PHILOSOPHICAL TRANSACTIONS B

Phil. Trans. R. Soc. B.
doi:10.1098/not yet assigned

The signal detection problem of aposematic prey revisited: integrating prior social and personal experience

Liisa Hämäläinen[1+], Rose Thorogood[1,2,3,*]

[1]*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.*
[2]*HiLIFE Helsinki Institute of Life Sciences, University of Helsinki, Helsinki FI-00011, Finland*
[3]*Research Programme in Organismal & Evolutionary Biology, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki FI-00011, Finland*
+ *https://orcid.org/0000-0002-3766-915X*
* *Corresponding author, https://orcid.org/0000-0001-5010-2177*

Keywords: Signal detection theory, predator-prey interactions, aposematism, social information use

Main Text

Summary

Ever since Alfred R. Wallace suggested brightly coloured, toxic insects warn predators about their unprofitability, evolutionary biologists have searched for an explanation of how these aposematic prey evolve and are maintained in natural populations. Understanding how predators learn about this widespread prey defence is fundamental to addressing the problem, yet individuals differ in their foraging decisions and the predominant application of associative learning theory largely ignores predators' prior experience. Here we revisit the suggestion made almost 15 years ago that signal detection theory (SDT) provides a useful framework to model predator learning by emphasising the integration of prior information into predation decisions. Using multiple experiments where we modified the availability of social information using video playback, we show that personal information (sampling aposematic prey) improves how predators (great tits, *Parus major*) discriminate between novel aposematic and cryptic prey. However, this relationship was not linear and beyond a certain point personal encounters with aposematic prey were no longer informative for prey discrimination. Social information about prey unpalatability reduced attacks on aposematic prey across learning trials, but it did not influence the relationship between personal sampling and discrimination. Our results suggest therefore that acquiring social information does not influence the value of personal information, but more experiments are needed to manipulate pay-offs and disentangle whether information sources affect response thresholds or change discrimination.

*Author for correspondence (rose.thorogood@helsinki.fi).

1. Introduction

The idea that conspicuous colouration could function as a warning signal to alert predators about prey toxicity was first described by Wallace over 150 years ago [1]. How conspicuous aposematic prey evolve and persist have puzzled evolutionary biologists ever since, and one of the key questions is to understand how predators learn about aposematic prey [2]. Most theoretical [e.g. 3,4,5,6,7] and empirical work [e.g. 8,9,10,11,12] has traditionally focused on associative learning by predators. Associative learning theories predict that predators require a fixed amount of experience to acquire avoidance, and the shape of this learning curve depends on characteristics of prey, such as the salience of the warning signal [9,13] and the strength of chemical defence [11,12,14]. While this provides a basic framework for predator behaviour, reality is more complex: the number of unpalatable prey that predators consume during learning varies among individuals [15,16,17,18] and depends on the abundance of different prey types [10,19,20,21]. How, then, do predators learn about aposematic prey?

(a) Signal detection theory for aposematic prey

Almost 15 years ago, Lynn [22] suggested that instead of using traditional learning theories, signal detection theory (SDT, [23,24]) could provide a useful tool to model the uncertainty that a predator experiences when making foraging decisions. This uncertainty is assumed to arise from the lack of prior experience with prey (rather than perceptual confusion), and avoidance learning is considered as a signal detection task where a predator discriminates between two prey types. The appropriate response to each prey varies over a continuum of prey appearance (figure 1) and predators place a response threshold on this continuum based on three signal parameters: the relative abundance of the two prey types, the costs and benefits for attacking and rejecting them, and the likelihood of appropriate responses towards each prey [22]. Signal detection theory has a history of being invoked in the context of Batesian mimicry, where predators need to discriminate between aposematic models and their palatable mimics [e.g. 25,26,27,28,29,30]. In his paper, however, Lynn also argued that the SDT approach could help us to understand how predators learn about aposematic prey initially, and potentially explain the previously counter-intuitive experimental findings that predators sample more aposematic prey when their relative abundance is higher than a cryptic palatable alternative [e.g. 10,19,20,21]. Although appealing, this second suggestion of how to use a SDT framework is yet to generate much empirical work.

More recent theoretical work has used an exploration-exploitation approach to model the uncertainty that a predator experiences when sampling unfamiliar prey [31,32,33,34]. This approach has much in common with SDT, but instead of considering a single decision, it models how predators iteratively revise their expectations about the profitability of prey when sampling them repeatably [31]. This also takes into account that continued sampling might not always be beneficial. If the prey is rare, for example, gaining information about its profitability might have little future value, which could provide an explanation for the positive correlation between the number of aposematic prey sampled and their abundance [31]. In contrast, SDT typically considers a single decision that an individual makes [23,24]. The assumption of a single decision is, however, often unrealistic in nature, and recent theoretical work shows that the classical predictions of SDT can be reversed when the model assumes that an individual makes repeated decisions [35]. In addition to considering iterative sampling [36], recent work has also incorporated speed-accuracy trade-offs and attention allocation into SDT to create more realistic models of a predator's behaviour [37].

(b) Integrating social and personal information about prey

One of the main benefits of SDT is that it considers how the frequency of each prey type and the payoff of attacking them influences predator decision-making [22]. However, previous work on SDT has not taken into account how social information from other predators influences prey discrimination. Information ecology theory predicts that animals should use multiple sources of information to reduce uncertainty about their environment [38] and we now have good experimental evidence that predators gather information about prey unprofitability by observing the foraging events of others [18,39,40,41,42,43,44]. This social information about prey defences reduces the initial predation risk for novel aposematic prey as predators consume fewer of the aposeme relative to cryptic alternative prey, and this effect persists across repeated foraging trials without any further social information [18,43,44]. Recent modelling shows that this may have important evolutionary consequences for aposematic prey, as social transmission among predators can influence the likelihood that the aposematic phenotype reaches fixation [18]. However, whether social information also alters the value of personal information gained from consuming prey directly remains untested.

