Social learning within and across predator species facilitates the evolution of aposematic prey

1. SUPPLEMENTARY METHODS

1.1 Prey symbol preference and visibility tests

Before conducting the learning trials, we tested whether blue tits had initial preferences towards the prey symbols, following similar methods as previous preference tests in great tits (Lindström *et al*., 2001a; Hämäläinen *et al*., 2019a). In the preference test blue tits were offered a choice between prey with a cross or a square symbol (both palatable) that were presented simultaneously on a white feeding tray, ensuring that both symbols were equally visible. This was repeated six times and we alternated which symbol was on the left and which on the right side of the plate. Individuals were always allowed to eat both prey items and we recorded their first choice. We then used a generalised linear mixed model with a binomial error distribution to investigate if blue tits preferred either of the symbols. The model included the order in which birds consumed prey items as a response variable (0/1) and this was explained by prey symbol (cross/square) and bird identity as a random effect. We found that blue tits preferred the prey with a square symbol during the six symbol pair presentations (estimate = -2.023 ± 0.413, Z = -4.900, $p < 0.001$). When the prey items were presented for the first time (i.e. first symbol pair), 8 individuals chose the prey with a square symbol and only 2 individuals the prey with a cross symbol. However, this preference was less clear during the last two symbol pair presentations (6 individuals chose a square and 4 individuals a cross), which suggests that positive experience of both symbols might have reduced birds' initial preference for squares.

We next tested the visibility of symbols using the same 10 individuals that participated in the preference test. Because each individual had consumed 6 crosses and 6 squares in the preference test, they had equal experience with both symbols and were therefore predicted to attack prey according to the visibility. Birds were required to find and eat 20 prey items from novel world backgrounds that contained only palatable prey. Each background contained 8 prey of each symbol type, and birds were presented with five backgrounds that were replaced once the bird had taken 4 prey items. We then used a paired sample t-test to compare the number of each prey type consumed. We found that blue tits attacked more squares than crosses (paired samples t-test: t = 7.632, df = 9, *p* < 0.001), consuming on average 15 squares and 5 crosses. This is similar to previous visibility tests in great tits (Lindström *et al*., 1999a; Hämäläinen *et al*., 2019a) and suggests that squares are more visible against the background, although the observed differences might be also explained by blue tits' initial preferences for squares and disentangling these two effects is difficult.

1.2 Demonstrator videos

We filmed eight demonstrators (four blue tits and four great tits) to provide observers social information about prey unpalatability. All demonstrators responded to aposematic prey by performing beak wiping and head shaking, but the length of these responses varied across demonstrators. To reduce this variation, the videos were edited to include 80 s of a demonstrator attacking (picking up and opening) an aposematic prey and showing a disgust response. However, the total number of beak wipes on the final video still varied across demonstrators, ranging from 50–120 in blue tits (mean = 73) and from 67–126 in great tits (mean = 86). Similarly, the number of head shakes on the videos varied from 4–22 in blue tits (mean = 9) and from 11–26 in great tits (mean = 19). We tested whether a demonstrator´s behaviour on the video influenced observers' (n = 48) foraging choices (i) in the first foraging trial (first 16 prey) and (ii) in all four trials (i.e. 64 prey) using a generalised linear model with a binomial error distribution. The number of aposematic and palatable prey attacked was used as a bound response variable and this was explained by the presented number of beak wipes and head shakes. We did not find evidence that the number of beak wipes on the video influenced how many aposematic prey observers attacked during the first trial (estimate = 0.002 ± 0.003, Z = 0.529, *p* = 0.60) or in total during the experiment (estimate = -0.002 ± 0.002, Z = -1.092, *p* = 0.27; Fig. 1a). Similarly, the number of head shakes did not influence the tendency to attack aposematic prey in the first trial (estimate = -0.002 ± 0.011, Z = -0.154, *p* = 0.88) or in total (estimate = 0.011 ± 0.006, Z = 1.715, *p* = 0.09; Fig. 1b). This suggests that even the videos with the lowest number of head shakes and beak wipes provided observers clear social information about prey unpalatability.

