JYX JYVÄSKYLÄN YLIOPISTO UNIVERSITY OF JYVÄSKYLÄ

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Hämäläinen, Liisa; Mappes, Johanna; Rowland, Hannah M.; Thorogood, Rose

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

Year: 2019

Version: Published version

Copyright: © 2019 The Authors.

Rights: CC BY 4.0

Rights url: https://creativecommons.org/licenses/by/4.0/

Please cite the original version:

Hämäläinen, L., Mappes, J., Rowland, H. M., & Thorogood, R. (2019). Social information use about novel aposematic prey is not influenced by a predator's previous experience with toxins. Functional Ecology, 33(10), 1982-1992. https://doi.org/10.1111/1365-2435.13395

Received: 28 February 2019 | Accepted: 17 June 2019

DOI: 10.1111/1365-2435.13395

RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

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

Liisa Hämäläinen[1] | Johanna Mappes[2] | Hannah M. Rowland[1,3,4] | Rose Thorogood[1,5,6]

[1]Department of Zoology, University of Cambridge, Cambridge, UK; [2]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland; [3]Max Planck Institute for Chemical Ecology, Jena, Germany; [4]Institute of Zoology, Zoological Society of London, London, UK; [5]HiLIFE Helsinki Institute of Life Sciences, University of Helsinki, Helsinki, Finland and [6]Research Programme in Organismal & Evolutionary Biology, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

Correspondence
Liisa Hämäläinen
Email: llh35@cam.ac.uk

Funding information
Finnish Cultural Foundation; Emil Aaltonen Foundation; Natural Environment Research Council UK, Grant/Award Number: NE/K00929X/1; Helsinki Institute of Life Science (HiLIFE), University of Helsinki; Institute of Zoology; Max Plank Society; Academy of Finland; Finnish Centre of Excellence Program; University of Jyväskylä

Handling Editor: Dana Hawley

Abstract

1. Aposematism is an effective antipredator strategy. However, the initial evolution and maintenance of aposematism are paradoxical because conspicuous prey are vulnerable to attack by naïve predators. Consequently, the evolution of aposematic signal mimicry is also difficult to explain.
2. 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.
3. It is currently unknown, however, how personal and social information combines to affect the fitness of aposematic prey. For example, does social information become more useful when predators have already ingested toxins and need to minimize further consumption?
4. 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).
5. 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.
6. 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

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2019 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

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.

KEYWORDS
aposematism, great tits, mimicry, predator–prey interactions, social learning, toxin load

1 | INTRODUCTION

Aposematism is a widespread antipredator defence where prey advertise their unprofitability with conspicuous warning signals (Poulton, 1890; Ruxton, Sherratt, & Speed, 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, Kokko, Ojala, & Lindström, 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, Giraldeau, Olsson, McNamara, & Stephens, 2005). When encountering novel prey, predators should attack them if the perceived value of a meal outweighs the potential cost of consuming toxins (Marples, Speed, & Thomas, 2018; Sherratt, 2011). 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, Svádová, Fuchs, Štys, & Exnerová, 2017) or negative foraging experiences of others (Johnston, Burne, & Rose, 1998; Mason & Reidinger, 1982; 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; Barnett, Skelhorn, Bateson, & Rowe, 2012; Skelhorn & Rowe, 2007), dietary wariness (Exnerová et al., 2007; Marples & Mappes, 2011) or the ability to learn about prey defences (Rowland, Fulford, & Ruxton, 2017) means 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 (Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004), 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 coloration of the model without having to pay the same costs of producing chemical defences (Speed, Ruxton, Mappes, & Sherratt, 2012), and at the same time, they degrade the protection the warning signal affords the model (Gamberale-Stille & Guilford, 2004; Lindström, Alatalo, & Mappes, 1997). 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 generalization 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 generalization 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 (a) how previous experience of toxic prey influences predators' likelihood to use social information about novel aposematic

prey, and (b) 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 (Alatalo & Mappes, 1996; Ihalainen, Lindström, & Mappes, 2007; Lindström, Alatalo, Mappes, Riipi, & Vertainen, 1999; Thorogood et al., 2018). Similar to many other bird species (Clark, 1970; Hämäläinen, Rowland, Mappes, & Thorogood, 2017), they respond to aversive food by wiping their beak 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, Mappes, Ruxton, & Speed, 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 (a) increase the costs of sampling prey and make predators more hesitant to attack any prey, but that (b) 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.