Individuals within species may also differ in how they use different information sources. This variation has been demonstrated in many studies of social learning and social information use more broadly [45], including studies on social avoidance learning [18,42,43,44]. However, thus far there has been little attempt to explain these individual differences. If juveniles use social information about novel prey more than adults, for example, this could help to explain why aposematic prey in nature quickly regain protection despite an influx of naïve predators every summer [46]. Or, if males show stronger responses than females then this would suggest that the sex composition of foraging flocks could be critical for modelling how social avoidance learning works in nature. Furthermore, the costs and benefits of attacking aposematic prey vary among predators depending on their current state [47,48,49], and dietary wariness [50] and personality [16] may influence a predator's likelihood to attack different prey types. While different cost-benefit ratios can create variation in the location of the response threshold [23,24,51] it remains unexplored whether they also affect how predators use personal and social information during discrimination learning.

Here, we investigate how personal and social information about aposematic prey influences the signal detection problem presented by novel aposematic prey types by integrating data from three different experiments [18,43,44]. Each experiment was originally designed to answer a separate research question, and although we used a 'novel world' method in all three experiments, the experimental protocols varied slightly.

In novel world experiments predators are presented with an artificial prey community that consists of cryptic palatable (cross signal) and conspicuous unpalatable (square signal) prey that are evolutionary novel to birds, ensuring that they do not have any initial biases towards them [8]. In each experiment, we used video playback to provide one group of great tits (*Parus major*) social information about novel aposematic prey, whereas other group could learn only through personal experience (they were presented with a control video). Birds were then allowed to forage in 'novel world' and we investigated how many novel aposematic prey they consumed. The strength of prey unpalatability, and the relative abundance of the two prey types was constant (50:50), but the size of the test arena differed among experiments, which might have affected the payoffs (e.g. search cost) of attacking each prey type [27]. Each experiment consisted of multiple foraging trials, but the total number of prey items that birds were allowed to attack varied. For each foraging trial, we calculated the change in consumption of aposematic prey (relative to cryptic prey) to represent how discrimination shifted from one trial to the next. We then asked whether increasing personal information explained the magnitude of this shift, whether there was a maximum number of aposematic prey that could be consumed beyond which increasing personal information had little effect, and whether both of these interacted with received social information. We made three predictions about how personal and social information about prey may shift discrimination:

1. Information is additive. As individuals consume more unpalatable prey, they will become increasingly more wary of making mistakes and show greater avoidance in the next trial.
2. Increasing personal experience with unpalatable prey may not be informative for prey discrimination beyond a certain number of prey consumed.
3. Social information may affect the magnitude of the shift in prey discrimination by either (i) increasing discrimination if it enhances information gained through direct consumption, or (ii) by reducing the magnitude of the shift because fewer unpalatable prey are consumed. Alternatively, social information may not alter the relationship between personal information and discrimination.

Finally, by combining data from our three experiments, we used this increased power to explore whether age, sex, mass, or seasonality can explain variation among individuals in how they used information to discriminate prey over repeated encounters.

2. Methods

(a) Birds

We used wild-caught great tits (N = 79) as predators, using different individuals in each of the three experiments (N = 27 [18]; N = 28, [43]; N = 24, [44]). Birds were sexed and aged according to plumage characteristics [52] (juvenile females: N = 13, juvenile males: N = 26, adult males: N = 22, adult females: N = 18). The experiments were conducted at the University of Jyväskylä Research Station, Konnevesi, Finland (62.6° N, 26.3° E) during three winters (2013-2014, 2016-2017, 2017-2018); the date a bird was involved in an experiment was recorded as days since the Autumn equinox. Birds were caught using feeding traps and housed individually in plywood cages after being weighed to the nearest 0.25g using a Pesola balance. They were provided food (sunflower seeds, tallow and peanuts) and fresh water ad libitum, except before experiments when food was restricted for 2 hours to ensure birds' motivation to forage. After the experiments (approximately one week) birds were weighed to measure change in mass, ringed, and released.

(b) The 'Novel world' set-up

We used an established 'novel world' experimental protocol [8,9] to investigate how predators learn about novel aposematic prey. Prey items were small pieces of almond that were glued inside a white paper packet (8 x 8 mm). Both sides of the packets were printed with black symbols that indicated prey profitability: palatable prey were printed with a cross symbol and unpalatable 'aposematic' prey (an almond soaked in bitter tasting quinine solution) with a square symbol. The foraging background was made of white paper sheets with printed crosses, which made palatable prey (crosses) cryptic and more difficult to find compared to aposematic prey (squares) [9,43]. The first learning experiment [18] was conducted in a large aviary (3.0 x 3.5 m). The floor of the aviary was covered in background sheets that contained 24 cryptic and 24 aposematic prey, and in each trial birds were allowed to attack 12 prey items. The other two experiments [43, 44] were conducted in a small-scale set-up (a 50 x 66 x 50 cm plywood cage) where birds were sequentially presented with A1 sized background sheets. Each sheet contained 8 cryptic and 8 aposematic prey, so the relative abundance of the two prey types was constant (50:50) in all experiments. For each trial, birds were presented with four backgrounds, allowing them to attack in total 16 prey (four from each of the four backgrounds).