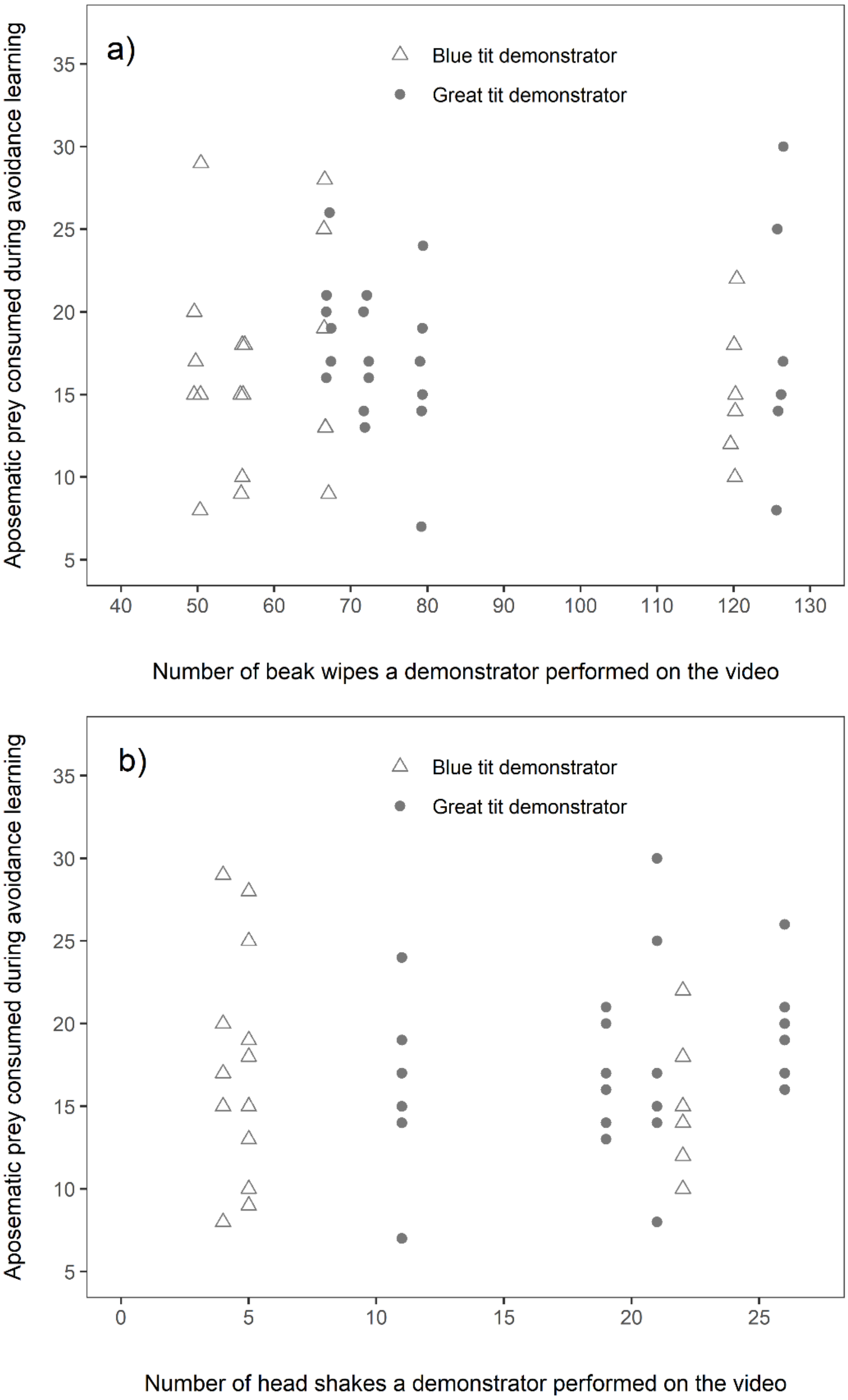


Figure 1. The number of (a) beak wipes or (b) head shakes that a demonstrator performed on the video (80 s) did not influence the total number of aposematic prey that observers (n = 48) consumed during the learning trials. Open triangles indicate that the demonstrator was a blue tit and filled circles represent great tit demonstrators.

2. SUPPLEMENTARY TABLES

Table 1. Cox regression model explaining the latency (s) to attack the first prey item in the experiment (n = 74).

The effect of conspecific (compared to blue tit control group, conspecific information * species: estimate = 0.367 ± 0.602, Z = 0.609, *p* = 0.54) or heterospecific information (compared to blue tit control group, heterospecific information * species: estimate = 0.420 ± 0.592, Z = 0.710, *p* = 0.48) did not differ between the species, and this interaction was excluded from the final model.

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Conspecific information	0.158	0.311	0.506	0.61
Heterospecific information	0.376	0.306	1.228	0.22
Species (great tit)	-0.411	0.244	-1.687	0.09
Age (juvenile)	0.162	0.260	0.625	0.53
Body condition	0.061	0.130	0.471	0.64

Appendix 4

Supplementary material for Chapter 6:

Social transmission of information about aposematic prey and palatable mimics in a wild predator community

1. SUPPLEMENTARY METHODS

1.1 Preference tests with green and red almonds

Before starting the experiment with green and red almonds, we investigated whether blue tits and great tits had initial biases towards the colours by conducting preference tests both in the wild and with wild birds in captivity. The captive tests were conducted at the Konnevesi Research Station in Central Finland during autumn 2017. We tested the colour preferences of 14 blue tits (5 adults and 9 juveniles) and 15 great tits (6 adults and 9 juveniles). Green and red almonds were prepared in a similar way as in the main experiment (by soaking them in a solution of water and food dye) and cut in small pieces (approximately 3 × 3 mm, 0.1 g). In the test birds were offered 8 almond pieces of each colour (i.e. altogether 16 pieces) on a white feeding tray. We waited for birds to eat all 16 pieces and recorded the order of their choices. To analyse the data, we first calculated a preference score for each colour by ranking the choices from 1–16 and calculating the average rank for each colour (Taplin, 2007). Low preference scores therefore indicate that birds preferred that colour. We then compared these preference scores using generalised linear models, with a preference score as a response variable. To investigate possible species- or age-specific differences in preferences, explanatory variables in the model included species * colour and age * colour interactions.

We found that blue tits and great tits did not differ in their preferences scores (species * colour: estimate = -1.931 ± 1.565, t = -1.234, *p* = 0.22), and this interaction was removed from the final model. We did, however, find significant differences between adult and juvenile birds (age * colour: estimate = -3.770 ± 1.603, t = -2.352, *p* = 0.02). Juveniles preferred red over green almonds (red vs. green: estimate = -2.611± 0.987, t = -2.644, *p* = 0.01), whereas adults did not have a preference towards either colour (red vs. green: estimate = 1.159 ± 1.263, t =0.918, *p* = 0.36; Fig. 1).