2 | MATERIALS AND METHODS

2.1 | 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 hatch-year birds, 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 1 week before release. Sunflower seeds, tallow and peanuts were provided ad libitum, except prior and during experiments when birds were food-deprived for 2 hr to ensure their motivation to forage. Fresh water was always available. Birds' sex and age were determined using 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.

2.2 | 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 S1). Aposematic prey were made bitter-tasting by soaking almonds in a chloroquine phosphate solution (2 g of chloroquine dissolved in 30 ml of water) for 1 hr, following previously validated methods (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 backgrounds that each contained eight cryptic prey items (crosses) and eight 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; Ihalainen et al., 2007; Lindström et al., 1999). 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 S1). Similar to previous experiments in a large aviary (Ihalainen et al., 2007; Lindström et al., 1999), we found that squares were approximately four times more visible against the background, compared to crosses.

2.3 | Filming demonstrators

Birds were provided with social information using video playback. All demonstrators (N = 10, six males and four 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 (a) a palatable prey (to provide social information about palatable mimics) and (b) 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.

2.4 | Avoidance learning

2.4.1 | 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 S1 for details). Birds received the last training in the test cage on the same day that the experiment started. They were presented 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 (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.

2.4.2 | 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.

2.4.3 | 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 (a) chloroquine-injected mealworms + social information (*n* = 14), (b) water-injected mealworms + social information (*n* = 15), (c) chloroquine-injected mealworms + control video (*n* = 14) and (d) water-injected mealworms + control video (*n* = 14; Figure 1).

2.4.4 | Foraging trials

The LCD monitor was removed immediately after the video ended, and the first background (containing eight palatable and eight aposematic prey) was placed on the cage floor. For each trial, birds were allowed to attack 16 prey items, with four taken from each of four backgrounds that were replaced sequentially. If birds did not attack all four prey items in 20 min, 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, that is 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.

2.5 | 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 (a) either received social information of previously toxic prey now being palatable (*n* = 29), or (b) 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.

2.6 | 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 generalized linear models with a negative binomial error distribution. We next analysed predation of aposematic prey in the first trial (number attacked) and avoidance learning across all five trials using generalized 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 S1 for model selections). When analysing learning across trials, trial number was included as an explanatory variable and bird identity as a random effect.