(c) Experimental protocol

Before the experiments, birds were trained to consume artificial prey items and forage in the experimental arena [18,43]. Birds were then divided into two treatments that (i) received social information about unpalatable prey signal, or (ii) did not receive information about prey profitability before the foraging trials. Social information was provided by presenting birds with video playback of a conspecific's aversive response to the unpalatable prey (a square symbol). This included a demonstrator attacking the prey and performing vigorous beak wiping and head shaking. The video also included an alternative cryptic prey (a cross) in an empty cage to ensure that birds were familiar with both prey items. Control groups were presented with a video of prey items only without a demonstrator bird. Both control and social information videos were 80 or 90 s long (depending on the experiment) and they were presented from an LCD monitor (Dell E198FPF, 19", resolution 1,280 × 1,024, 75 Hz refresh rate, 300 cd/m2) that was placed against the plexiglass wall of the test cage (50 x 66 x 50 cm). Our previous work with the same set-up shows that blue tits pay attention to video playback of a demonstrator bird [53], and videos therefore provide a good method to manipulate the presented information. Birds were allowed to forage in the novel world immediately after the video, and we recorded the prey types that they attacked. The first experiment consisted of three foraging trials that were conducted over three consecutive days, and in each trial birds were allowed to attack 12 prey [18]. The two other experiments consisted of four trials conducted over two days [44] and five trials conducted over three days [43], and birds were allowed to attack 16 prey in a trial.

Birds did not receive further social information after the first day to investigate whether the effect of social information persisted across days. For more detailed methods, see the original research articles [18,43,44].

(d) Statistical analysis

Before proceeding with analyses of changes in discrimination, or the effects of potential pay-offs on information use, we checked that social information had similar effects on the relative sampling of prey types across all three experiments. We used a generalised linear mixed effects model (GLMM, using the lme4 package, [54]) where the relative number of aposematic and cryptic prey taken was modelled as a binomial response variable; trial, information treatment and experiment were included as fixed effects, and a random slope (trial) and intercept (bird identity) were included to account for multiple trials with individual birds. Any significant differences among experiments were estimated by comparing models with and without interaction terms of information treatment, trial, and experiment.

To measure how personal and social information shifted discrimination (Δd', figure 1), we then calculated the relative change in consumption of aposematic prey from the previous trial:

$$\Delta d' = \frac{aposematic\ prey\ taken\ in\ trial_i}{total\ prey\ taken\ in\ trial_i} - \frac{aposematic\ prey\ taken\ in\ trial_{i-1}}{total\ prey\ taken\ in\ trial_{i-1}}$$

where $trial_i$ varied between 2 and 5, depending on the experiment. We modelled how information influenced the magnitude of this Δd' using GLMMs, where individual bird and trial were included as random effects to account for repeated testing, and Δd' was modelled according to a Gaussian distribution. Experiment number was included as a random effect in all analyses. We first built main effect models with total sampling of aposematic prey prior to trial (i.e. personal information) versus social information treatment (with or without social information) included as an interaction term. Although sampling cryptic prey would also provide personal information, birds sampled a fixed total number of prey in each experiment so here we present only aposematic prey. Visual inspection of polynomial fits (using sjPlot package, [55]) suggested a second-order polynomial would explain variation in our data better than a linear term, so this was included in all models.

Next we investigated whether putative variables affecting pay-offs (age, sex, days since the Autumn equinox, mass at time of capture, or change in mass while held in captivity) could explain variation in the effects of personal and/or social information on d′ and Δd'. The effect of each was tested in turn, in models containing either 3-way (e.g. age*information treatment*number of prior aposematic prey sampled) or 2-way interactions (e.g. age*number of prior aposematic prey sampled), or as single covariates (e.g. age) while maintaining the model structure identified in the previous analyses.

Likelihood ratio tests were used to assess the significance of all terms by comparison with models with the term of interest removed, and then adjusted for multiple comparisons where relevant using the Benjamini and Hochberg False Discovery Rate [56]. All data analyses were conducted using R version 3.6.1 [57].

3. Results

(a) Consistency of effects of social information across experiments

Despite differences in arena size and the number and duration of trials, social information consistently reduced the relative number of aposematic prey taken in a similar way across all three of our experiments (experiment*information treatment, $\chi^2 = 0.231$, df = 2, p = 0.89; information treatment, $\chi^2 = 9.348$, df = 1, p = 0.002), and across the repeated trials (experiment*information treatment*trial, $\chi^2 = 0.546$, df = 2, p = 0.76; trials, $\chi^2 = 109.20$, df = 1, p < 0.001; figure 2). Therefore, we continued with our next analyses to explain how experience with prey shifts discrimination.

(b) Effects of social and personal information on changes in discrimination

The number of aposematic prey that an individual consumed in the past ('personal information') predicted the direction and magnitude of changes in foraging responses ($\Delta d'$), however this relationship was curvilinear (prior consumption of aposematic prey 2nd-order polynomial, $\chi^2 = 15.563$, df = 1, p < 0.001, table 1). Personal information altered the magnitude of discrimination in the following trial, but cumulative personal information gained by sampling 7 or fewer aposematic prey (i.e. where the line of best fit crossed 0.0, 95% CI = 2 – 12 prey) did not improve prey discrimination (figure 3*a*). The discrimination of aposematic prey only improved (i.e. negative values) if between 8 to 20 aposematic prey were taken; after this inflection point, the magnitude of the shift in discrimination did not depend on the number of aposematic prey consumed prior to the trial (linear term for a model including > 20 prey consumed, estimate = -0.003 ± 0.004, $t = -0.877$; $\chi^2 = 0.797$, df = 1, p = 0.37). There was no effect of social information on the shape (polynomial prior consumption* information treatment, $\chi^2 = 3.254$, df = 2, p = 0.20) or intercept (information treatment, $\chi^2 = 2.247$, df = 1, p = 0.14) of this relationship between the number of prey consumed and changing discrimination (figure 3*a*).