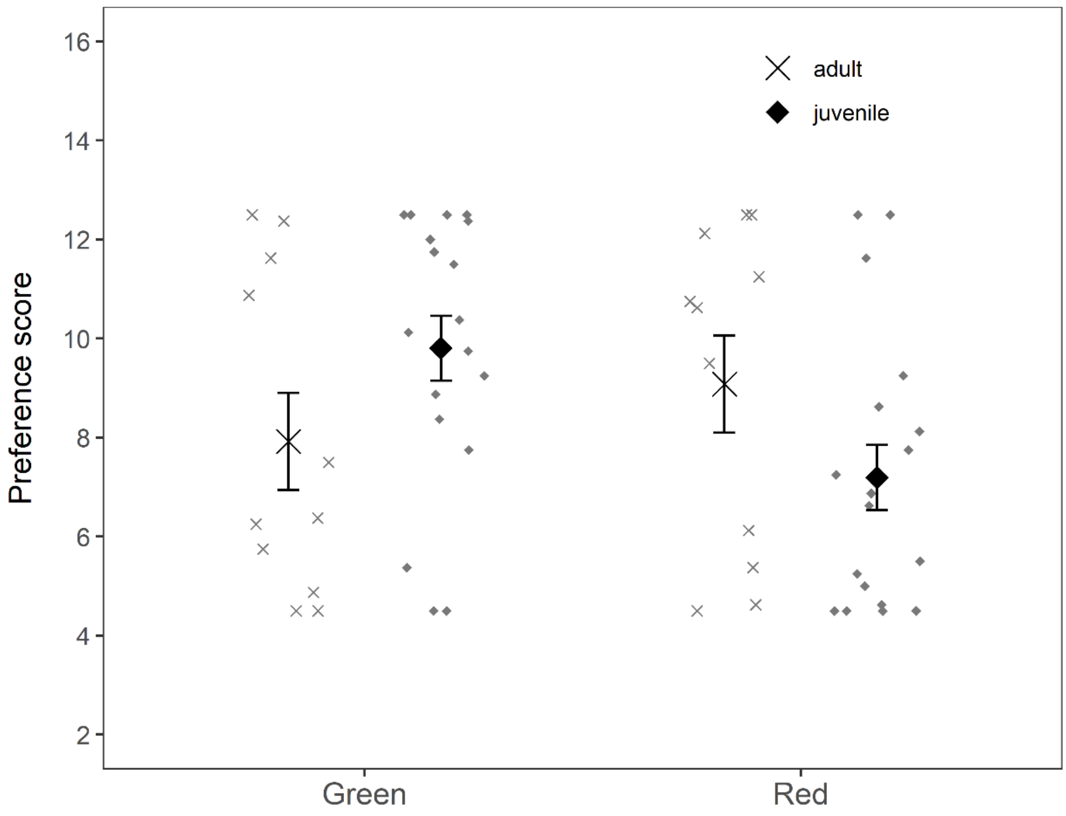


Figure 1. Birds' (n = 29) preference scores for red and green almonds in the captive experiment. Low scores indicate that birds preferred that colour, i.e. consumed it first. The preference scores differed between adults (cross symbol, n = 11) and juveniles (square symbol, n = 18). Big symbols show the mean (± s.e.) preference score and smaller symbols present individual variation.

In addition to testing colour preferences with birds in captivity, we conducted a preference test in the wild during winter 2017–2018. Because we did not want the birds in our study population to have any experience of the colours before the main experiment, this pilot study was conducted in Newbury, which is 130 km from our main study site. In the preference test birds were simultaneously presented with two feeders with red and green almonds (both palatable) for 30 min. The side of the feeders was switched after 15 min to control any preferences for feeder location. The feeders were observed with binoculars from the distance and the number of each colour taken by blue tits and great tits was recorded. The test was repeated on 9 different days. The number of visits to the feeders was relatively low and varied across the days. Nevertheless, we did not find any evidence that birds had initial preferences for the colours (t-test: t = 0, df = 15.69, *p* = 1; Fig. 2), which was important for our main experiment in the field. In our main experiment we used green as palatable and red as unpalatable colour, and our main concern was that birds might show initial wariness towards red (typical warning colour). This would have made it difficult to detect social avoidance learning, but we did not find any evidence of birds avoiding red in either of our preference tests. In fact, juvenile birds preferred red over green almonds in our captive test. However, even if juveniles showed the same preference for red in the wild, this should not prevent us detecting social learning, but it might instead make the effect of social information stronger (birds would need to change their initial preference).