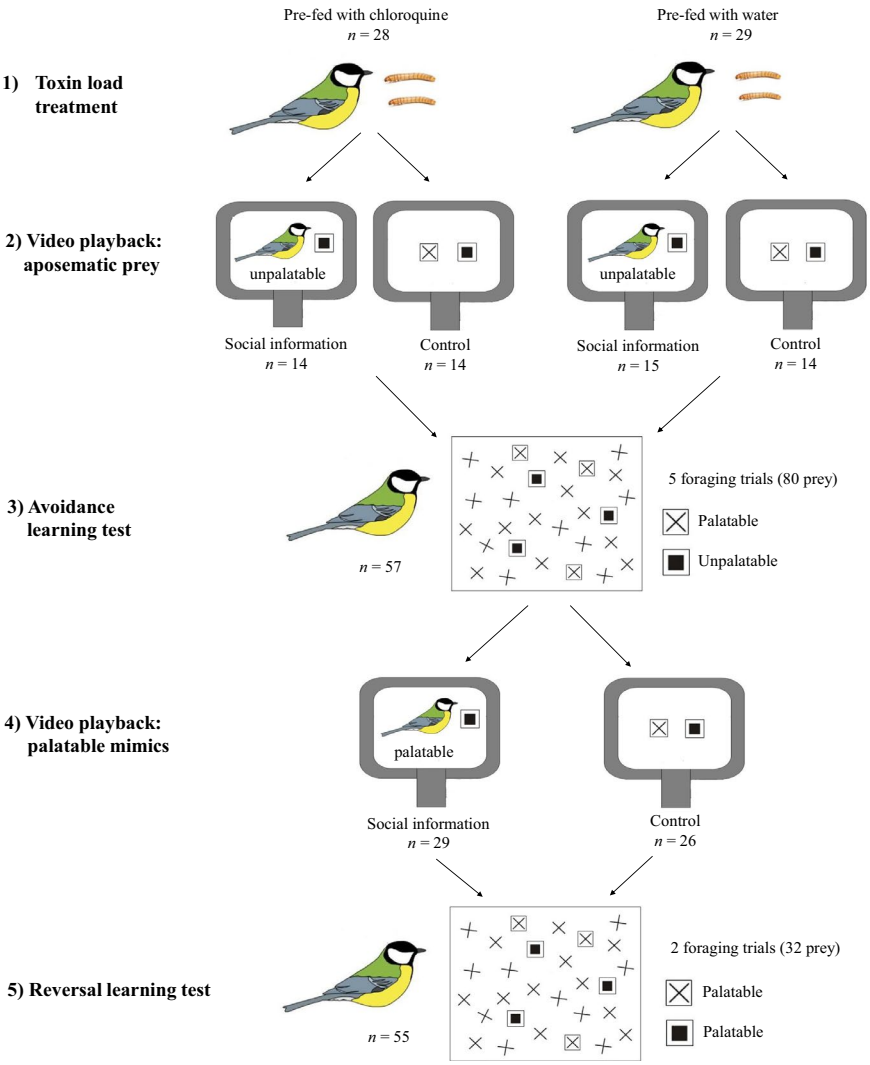

FIGURE 1 Experimental set-up. In the first part of the experiment, birds were pre-fed with two chloroquine- or water-injected mealworms. Half of the individuals in each treatment were then provided with social information about novel aposematic prey (the other half saw a control video) before five foraging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

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 generalized 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, Mächler, Bolker, & Walker, 2015) and *MASS* (Venables & Ripley, 2002) packages.

3 | RESULTS

3.1 | 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 (χ^2 = 0.150, *df* = 1, *p* = 0.70) or toxin load treatment (χ^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; Figure 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 min, so