(c) Individual differences in signal detection

The effects of social information on discrimination did not differ according to age (adults versus 1st year birds), sex, mass, or change in mass, and nor did it vary during the season (table 2). Similarly, we also found no evidence that age or seasonality altered how individuals changed discrimination from one encounter to the next after sampling aposematic prey (table 3), or in their response to social information (table 3). There was, however, a marginally significant interaction between sex and prior sampling of aposematic prey (table 3), with males showing a stronger shift in discrimination towards cryptic prey as their personal information increased (figure 3b) but this relationship was weak and was no longer significant after controlling for multiple comparisons (p = 0.52).

4. Discussion

When encountering novel aposematic and palatable prey, predators face a signal detection problem to discriminate between them [22]. Our results suggest that gathering personal information about aposematic prey improves prey discrimination, but this relationship is not linear. We found that sampling 8 to 20 aposematic prey increased discrimination of two novel prey types that great tits encountered in foraging trials. The first 7 aposematic prey sampled did not consistently improve discrimination, which suggests that predators require multiple encounters with aposematic prey before associating their signal with unpalatability. Sampling more than 20 prey, in turn, did not further improve discrimination. This indicates that even though continued sampling beyond this point can provide predators information about possible changes in prey profitability [59], it does not appear to be informative for prey discrimination. Although we found a consistent effect of social information reducing the attacks on aposematic prey in all experiments (as reported previously, [18,43,44]), this did not influence how personal information changed prey discrimination. Our results therefore suggest that social information is important in reducing the initial number of aposematic prey attacked, but it does not affect the value of information gathered by personally sampling aposematic prey.

(a) Effects of social and personal information on changes in discrimination

Traditional associative learning theory predicts that after the initial learning phase, predators should continue to attack prey at an asymptotic rate and therefore not change their discrimination further (reviewed in [49]). However, in our experiments attacks on aposematic prey continued to decrease throughout trials, which suggests that birds were not given sufficient learning opportunities to reach an asymptotic attack level. Nevertheless, by looking at changes in discrimination we found that after sampling approximately 20 aposematic prey, further encounters with prey did not continue to influence how well birds discriminated between the two prey types. In other words, even though birds still improved their discrimination after this inflection point (figure 3, the mean change is < 0 after the inflection point), this did not depend on further personal experience with aposematic prey or on individual-level variables. This curvilinear relationship suggests that any further improvements in discrimination were due to movement in the response threshold, and not as a response to personal (or social) information, supporting our second prediction that personal encounters with aposematic prey are not informative beyond a certain point for prey discrimination. Continued sampling may, however, be beneficial if prey profitability changes through time [59], for example. This information might be particularly valuable when defended prey is abundant and likely to be encountered in the future [31], influencing pay-offs and placement of response thresholds.

Receiving social information about prey unpalatability did not influence the relationship between personal information and prey discrimination. We have previously demonstrated that observing a negative feeding experience of a conspecific reduces the number of novel aposematic prey that great tits attack [18,43,44], and here we confirm that this effect is consistent across three different experiments, providing a rare example of replication [60] across years (experiments were conducted in 3 different years between 2014 and 2018), time (experiments varied in duration from 3 to 5 trials over 3 days to 4 trials over 2 days), and foraging space (experimental arenas varied from 0.25 m^2 to 10.5 m^2). Our previous work also indicated that even though socially educated birds initially sample fewer aposematic prey, their learning rate across foraging trials is similar to control birds. Here we extend this idea to show that social information does not interact with personal information in prey discrimination, which suggests that acquiring social information does not alter the value of personal encounters with prey. Indeed, even though social information can be cheaper to gather, it comes at a risk that it may be less accurate than personal information [38,61,62]. Observing foraging behaviour of others can therefore provide predators information about prey quality, but learning about more accurate toxin and nutrient quantity requires personal sampling, which could explain the similar effect of personal information in socially educated birds. Furthermore, our results suggest that personal and social information influence predator decision-making independently. However, the cognitive processes involved in learning about physiological effects of prey toxins and nutrients [49], as well as the mechanisms involved in social learning about prey defences are still poorly understood.

(b) Individual differences in signal detection

A recently proposed framework for predator decision-making suggests that both internal and external modifiers shape how predators discriminate between two stimuli [36]. We minimised any variation in external factors by using constant toxin and nutrient levels and same prey signals across experiments. The costs to detect prey items might have differed slightly because of a larger foraging arena in one of the experiments [18], but there was no evidence of any visibility differences [9,43], or that this would have influenced prey discrimination. Similarly, we did not find strong support that any internal factors influenced how personal or social information changed prey discrimination, although there was some evidence that males responded to personal information stronger than females. However, this effect was weak, and the effect sizes here indicate that we would need to test a much larger number of individuals before making strong conclusions about this difference between the sexes. Internal factors might have also influenced the payoffs to attack each prey type. For example, previous work has demonstrated that energetic reserves affect an individual's likelihood to attack defended prey [48,63], however, here we did not find evidence that an individual's mass influenced foraging decisions. Furthermore, individual differences might interact with social information [45], with previous work demonstrating that age and sex [64,65] or personality [66,67,68] can influence social information use. We did not, however, find that any of our individual-level variables influenced how birds used social information, even when the power to detect these effects was increased due to a larger sample size from three different experiments. This suggests that social information about prey profitability is valuable to all naive predators, regardless of their age, sex or current state [43].