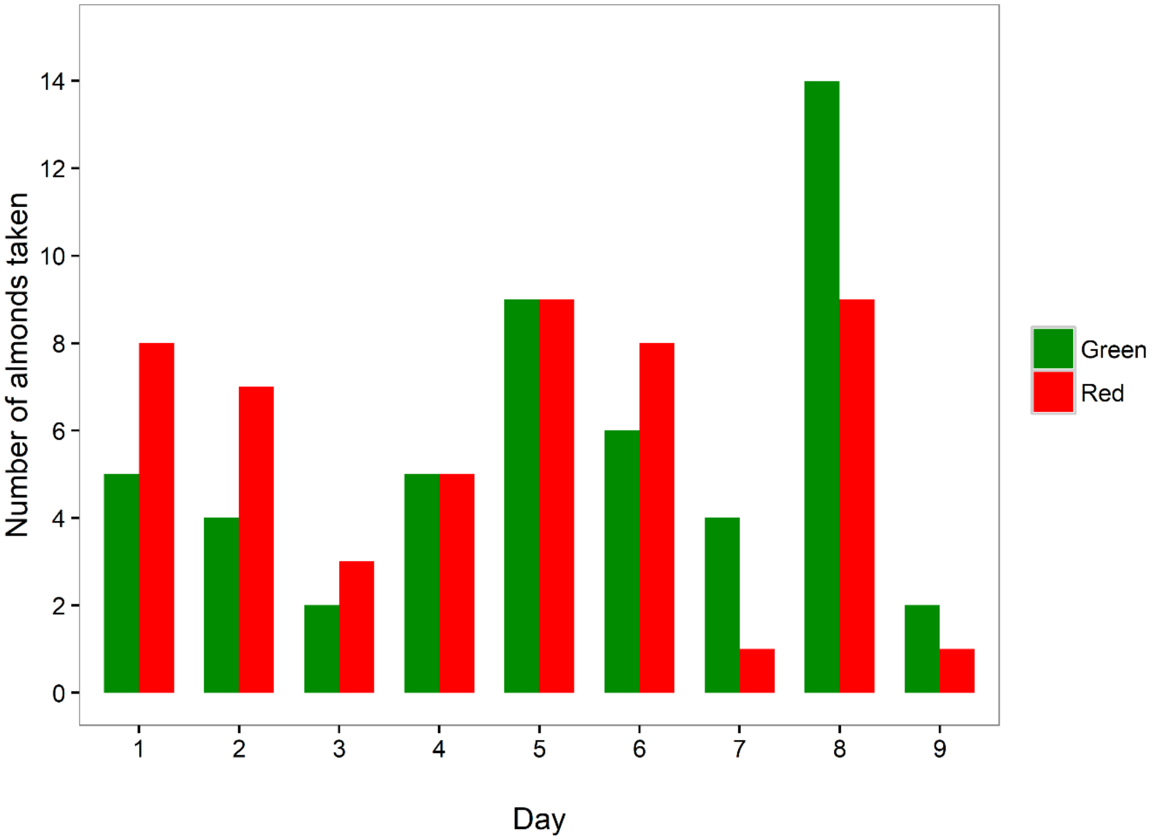


Figure 2. Number of green and red almonds taken during the initial preference test in the wild.

1.2 PIT tag coverage during the experiments

We estimated what proportion of blue tits and great tits that visited the feeders during the experiments were RFID tagged, based on the video recordings at the feeders. We calculated the estimated RFID tag coverage for each day of the experiments by watching at least 100 visits to the feeders (divided equally among the three feeding stations) and recording from the videos whether visiting blue tits and great tits had a RFID tag or not. During the first colour pair (red/green), the RFID tag coverage was low in the beginning of the experiment, but during the other experiments approximately 89 % of the individuals were RFID tagged (Fig. 3).