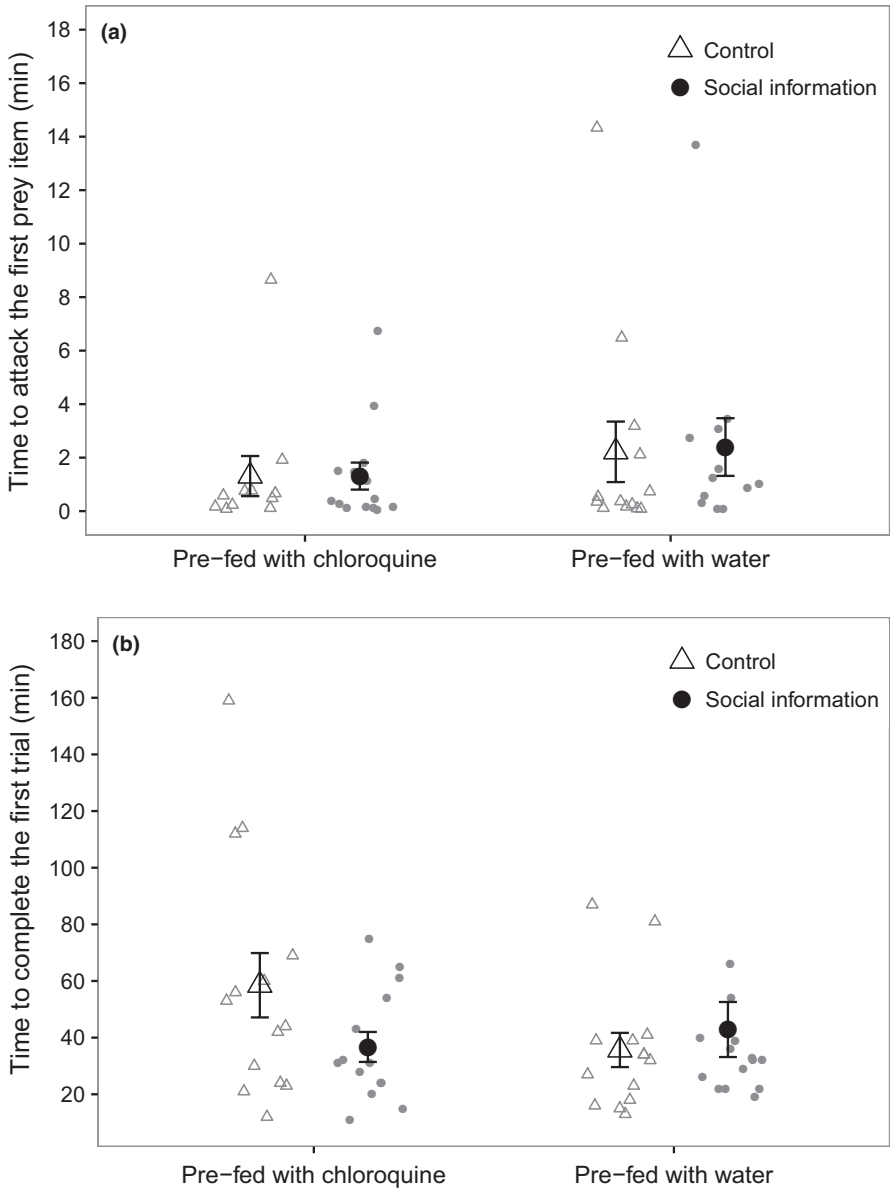

FIGURE 2 Birds' wariness to attack novel prey in the first foraging trial (first 16 prey items). Birds (n = 57) were pre-fed with two mealworms injected with chloroquine or water. Half of the individuals in both treatments received social information of aposematic prey (circles) and half were presented a control video (triangles). Big symbols represent mean (±*SE*) for each treatment and small grey 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 min 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)

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; Figure 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; Figure 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 seven 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 hatch-year birds completed the first trial faster than adults (estimate = −0.370 ± 0.156, Z = −2.368, p = 0.02).

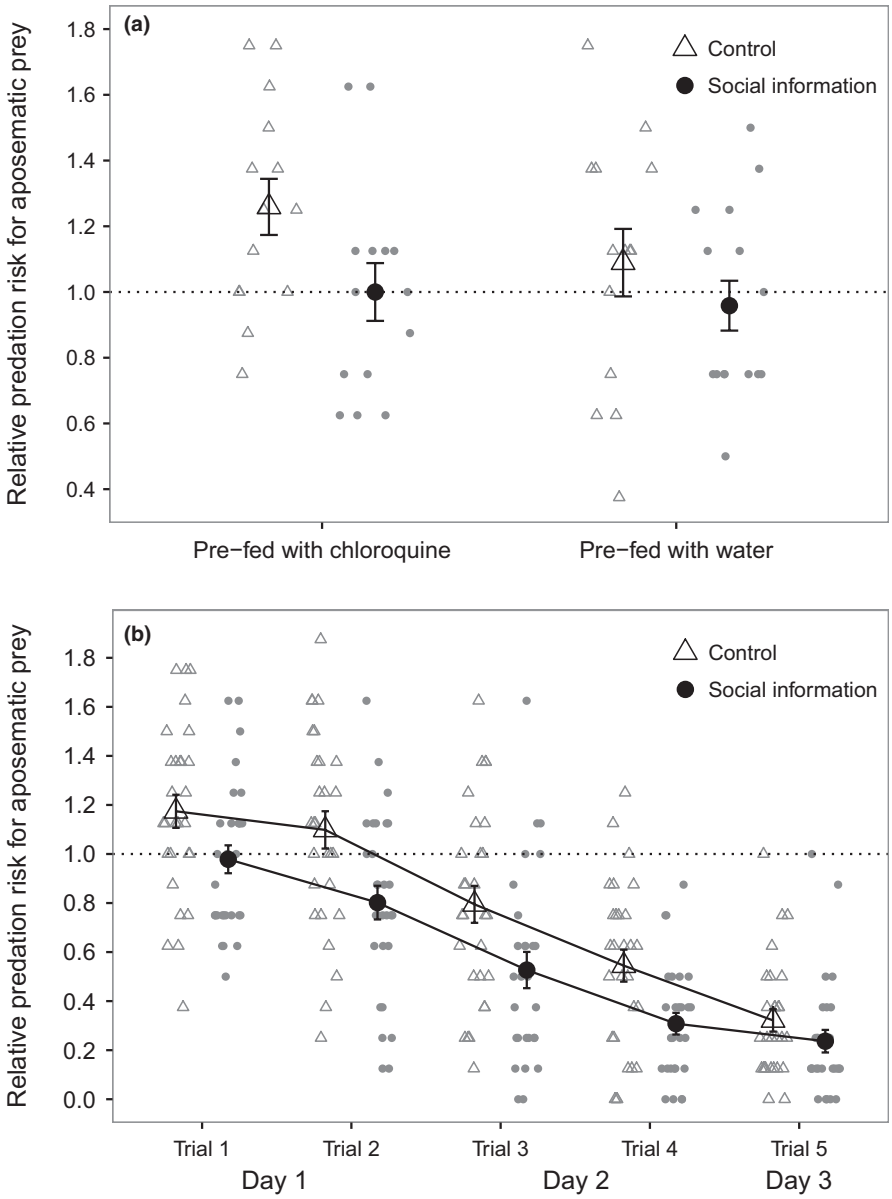

FIGURE 3 Relative predation risk for aposematic prey (number of aposematic prey attacked/ number expected by chance): (a) in the foraging first trial, and (b) across five foraging trials (conducted over three days). Birds (n = 57) were pre-fed with two mealworms injected with chloroquine or water. Half of the individuals in both treatments received social information of aposematic prey (circles) and half were presented a control video (triangles). Big symbols represent mean (±*SE*) for each treatment and small grey 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)

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; Figure 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).