External and internal factors have potential to influence shifts in both prey discrimination and the response threshold, and determining to what extent avoidance learning is attributed to improved discrimination, shifting response thresholds, or their combination is often difficult [36]. In our experiment, we defined discrimination between prey types as a change in foraging choices from trial to trial, however, this change might also depend on the birds' response threshold. Recent mathematical work suggests that disentangling these could be critical for explaining inconsistencies in iterative responses to repeated encounters [35]. This would require us to quantify four types of foraging decisions: i) correct detections (attacks on cryptic prey), ii) false alarms (attacks on aposematic prey), iii) missed detections (rejections of cryptic prey) and iv) correct rejections (rejections of aposematic prey, [22]). However, in our experiments we could only be certain about the prey that birds attacked as we could not assess whether a prey item was seen but ignored (correct rejection). Future studies should therefore aim to quantify the rejections of both prey types, which would enable us to better estimate the cost-benefit ratios for making different types of mistakes, as well as to investigate variation in response thresholds.

5. Conclusions

Social information about prey defences can facilitate the evolution and maintenance of aposematic prey by reducing predation pressure exerted by naïve individuals [18]. In addition to great tits [18,42,43,44], other avian species have been similarly demonstrated to shift their foraging preferences after receiving social information about prey unpalatability [39,40,41,69], and there is mounting evidence that social information use about palatable foraging opportunities could effect rapid evolutionary change [70] as well as have broad ecological consequences [71]. How social information interacts with and shapes the value of personal information under such scenarios, however, remains largely untested. Here we used a SDT approach to demonstrate that even though social information reduces the initial number of prey attacked, it does not change the relationship between personal information and prey discrimination. This suggests that some prey in a population will always need to be sampled for predators to learn how to discriminate them from alternatives, even if social information is available. However, the effect of personal and social information on predators' foraging decisions is likely to depend on the foraging context which can influence both prey discrimination and the response threshold. In addition to internal modifiers, such as a predator's current state [46,47,62], external payoffs, such as toxin [14,72] and nutrient content of the defended prey [73], or the abundance [74,75] or size [76] of alternative prey can influence a predator's decisions to attack each prey type. How these external payoffs influence the relationship between different information sources and prey discrimination, however, remains unknown but could represent a major ecological feedback in the evolutionary dynamics of predators and prey [18]. We suggest that SDT can be a useful approach to answer this question, and future studies should design experiments that manipulate the payoffs to attack different prey types to better understand how these influence the value of personal and social information and predator decision-making.

Acknowledgments

We thank Helinä Nisu and the staff at the Konnevesi research station for hosting the experiments, Hannah Rowland and Johanna Mappes for assistance in designing the original experiments, and David Kikuchi for helpful comments on the manuscript. 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 (grant number NE/K00929X/1) and a start-up grant from the Helsinki Institute of Life Science (HiLIFE), University of Helsinki.

References

1. Wallace, A. 1867. *Proceedings Of The Entomological Society Of London*: IXXX–IXXXi.
2. Ruxton, G. D., Allen, W. L., Sherratt, T. N. & Speed, M. P. 2018. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry* (2nd edition). Oxford University Press.
3. Müller, F. 1879. *Ituna and Thyridia*: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*.
4. Leimar, O., Enquist, M. & Sillen-Tullberg, B. 1986. Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. *The American Naturalist*, 128, 469–490. https://doi.org/10.1086/284581
5. Speed, M. P. 1993. Muellerian mimicry and the psychology of predation. *Animal Behaviour*, 45, 571–580. https://doi.org/10.1006/anbe.1993.1067
6. Speed, M. P. & Turner, J. R. G. 1999. Learning and memory in mimicry: II. Do we understand the mimicry spectrum? *Biological Journal of the Linnean Society*, 67, 281–312. https://doi.org/10.1006/bijl.1998.0310
7. Servedio, M. R. 2000. The effects of predator learning, forgetting, and recognition errors on the evolution of warning coloration. *Evolution*, 54, 751–763. https://doi.org/10.1111/j.0014-3820.2000.tb00077.x
8. Alatalo, R. V. & Mappes, J. 1996. Tracking the evolution of warning signals. *Nature*, 382, 708–710. https://doi.org/10.1038/382708a0
9. 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
10. Speed, M. P., Alderson, N. J., Hardman, C. & Ruxton, G. D. 2000. Testing Mullerian mimicry: an experiment with wild birds. *Proceedings of the Royal Society B: Biological Sciences*, 267, 725–731. https://doi.org/10.1098/rspb.2000.1063
11. 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
12. 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
13. Forsman, A. & Merilaita, S. 1999. Fearful symmetry: Pattern size and asymmetry affects aposematic signal efficacy. *Evolutionary Ecology*, 13, 131–140. https://doi.org/10.1023/A:1006630911975
14. Barnett, C. A, Bateson, M. & Rowe, C. 2014. Better the devil you know: avian predators find variation in prey toxicity aversive. *Biology Letters*, 10. https://doi.org/10.1098/rsbl.2014.0533