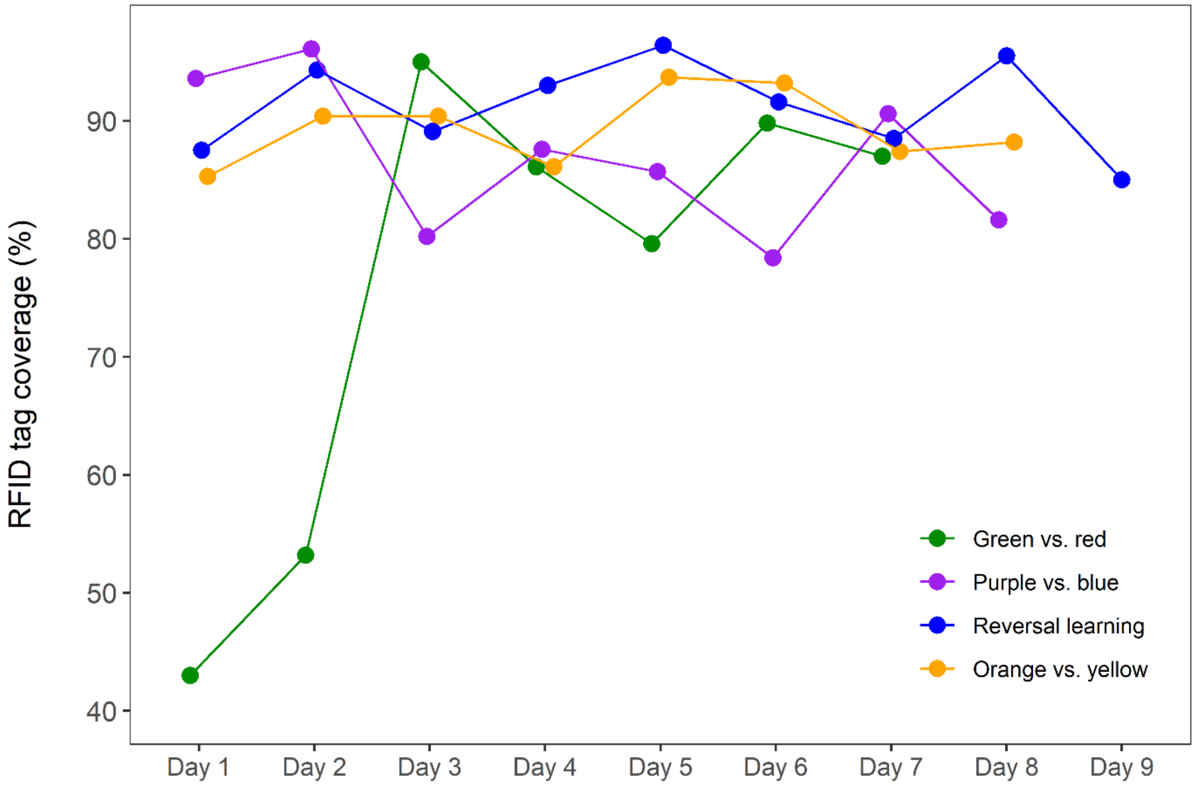


Figure 3. RFID tag coverage across days in each of the experiments (the number of visiting blue tits and great tits that had RFID tags, divided by the number of all visiting blue tits and great tits). In the first experiment (red/green) the RFID tag coverage was low during the first two days and we conducted a mist netting session after day 2 before continuing the experiment. To maintain a high proportion of birds RFID tagged for the other colour pairs, we conducted a mist netting session a day before starting a new experiment (new colour pair), as well as four (reversal learning) or five days (blue/purple and yellow/orange) after each experiment was started. During these mist netting sessions feeders were switched back to containing of plain almonds to ensure that mist netting would not interfere with the learning experiments.

2. SUPPLEMENTARY TABLES

2.1 Foraging choices in learning experiments: model summaries and selections

Table 1. Best-fit generalised linear mixed effects model explaining birds' foraging choices during avoidance learning experiments (across 8 days) and the comparison of models.

A) Summary of the best-fitting GLMM model. Birds' (n = 189) choices were modeled using a binomial error distribution, with the number of visits to palatable and unpalatable feeders as a bound response variable, and this was explained by an interaction between individuals' age and the day of the experiment (a second order polynomial term). Bird identity (variance = 0.807) and experiment (red/green, blue/purple, orange/yellow; variance = 0.012) were included as random effects.

B) Comparison of GLMMs explaining birds' foraging choices. Abbreviations of the explanatory variables are: A = age, S = species, D = day, ID = bird identity, E = experiment. We started a model selection with a model that included a three-way interaction between the species, age and day (a second order polynomial term), and selected the best-fit model based on Akaike's information criterion.

A) Best-fit model

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-2.182	0.166	-13.116	< 0.001
Age (juvenile)	0.573	0.173	3.312	< 0.001
Day (linear)	-39.262	2.922	-13.439	< 0.001
Day (polynomial)	31.867	2.782	11.453	< 0.001
Day (linear) * Age (juvenile)	3.166	3.103	1.020	0.31
Day (polynomial) * Age (juvenile)	-22.981	2.947	-7.798	< 0.001

B) Model selection

Alternative models	**AIC**	**∆AIC**
~A * D (poly) + 1|ID + 1|E (final model)	9480.8	0
~A * D (poly) + S + 1|ID + 1|E	9482.8	+2.0
~A * D (poly) + S * D (poly) + 1|ID + 1|E	9482.2	+1.4
~A * D (poly) + S * D (poly) + A * S + 1|ID + 1|E	9483.3	+2.5
~A * S * D (poly) + 1|ID + 1|E	9483.8	+3.0
~A * D (linear) + 1|ID + 1|E (best model with linear terms only)	9675.7	+194.9

Table 2. Best-fit generalised linear mixed effects model explaining birds' foraging choices during reversal learning experiment (across 9 days) and the comparison of models.

A) Summary of the best-fitting GLMM model. Birds' (n = 118) choices were modeled using a binomial error distribution, with the number of visits to purple and blue feeders as a bound response variable, and this was explained by the interactions between individuals' age and the day of the experiment (linear term), and species and the day of the experiment (a second order polynomial term). Bird identity (variance = 1.950) was included as random effect.

B) Comparison of GLMMs explaining birds' foraging choices. Abbreviations of the explanatory variables are: A = age, S = species, D = day, ID = bird identity. We started a model selection with a model that included a three-way interaction between the species, age and day (a second order polynomial term), and selected the best-fit model based on Akaike's information criterion.

A) Best-fit model

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-1.268	0.311	-4.082	< 0.001
Age (juvenile)	1.119	0.360	3.104	0.002
Species (great tit)	-0.011	0.278	-0.040	0.97
Day (linear)	20.036	2.276	8.805	< 0.001
Day (polynomial)	0.655	0.994	0.659	0.51
Day (linear) * Species (great tit)	9.077	1.314	6.908	< 0.001
Day (polynomial) * Species (great tit)	-2.999	1.256	-2.388	0.02
Day (linear) * Age (juvenile)	-0.128	0.028	-4.648	< 0.001

B) Model selection

Alternative models	**AIC**	**∆AIC**
~A * D (linear) + S * D (poly) + 1|ID (final model)	6778.5	0
~A * D (poly) + S * D (poly) + 1|ID	6778.8	+0.3
~A * S * D (poly) + 1|ID	6780.7	+2.2
~A * D (linear) + S * D (linear) + 1|ID (best model with linear terms only)	6784.2	+5.7

2.2 Social information use during avoidance learning: model summaries and selections

Table 3. Best-fit generalised linear mixed effects model explaining the effect of personal and social information on birds' foraging choices in the red/green experiment and the comparison of models.