3.2 | 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 (Figure 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

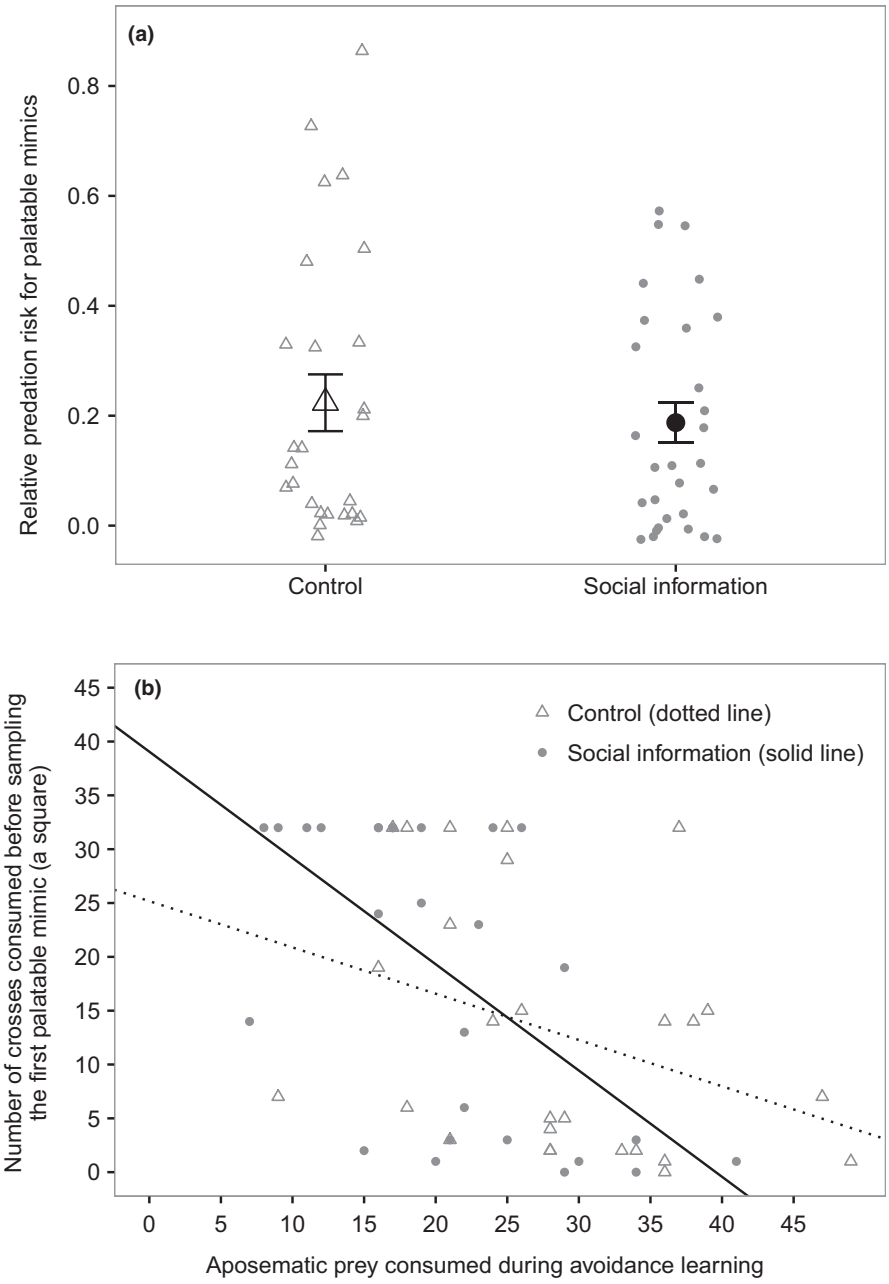

FIGURE 4 Birds' (n = 55) foraging choices in the reversal learning test. (a) Relative predation risk for the palatable mimic (prey with square symbol). Half of the individuals (circles) received social information about palatable mimics and half were presented a control video (triangles). Big symbols represent mean (±*SE*) for each treatment and small grey 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; that is, 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

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, Figure 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.