15. 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
16. Exnerová, A., Svádová, K. H., Fucíková, E., Drent, P. & Stys, 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
17. Halpin, C. G., Skelhorn, J. & Rowe, C. 2012. The relationship between sympatric defended species depends upon predators' discriminatory behaviour. *PLoS ONE*, 7, e44895. https://doi.org/10.1371/journal.pone.0044895
18. 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
19. Lindström, L., Alatalo, R. V, Lyytinen, A. & Mappes, J. 2001. Strong antiapostatic selection against novel rare aposematic prey. *Proceedings of the National Academy of Sciences*, 98, 9181–9184. https://doi.org/10.1073/pnas.161071598
20. Beatty, C. D., Beirinckx, K. & Sherratt, T. N. 2004. The evolution of mullerian mimicry in multispecies communities. *Nature*, 431, 63–66. https://doi.org/10.1038/nature02818.
21. Rowland, H. M., Wiley, E., Ruxton, G. D., Mappes, J. & Speed, M. P. 2010. When more is less: the fitness consequences of predators attacking more unpalatable prey when more are presented. *Biology Letters*, 6, 732–735. https://doi.org/10.1098/rsbl.2010.0207
22. Lynn, S. K. 2005. Learning to avoid aposematic prey. *Animal Behaviour*, 70, 1221–1226. https://doi.org/10.1016/j.anbehav.2005.03.010
23. Green, D. M. & Swets, J. A. 1966. *Signal detection theory and psychophysics.* New York: Wiley.
24. Macmillan, N. A. & Creelman, C. D. 2004. *Detection theory: A user's guide* (2nd edition). Lawrence Erlbaum Associates.
25. Duncan, C. J. & Sheppard, P. M. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour*, 24, 269–282. https://doi.org/10.1163/156853965X00066
26. Oaten, A., Pearce, C. E. M. & Smyth, M. E. B. 1975. Batesian mimicry and signal detection theory. *Bulletin of Mathematical Biology*, 37, 367–387. https://doi.org/10.1007/BF02459520
27. Getty, T. 1985. Discriminability and the sigmoid functional response: how optimal foragers could stabilize model-mimic complexes. *American Naturalist*, 125, 239–256. https://doi.org/10.1086/284339
28. Sherratt, T. N. 2002. The evolution of imperfect mimicry. *Behavioral Ecology,* 13, 821–826. https://doi.org/10.1093/beheco/13.6.821
29. McGuire, L., Van Gossum, H., Beirinckx, K. & Sherratt, T. N. 2006. An empirical test of signal detection theory as it applies to Batesian mimicry. *Behavioural Processes*, 73, 299–307. https://doi.org/10.1016/j.beproc.2006.07.004
30. Kikuchi, D. W., Malick, G., Webster, R. J., Whissell, E. & Sherratt, T. N. 2015. An empirical test of 2-dimensional signal detection theory applied to Batesian mimicry. *Behavioral Ecology*, 26, 1226–1235.

https://doi.org/10.1093/beheco/arv072

31. 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
32. Aubier, T. G. & Sherratt, T. N. 2015. Diversity in Müllerian mimicry: The optimal predator sampling strategy explains both local and regional polymorphism in prey. *Evolution*, 69, 2831–2845. https://doi.org/10.1111/evo.12790
33. Kikuchi, D. W. & Sherratt, T. N. 2015. Costs of learning and the evolution of mimetic signals. *The American Naturalist*, 186, 321–332. https://doi.org/10.1086/682371
34. Aubier, T. G., Joron, M. & Sherratt, T. N. 2017. Mimicry among unequally defended prey should be mutualistic when predators sample optimally. *American Naturalist*, 189, 267–282. https://doi.org/10.1086/690121
35. McNamara, J. M. & Trimmer, P. C. 2019. Sequential choices using signal detection theory can reverse classical predictions. *Behavioral Ecology*, 30, 16–19. https://doi.org/10.1093/beheco/ary132
36. Leavell, B. C. & Bernal, X. E. 2019. The cognitive ecology of stimulus ambiguity: a predator–prey perspective. *Trends in Ecology & Evolution*, 34, 1048–1060. https://doi.org/10.1016/j.tree.2019.07.004
37. Abbott, K. R. & Sherratt, T. N. 2013. Optimal sampling and signal detection: Unifying models of attention and speed-accuracy trade-offs. *Behavioral Ecology*, 24, 605–616. https://doi.org/10.1093/beheco/art001
38. Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, 20, 187–193. https://doi.org/10.1016/j.tree.2005.01.010
39. Mason, J Russell & Reidinger, R. 1982. Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *The Auk*, 99, 548–554.
40. 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
41. 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
42. 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
43. 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, 1982–1992. https://doi.org/10.1111/1365-2435.13395
44. Hämäläinen, L., Mappes, J., Rowland, H. M., Teichmann, M. & Thorogood, R. Social learning within and across predator species reduces attacks on novel aposematic prey. *Journal of Animal Ecology*. In press.

45. Mesoudi, A., Chang, L., Dall, S. R. X. & Thornton, A. 2016. The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, 31, 215–225. https://doi.org/10.1016/j.tree.2015.12.012
46. 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
47. 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
48. 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
49. Skelhorn, J., Halpin, C. G. & Rowe, C. 2016. Learning about aposematic prey. *Behavioral Ecology*, 27, 955–964. https://doi.org/10.1093/beheco/arw009
50. 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
51. Lynn, S. K. & Barrett, L. F. 2014. "Utilizing" signal detection theory. *Psychological Science*, 25, 1663–1673. https://doi.org/10.1177/0956797614541991
52. Svensson, L. 1992. *Identification Guide to European Passerines*. Stockholm.
53. 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
54. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. https://doi.org/10.18637/jss.v067.i01
55. Lüdecke, D. 2019. sjPlot: Data visualization for statistics in social science. R package version 2.7.2. https://doi.org/10.5281/zenodo.1308157
56. Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x
57. R Core Team. 2019. R: A language and environment for statistical computing (Vienna: R Foundation for Statistical Computing). Version 3.1.0. http://www.r-project.org
58. Nakagawa, S., Johnson, P. & Schielzeth, H. 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface,* 14. https://doi.org/10.1098/rsif.2017.0213
59. Lloyd, K. & Leslie, D. S. 2013. Context-dependent decision-making: A simple Bayesian model. *Journal of the Royal Society Interface*, 10. https://doi.org/10.1098/rsif.2013.0069
60. Hatchwell, B. J. 2017. Replication in behavioural ecology: A comment on Ihle et al. *Behavioral Ecology* 28, 360. https://doi.org/10.1093/beheco/arx009