A) Summary of the best-fitting GLMM model. Birds' (n = 86) choices were modeled using each choice as a binary response variable, with an intercept giving a likelihood to choose an unpalatable colour (red). This was explained by birds' previous visits to the palatable (green) and unpalatable (red) feeder, as well as observations of negative and positive feeding events of others, split between observations of adults and juveniles. Observations of positive feeding events were further divided to observations of conspecifics (CS) and heterospecifics (HS). Bird identity (variance = 3.067) was included as a random effect. Coefficients give an estimate of the effect of one visit or observation on the likelihood to choose an unpalatable option.

B) Comparison of GLMMs explaining birds' foraging choices in the red/green experiment.

A) Final model

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-0.295	0.026	-11.159	< 0.001
Visit to palatable feeder (green)	-0.042	0.015	-2.814	0.005
Visit to unpalatable feeder (red)	-0.053	0.011	-5.007	< 0.001
Positive observation of CS juvenile	0.003	0.009	0.354	0.72
Positive observation of CS adult	-0.111	0.046	-2.422	0.02
Positive observation of HS juvenile	0.041	0.008	5.324	< 0.001
Positive observation of HS adult	-0.058	0.091	-0.638	0.52
Negative observation of juvenile	-0.061	0.028	-2.152	0.03
Negative observation of adult	-1.287	0.603	-2.135	0.03

B) Model selection

Alternative models	**AIC**	**∆AIC**
Final model (Table 3A)	4367.9	0
Different conspecific/heterospecific positive effect, no age differences in social effects	4393.3	+25.4
Different conspecific/heterospecifics social effects, no age differences in social effects	4393.5	+25.6
No conspecific/heterospecific or age differences in social effects	4406.3	+38.4

Table 4. Generalised linear mixed effects model explaining the effect of personal and social information on birds' foraging choices in the blue/purple experiment and the comparison of models.

A) Summary of the GLMM model. Birds' (n = 90) choices were modeled using each choice as a binary response variable, with an intercept giving a likelihood to choose an unpalatable colour (blue). This was explained by birds' previous visits to the palatable (purple) and unpalatable (blue) feeder, as well as observations of negative and positive feeding events of others, split between observations of adults and juveniles. Observations of positive feeding events were further divided to observations of conspecifics (CS) and heterospecifics (HS). Bird identity (variance = 1.817) was included as a random effect. Coefficients give an estimate of the effect of one visit or observation on the likelihood to choose an unpalatable option.

B) Comparison of GLMMs explaining birds' foraging choices in the blue/purple experiment. Adding age differences in social effects did not improve the model, but we decided to include them, so that the final model was comparable to other two avoidance learning experiments.

A) Final model

Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-0.200	0.016	-12.898	< 0.001
Visit to palatable feeder (purple)	-0.023	0.112	-2.046	0.04
Visit to unpalatable feeder (blue)	-0.038	0.008	-4.560	< 0.001
Positive observation of CS juvenile	0.000	0.006	-0.007	0.99
Positive observation of CS adult	-0.042	0.029	-1.429	0.15
Positive observation of HS juvenile	0.005	0.007	0.812	0.42
Positive observation of HS adult	-0.025	0.042	-0.603	0.55
Negative observation of juvenile	-0.048	0.023	-2.095	0.04
Negative observation of adult	-0.087	0.273	-0.319	0.74

B) Model selection

Alternative models	**AIC**	**∆AIC**
Final model (Table 4A)	5494.2	0
Different conspecific/heterospecific positive effect, no age differences in social effects	5490.9	-3.3
Different conspecific/heterospecifics social effects, no age differences in social effects	5492.9	-1.3
No conspecific/heterospecific or age differences in social effects	5489.1	-5.1

Table 5. Best-fit generalised linear mixed effects model explaining the effect of personal and social information on birds' foraging choices in the yellow/orange experiment and the comparison of models.

A) Summary of the best-fitting GLMM model. Birds' (n = 168) choices were modeled using each choice as a binary response variable, with an intercept giving a likelihood to choose an unpalatable colour (yellow). This was explained by birds' previous visits to the palatable (orange) and unpalatable (yellow) feeder, as well as observations of negative and positive feeding events of others, split between observations of adults and juveniles. Observations of positive feeding events were further divided to observations of conspecifics (CS) and heterospecifics (HS). Bird identity (variance = 0.812) was included as a random effect. Coefficients give an estimate of the effect of one visit or observation on the likelihood to choose an unpalatable option.

B) Comparison of GLMMs explaining birds' foraging choices in the yellow/orange experiment.