4 | 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 (Kendal et al., 2005; Laland, 2004), 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 set-up has been implemented in a small test cage; nevertheless, our results are consistent with previous experiments in a larger aviary (Lindström et al., 1999; 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 (Fryday & Greig-Smith, 1994; Johnston et al., 1998; Mason, Arzt, & Reidinger, 1984; Mason & Reidinger, 1982; 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; Rowland, Ruxton, & Skelhorn, 2013; Skelhorn, Griksaitis, & Rowe, 2008). 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 (Figure 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 (van Bergen, Coolen, & Laland, 2004; Fryday & Greig-Smith, 1994). 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, Alatalo, Lyytinen, & Mappes, 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, 2012) or personality type (Exnerova, Svádová, Fučíková, Drent, & Štys, 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.

ACKNOWLEDGEMENTS

We are grateful to Tuuli Salmi for helping with the experiment, Helinä Nisu for taking care of the birds, staff at the Konnevesi Research Station for providing facilities for the experiments and Victoria Franks for providing illustrations. LH was funded by the Finnish Cultural Foundation and Emil Aaltonen Foundation. RT was supported by an Independent Research Fellowship from the Natural Environment Research Council UK (NE/K00929X/1) and a start-up grant from the Helsinki Institute of Life Science (HiLIFE), University of Helsinki. HMR was supported by a research fellowship from the Institute of Zoology and is currently supported by the Max Plank Society. JM was supported by the Academy of Finland via the Finnish Centre of Excellence Program and the University of Jyväskylä which also offered facilities for the experiments. Wild birds were used with permission from the Central Finland Centre for Economic Development, Transport and Environment and licence from the National Animal Experiment Board (ESAVI/9114/04.10.07/2014) and the Central Finland Regional Environmental Centre (VARELY/294/2015).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived and designed the experiment. L.H. collected the data. L.H. and R.T. analysed the data. L.H. led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data is available from the Cambridge University Data Repository: https://doi.org/10.17863/CAM.40827 (Hamalainen, Mappes, Rowland & Thorogood, 2019).

ORCID

Liisa Hämäläinen https://orcid.org/0000-0002-3766-915X

REFERENCES

Alatalo, R. V., & Mappes, J. (1996). Tracking the evolution of warning signals. *Nature*, *382*, 708–710. https://doi.org/10.1038/382708a0

Alcock, J. (1969). Observational learning by fork-tailed flycatchers (*Muscivora tyrannus*). *Animal Behaviour*, *17*, 652–657. https://doi.org/10.1016/S0003-3472(69)80007-2

Alcock, J. (1970). Punishment levels and the response of black-capped chickadees (*Parus atricapillus*) to three kinds of artificial seeds. *Animal Behaviour*, *18*, 592–599. https://doi.org/10.1016/0003-3472(70)90057-6

Barnett, C. A., Bateson, M., & Rowe, C. (2007). State-dependent decision making: Educated predators strategically trade off the costs and benefits of consuming aposematic prey. *Behavioral Ecology*, *18*, 645–651. https://doi.org/10.1093/beheco/arm027

Barnett, C. A., Skelhorn, J., Bateson, M., & Rowe, C. (2012). Educated predators make strategic decisions to eat defended prey according to their toxin content. *Behavioral Ecology*, *23*, 418–424. https://doi.org/10.1093/beheco/arr206

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Bates, H. W. (1862). Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London*, *23*, 495–566. https://doi.org/10.1111/j.1096-3642.1860.tb00146.x

Bosque, R. J., Lawrence, J. P., Buchholz, R., Colli, G. R., Heppard, J., & Noonan, B. (2018). Diversity of warning signal and social interaction influences the evolution of imperfect mimicry. *Ecology and Evolution*, *8*, 7490–7499. https://doi.org/10.1002/ece3.4272

Brower, L. P., Brower, J. V. Z., & Corvino, J. M. (1967). Plant poisons in a terrestrial food chain. *Proceedings of the National Academy of Sciences*, *57*, 893–898. https://doi.org/10.1073/pnas.57.4.893

Clark, G. J. (1970). Avian bill-wiping. *The Wilson Bulletin*, *82*, 279–288.

Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*, 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Endler, J. A., & Mappes, J. (2004). Predator mixes and the conspicuousness of aposematic signals. *American Naturalist*, *163*, 532–547. https://doi.org/10.1086/382662

Exnerová, A., Štys, P., Fučíková, E., Veselá, S., Svádová, K., Prokopová, M., … Landová, E. (2007). Avoidance of aposematic prey in European tits (Paridae): Learned or innate? *Behavioral Ecology*, *18*, 148–156. https://doi.org/10.1093/beheco/arl061

Exnerova, A., Svádová, K. H., Fučíková, E., Drent, P., & Štys, P. (2010). Personality matters: Individual variation in reactions of naive bird predators to aposematic prey. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 723–728. https://doi.org/10.1098/rspb.2009.1673

Fryday, S. L., & Greig-Smith, P. W. (1994). The effects of social learning on the food choice of the house sparrow (*Passer domesticus*). *Behaviour*, *128*, 281–300. https://doi.org/10.1163/156853994X00299

Gamberale-Stille, G., & Guilford, T. (2004). Automimicry destabilizes aposematism: Predator sample-and-reject behaviour may provide a solution. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 2621–2625. https://doi.org/10.1098/rspb.2004.2893

Hämäläinen, L., Mappes, J., Rowland, H. M., & Thorogood, R. (2019). Research data supporting "Social information use about novel aposematic prey is not influenced by a predator's previous experience with toxins" [Dataset]. https://doi.org/10.17863/CAM.40827

Hämäläinen, L., Rowland, H. M., Mappes, J., & Thorogood, R. (2017). Can video playback provide social information for foraging blue tits? *PeerJ*, *5*, e3062. https://doi.org/10.7717/peerj.3062

Ihalainen, E., Lindström, L., & Mappes, J. (2007). Investigating Müllerian mimicry: Predator learning and variation in prey defences. *Journal of Evolutionary Biology*, *20*, 780–791. https://doi.org/10.1111/j.1420-9101.2006.01234.x

Johnston, A., Burne, T., & Rose, S. (1998). Observation learning in day-old chicks using a one-trial passive avoidance learning paradigm. *Animal Behaviour*, *56*, 1347–1353. https://doi.org/10.1006/anbe.1998.0901

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, *35*, 333–379. https://doi.org/10.1016/S0065-3454(05)35008-X

Kokko, H., Mappes, J., & Lindström, L. (2003). Alternative prey can change model-mimic dynamics between parasitism and mutualism. *Ecology Letters*, *6*, 1068–1076. https://doi.org/10.1046/j.1461-0248.2003.00532.x

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, *32*, 4–14. https://doi.org/10.3758/BF03196002

Landová, E., Svádová, K. H., Fuchs, R., Štys, P., & Exnerová, A. (2017). The effect of social learning on avoidance of aposematic prey in juvenile great tits (*Parus major*). *Animal Cognition*, *20*, 855–866. https://doi.org/10.1007/s10071-017-1106-6

Lindström, L., Alatalo, R. V., Lyytinen, A., & Mappes, J. (2004). The effect of alternative prey on the dynamics of imperfect Batesian and Müllerian mimicries. *Evolution*, *58*, 1294–1302. https://doi.org/10.1111/j.0014-3820.2004.tb01708.x

Lindström, L., Alatalo, R. V., & Mappes, J. (1997). Imperfect Batesian mimicry—The effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society B: Biological Sciences*, *264*, 149–153. https://doi.org/10.1098/rspb.1997.0022

Lindström, L., Alatalo, R. V., Mappes, J., Riipi, M., & Vertainen, L. (1999). Can aposematic signals evolve by gradual change? *Nature*, *397*, 249–251. https://doi.org/10.1038/16692

Mappes, J., Kokko, H., Ojala, K., & Lindström, L. (2014). Seasonal changes in predator community switch the direction of selection for prey defences. *Nature Communications*, *5*, 5016. https://doi.org/10.1038/ncomms6016

Mappes, J., & Lindström, L. (2012). How did cuckoo get its polymorphic plumage? *Science*, *337*, 532–533. https://doi.org/10.1126/science.1225997

Mappes, J., Marples, N., & Endler, J. A. (2005). The complex business of survival by aposematism. *Trends in Ecology & Evolution*, *20*, 598–603. https://doi.org/10.1016/j.tree.2005.07.011

Marples, N. M., & Mappes, J. (2011). Can the dietary conservatism of predators compensate for positive frequency dependent selection against rare, conspicuous prey? *Evolutionary Ecology*, *25*, 737–749. https://doi.org/10.1007/s10682-010-9434-x

Marples, N. M., Speed, M. P., & Thomas, R. J. (2018). An individual-based profitability spectrum for understanding interactions between predators and their prey. *Biological Journal of the Linnean Society*, *125*, 1–13. https://doi.org/10.1093/biolinnean/bly088

Mason, J. R., Arzt, A. H., & Reidinger, R. F. (1984). Comparative assessment of food preferences and aversions acquired by blackbirds via observational learning. *The Auk*, *101*, 796–803. https://doi.org/10.2307/4086906

Mason, J. R., & Reidinger, R. F. (1982). Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *The Auk*, *99*, 548–554.