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

62. 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

63. 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

64. Aplin, L. M., Sheldon, B. C. & Morand-Ferron, J. 2013. Milk bottles revisited: Social learning and individual variation in the blue tit, Cyanistes caeruleus. *Animal Behaviour*, 85, 1225–1232. https://doi.org/10.1016/j.anbehav.2013.03.009

65. Guillette, L. M. & Healy, S. D. 2014. Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, 108, 177–182. https://doi.org/10.1016/j.beproc.2014.10.011

66. Marchetti, C. & Drent, P. 2000. Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60, 131–140. https://doi.org/10.1006/anbe.2000.1443

67. Kurvers, R. H. J. M., van Oers, K., Nolet, B. A., Jonker, R. M., van Wieren, S. E., Prins, H. H. T. & Ydenberg, R. C. 2010. Personality predicts the use of social information. *Ecology Letters*, 13, 829–837. https://doi.org/10.1111/j.1461-0248.2010.01473.x

68. Smit, J. A. H. & van Oers, K. 2019. Personality types vary in their personal and social information use. *Animal Behaviour*, 151, 185–193. https://doi.org/10.1016/j.anbehav.2019.02.002

69. 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

70. Whitehead, H., Laland, K.N., Rendell, L., Thorogood, R. & Whiten, A. 2019. The reach of gene–culture coevolution in animals. *Nature Communications*, 10, 2405. https://doi.org/10.1038/s41467-019-10293-y

71. Gil, M.A., Hein, A.M., Spiegel, O., Baskett, M.L. & Sih, A. 2018. Social information links individual behavior to population and community dynamics. *Trends in Ecology and Evolution*, 33, 535–548. https://doi.org/10.1016/j.tree.2018.04.010

72. Skelhorn, J. & Rowe, C. 2006. Avian predators taste-reject aposematic prey on the basis of their chemical defence. *Biology Letters*, 2, 348–350. https://doi.org/10.1098/rsbl.2006.0483

73. Halpin, C. G., Skelhorn, J. & Rowe, C. 2014. Increased predation of nutrient-enriched aposematic prey. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, https://doi.org/10.1098/rspb.2013.3255

74. 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

75. 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

76. Halpin, C. G., Skelhorn, J. & Rowe, C. 2013. Predators' decisions to eat defended prey depend on the size of undefended prey. *Animal Behaviour*, 85, 1315–1321. https://doi.org/10.1016/j.anbehav.2013.03.021

Additional Information

Ethics

Wild birds were used 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).

Data Accessibility

All data are available from Dryad (https://doi.org/10.5061/dryad.573n5tb42).

Authors' Contributions

L.H. and R.T. conceived and designed the study, collected and analysed the data, and wrote the manuscript. Both authors approved the final version of the manuscript.

Competing Interests

We have no competing interests.

Tables

Table 1: The effects of personal and social information on changes in discrimination towards aposematic versus cryptic prey. Social information was provided before the first foraging trial to half of the birds (N = 39, N = 79 in total) and personal information (number of aposematic prey eaten previously) was modelled as a 2nd order polynomial. Interactions between these terms did not improve model fit and were removed. Number of trials varied from 3 to 5 across three experiments (trial and experiment were included as random effects with bird identity, N = 236 trials in total). Significance was determined via a simple approximation based on the *t*-statistic, significant terms are shown in bold. Conditional R^2 indicates model fit given the random effects [58].

Predictors	Estimate ± standard error	*t*-statistic	*p*
(Intercept – no social information)	-0.08 ± 0.06	-1.40	0.16
Personal information, 1st -order	-1.55 ± 0.23	-6.82	**<0.001**
Personal information, 2nd -order	0.71 ± 0.17	4.14	**<0.001**
Social information treatment	-0.03 ± 0.02	-1.55	0.12
Marginal R^2 / Conditional R^2	0.28 / 0.53		

Table 2: Likelihood ratio statistics for GLMM models testing how (a) individual-level covariates of age (adult *N* = 40 vs. juvenile *N* = 39), sex (male *N* = 48 vs. female *N* = 31), seasonality (days since Autumn equinox when tested, *N* = 79), mass at capture from the wild (*N* = 74), and percent change in mass during captivity (*N* = 74) influenced great tits' discrimination of aposematic prey from a cryptic alternative (proportion of prey taken that were aposematic, d'), and (b) depending on whether individuals had been provided social information before their first foraging trial versus a control. All models contained a fixed effect for trial and random slopes and intercepts for individual bird identity (model estimates are in Supplementary tables 1 and 2). Significance was determined via a Likelihood Ratio Test statistic (LRT, χ^2 distribution) compared to a reduced model without the variable of interest (df, degrees of freedom of both models shown), and then adjusted for multiple comparisons (p_{FDR}). The estimated effect size (± S.E.) of each covariate and its interaction with social information treatment are provided. Only models with the same sample sizes were compared using LRT.