A) Final model

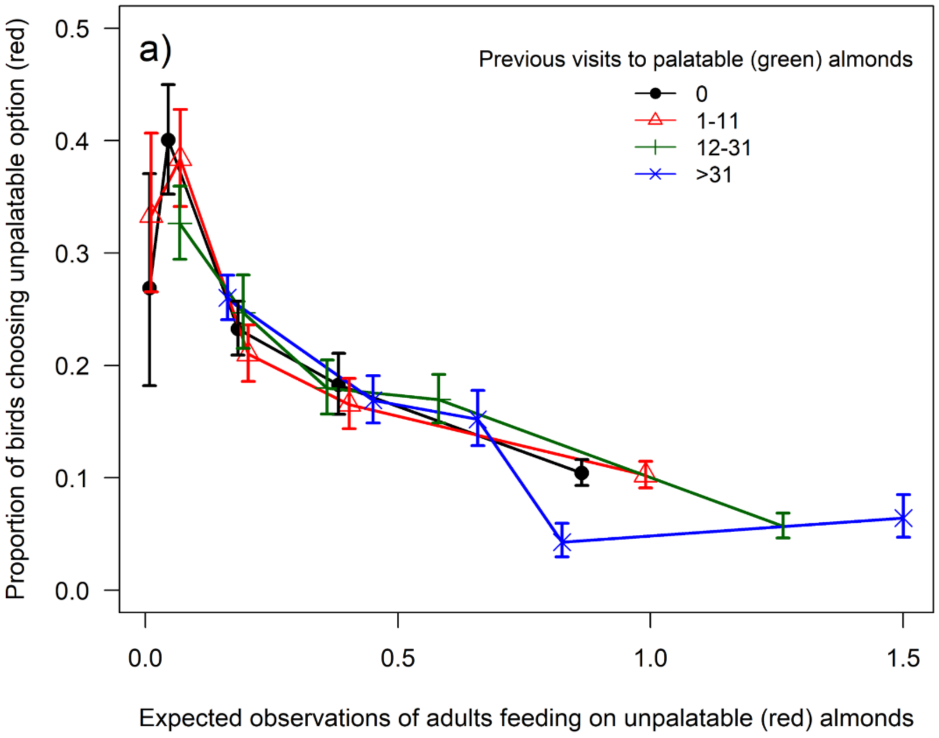
Terms in the model	**Estimate**	**SE**	**Z**	***P***
Intercept	-0.041	0.002	-22.651	< 0.001
Visit to palatable feeder (orange)	-0.005	0.001	-3.266	0.001
Visit to unpalatable feeder (yellow)	-0.001	0.001	-1.098	0.27
Positive observation of CS juvenile	-0.004	0.001	-2.527	0.01
Positive observation of CS adult	-0.039	0.007	-5.987	< 0.001
Positive observation of HS juvenile	0.011	0.002	6.736	< 0.001
Positive observation of HS adult	-0.042	0.008	-5.620	< 0.001
Negative observation of juvenile	0.005	0.004	1.276	0.20
Negative observation of adult	-0.239	0.043	-5.502	< 0.001

B) Model selection

Alternative models	**AIC**	**∆AIC**
Final model (Table 5A)	18153.0	0
Different conspecific/heterospecific positive effect, no age differences in social effects	18278.0	+125.0
Different conspecific/heterospecifics social effects, no age differences in social effects	18279.9	+126.9
No conspecific/heterospecific or age differences in social effects	18314.8	+161.8