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, *118*, 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Pfennig, D. W., & Mullen, S. P. (2010). Mimics without models: Causes and consequences of allopatry in Batesian mimicry complexes. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2577–2585. https://doi.org/10.1098/rspb.2010.0586

Poulton, E. B. (1890). *The colours of animals: Their meaning and use especially considered in the case of insects*. London, UK: Kegan Paul, Trench, Trübner & Co.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rowe, C., & Skelhorn, J. (2005). Colour biases are a question of taste. *Animal Behaviour*, *69*, 587–594. https://doi.org/10.1016/j.anbehav.2004.06.010

Rowland, H. M., Fulford, A. J. T., & Ruxton, G. D. (2017). Predator learning differences affect the survival of chemically defended prey. *Animal Behaviour*, *124*, 65–74. https://doi.org/10.1016/j.anbehav.2016.11.029

Rowland, H. M., Mappes, J., Ruxton, G. D., & Speed, M. P. (2010). Mimicry between unequally defended prey can be parasitic: Evidence for quasi-Batesian mimicry. *Ecology Letters*, *13*, 1494–1502. https://doi.org/10.1111/j.1461-0248.2010.01539.x

Rowland, H. M., Ruxton, G. D., & Skelhorn, J. (2013). Bitter taste enhances predatory biases against aggregations of prey with warning coloration. *Behavioral Ecology*, *24*, 942–948. https://doi.org/10.1093/beheco/art013

Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2018). *Avoiding attack. Evolutionary ecology of crypsis, warning signals and mimicry* (2nd ed.). Oxford, UK: Oxford University Press.

Sherratt, T. N. (2011). The optimal sampling strategy for unfamiliar prey. *Evolution*, *65*, 2014–2025. https://doi.org/10.1111/j.1558-5646.2011.01274.x

Skelhorn, J. (2011). Colour biases are a question of conspecifics taste. *Animal Behaviour*, *81*, 825–829. https://doi.org/10.1016/j.anbehav.2011.01.017

Skelhorn, J. (2016). Bitter tastes can influence birds' dietary expansion strategies. *Behavioral Ecology*, *27*, 725–730. https://doi.org/10.1093/beheco/arv216

Skelhorn, J., Griksaitis, D., & Rowe, C. (2008). Colour biases are more than a question of taste. *Animal Behaviour*, *75*, 827–835. https://doi.org/10.1016/j.anbehav.2007.07.003

Skelhorn, J., Halpin, C. G., & Rowe, C. (2016). Learning about aposematic prey. *Behavioral Ecology*, *27*, 955–964. https://doi.org/10.1093/beheco/arw009

Skelhorn, J., & Rowe, C. (2006). Prey palatability influences predator learning and memory. *Animal Behaviour*, *71*, 1111–1118. https://doi.org/10.1016/j.anbehav.2005.08.011

Skelhorn, J., & Rowe, C. (2007). Predators' toxin burdens influence their strategic decisions to eat toxic prey. *Current Biology*, *17*, 1479–1483. https://doi.org/10.1016/j.cub.2007.07.064

Speed, M. P., Ruxton, G. D., Mappes, J., & Sherratt, T. N. (2012). Why are defensive toxins so variable? An evolutionary perspective. *Biological Reviews*, *87*, 874–884. https://doi.org/10.1111/j.1469-185X.2012.00228.x

Thorogood, R., & Davies, N. B. (2012). Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science*, *337*, 578–580. https://doi.org/10.1126/science.1220759

Thorogood, R., Kokko, H., & Mappes, J. (2018). Social transmission of avoidance among predators facilitates the spread of novel prey. *Nature Ecology & Evolution*, *2*, 254–261. https://doi.org/10.1038/s41559-017-0418-x

van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 957–962. https://doi.org/10.1098/rspb.2004.2684

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Hämäläinen L, Mappes J, Rowland HM, Thorogood R. Social information use about novel aposematic prey is not influenced by a predator's previous experience with toxins. *Funct Ecol*. 2019;33:1982–1992. https://doi.org/10.1111/1365-2435.13395