3. SUPPLEMENTARY FIGURES

Social information use during avoidance learning: the effect of observing adults



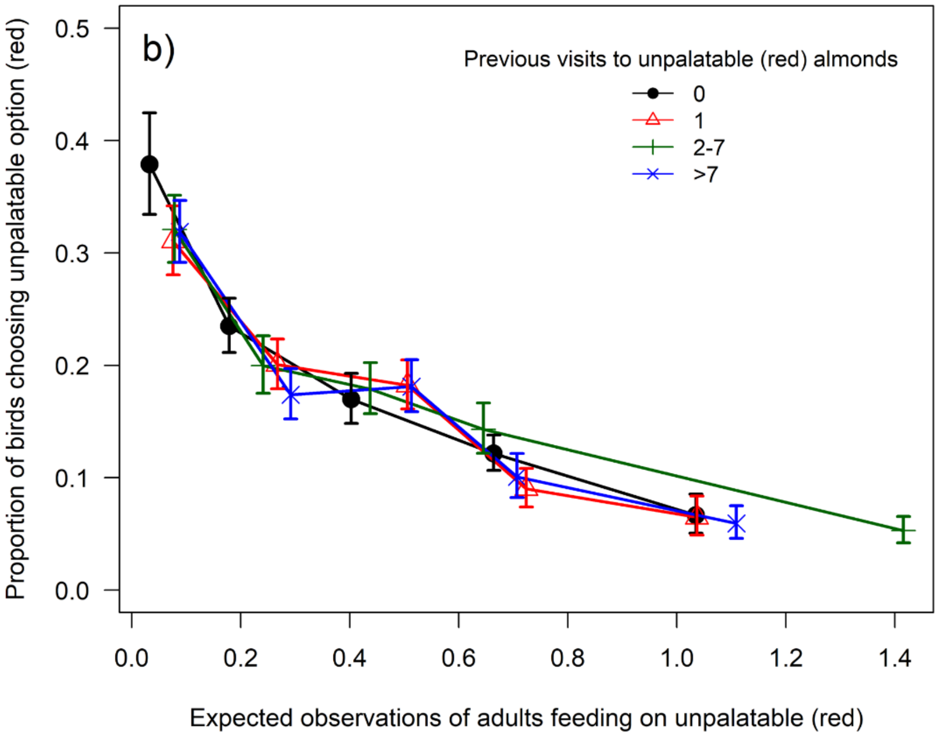


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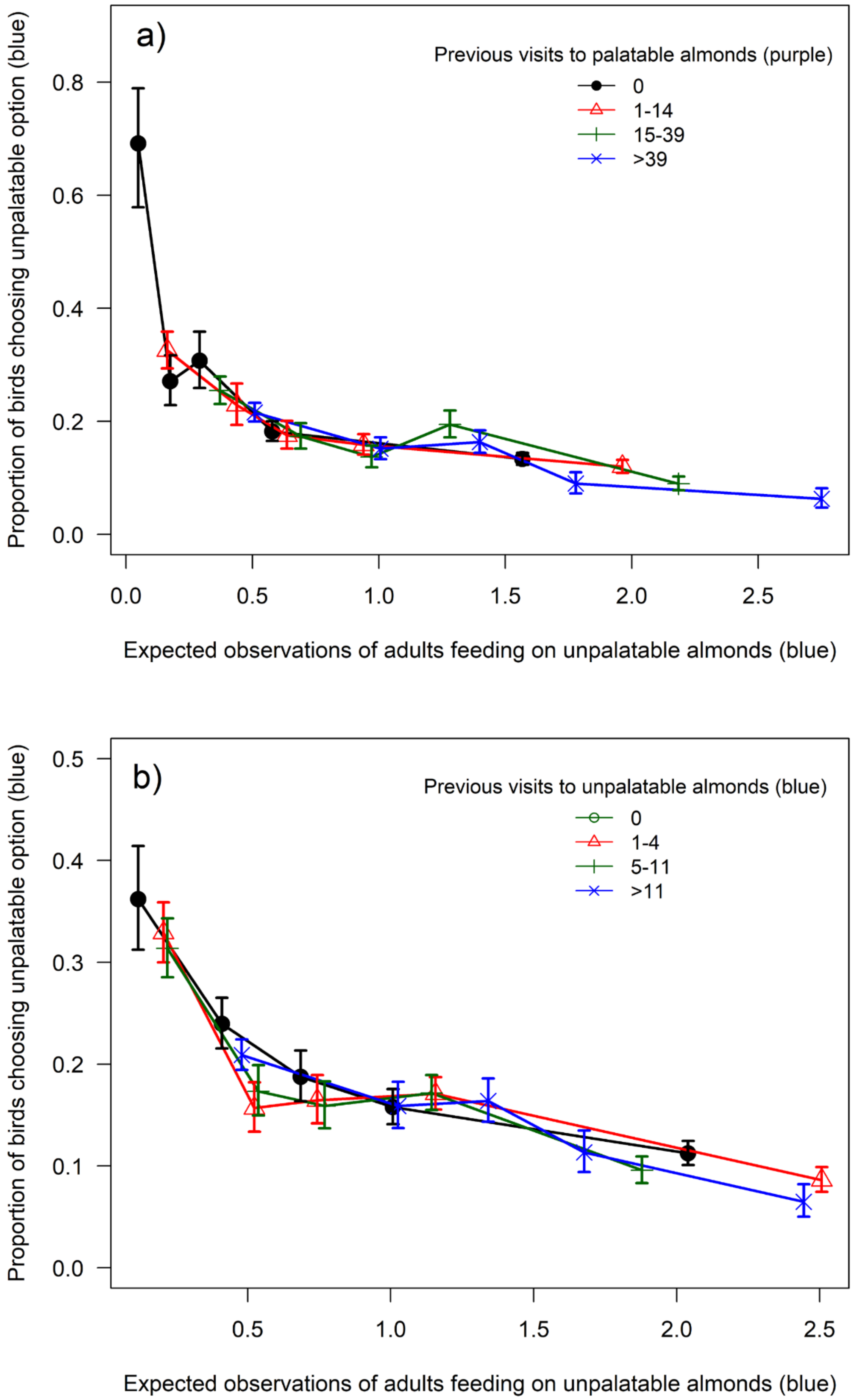
Figure 3. Proportion of individuals choosing the unpalatable (red) option in the red/green experiment decreased when birds (n = 86) observed adults feeding on unpalatable almonds, and this was not explained by birds' personal experience of (a) palatable or (b) unpalatable almonds. In each graph, the data is divided to quartiles based on how many times birds had personally sampled (a) palatable or (b) unpalatable almonds before their current choice (represented by different symbols and colours). Within these 'personal experience categories', the data is further split to quartiles based on the expected number of observed unpalatable feeding events of adults (including the minimum value, i.e. five points for each personal experience category). Symbols show the mean and 95 % CI for the proportion of birds choosing the unpalatable option. If birds used only personal information, we would expect to see differences between each personal experience category and no decreasing trend when birds had not personally visited feeders (circles + black line).



(Figure caption on following page)

Figure 4. Proportion of individuals choosing the unpalatable (blue) option in the blue/purple experiment decreased when birds (n = 90) observed adults feeding on unpalatable almonds, and this was not explained by birds' personal experience of (a) palatable or (b) unpalatable almonds. In each graph, the data is divided to quartiles based on how many times birds had personally sampled (a) palatable or (b) unpalatable almonds before their current choice (represented by different symbols and colours). Within these 'personal experience categories', the data is further split to quartiles based on the expected number of observed unpalatable feeding events of adults (including the minimum value, i.e. five points for each personal experience category). Symbols show the mean and 95 % CI for the proportion of birds choosing the unpalatable option. If birds used only personal information, we would expect to see differences between each personal experience category and no decreasing trend when birds had not personally visited feeders (circles + black line).