	Effect size	LRT χ^2 (df)	p	p_{FDR}
(a) Covariates				
Age	-0.226 ± 0.135	2.767 (6,7)	0.096	0.56
Sex	-0.069 ± 0.140	0.248 (6,7)	0.62	0.88
Seasonality	0.045 ± 0.070	0.400 (6,7)	0.53	0.88
Mass at capture	-0.099 ± 0.070	1.998 (6,7)	0.16	0.56
Percent mass change	1.067 ± 1.502	0.504 (6,7)	0.48	0.88
(b) Depending on social information				
Social information§ * Age	0.370 ± 0.267	1.898 (7,8)	0.17	0.56
Social information§ * Sex	-0.070 ± 0.281	0.062 (7,8)	0.80	0.89
Social information§ * Seasonality	-0.051 ± 0.141	0.132 (7,8)	0.72	0.89
Social information+ * Mass at capture	-0.163 ± 0.141	1.338 (7,8)	0.25	0.62
Social information+ * Percent mass change	-0.229 ± 3.043	0.006 (7,8)	0.94	0.94

§ Social information treatment, N = 39; Control treatment, N = 40

+ Social information treatment, N = 37; Control treatment, N = 37

Table 3: Likelihood ratio statistics for GLMM models testing how great tits' use of prior personal information (number of aposematic prey previously eaten, modelled as a 2nd order polynomial) and/or social information (provided prior to the first foraging trial) when changing discrimination (Δd') towards aposematic prey varied according to individual-level covariates of (i) age (adult vs. juvenile), (ii) sex (male vs. female), (iii) seasonality (days since Autumn equinox when tested) on change in discrimination, (iv) mass at capture from the wild, and (v) percentage change in mass during captivity (sample sizes as in table 2). Significance was determined via a Likelihood Ratio Test statistic (χ^2 distribution) compared to a reduced model without the variable of interest (df, degrees of freedom of both models shown), and then adjusted for multiple comparisons (p_{FDR}). The estimated effect size (± S.E.) of each covariate in its interaction with personal and/or social information are provided (full model estimates are in Supplementary tables 3 – 7).

	Effect size	LRT χ^2 (df)	p	p_{FDR}
(i) Age:				
Personal information^2 * Social information * Age	0.277 ± 0.687	2.001 (14,16)	0.37	0.88
Personal information^2 * Age	-0.027 ± 0.312	0.216 (8,10)	0.90	0.91
Social information * Age	-0.015 ± 0.042	0.130 (7,8)	0.72	0.88
(ii) Sex:				
Personal information^2 * Social information * Sex	-0.070 ± 0.713	0.190 (14,16)	0.91	0.91
Personal information^2 * Sex	0.558 ± 0.292	6.713 (8,10)	0.035	0.52
Social information * Sex	-0.014 ± 0.043	0.110 (7,8)	0.74	0.91
(iii) Seasonality:				
Personal information^2 * Social information * Days	0.445 ± 0.554	0.746 (14,16)	0.69	0.91
Personal information^2 * Days	-0.449 ± 0.247	3.560 (8,10)	0.17	0.88
Social information * Days	0.013 ± 0.021	0.397 (7,8)	0.53	0.88
(iv) Mass at capture:				
Personal information^2 * Social information * Mass	-0.060 ± 0.339	0.505 (14,16)	0.78	0.91
Personal information^2 * Mass	-0.156 ± 0.150	1.618 (8,10)	0.45	0.88
Social information * Mass	0.022 ± 0.022	1.016 (7,8)	0.31	0.88
(v) Percentage change in mass:				
Personal information^2 * Social information * Mass change	0.256 ± 0.465	0.368 (14,16)	0.83	0.91
Personal information^2 * Mass change	0.070 ± 0.149	2.392 (8,10)	0.30	0.88
Social information * Mass change	-0.026 ± 0.022	1.458 (7,8)	0.23	0.88

Figures

Figure 1: The signal detection task of avoidance learning. According to Signal Detection Theory, the likelihood of responding appropriately (i.e. attack or avoid) to two prey types that vary in some intrinsic cue (e.g. visual appearance), cryptic but beneficial to attack S+ (grey lines) versus aposematic and costly S- (black lines), depends on 'stimulus generalisation gradients' which are described by probability distribution functions that tend to be bell-shaped and decrease in variance as predators learn over sequential trials (e.g. solid lines indicate trial 1, dotted lines indicate trial 2). This shifts potential for discrimination among prey types (d', horizontal lines) as experience increases from trial to trial (Δd'), although Δd' need not increase linearly across iterative learning opportunities [35]. The overlap of S+ and S- distributions indicates uncertainty about whether predators should attack or avoid S- prey, but the response threshold (RT, vertical red lines) of predators depends on the relative abundances of prey types and individual pay-offs. Prey that fall to the right of the threshold will be avoided while those to the left will be attacked.

Figure 2: The mean (± s.e.) number of aposematic prey sampled, relative to a cryptic alternative (discrimination, d'), by great tits during learning trials in three experiments designed to test the effects of social information (triangle, [18]; square, [43]; circle, [44]). Half of the individuals in each experiment received social information about prey signals via video playback (filled symbols, N = 39) and half were presented a control video (open symbols, N = 40). Grey symbols represent individual data points within each experiment and treatment.

Figure 3: The effect of personal information (sampling of aposematic prey) on the change in predators' discrimination of novel aposematic prey during repeated encounters, depending on whether they (*a*) received social information about signal unpalatability before encountering prey (filled circles, dashed line; controls = open circles, dotted line), or (*b*) whether they are male (filled diamonds, solid line) or female (open diamonds, dotted dashed line). Only the interaction shown in (*b*) is marginally significant (see table 3). The horizontal grey line indicates 0.0 change in discrimination, polynomial fit lines indicate the estimated lines of best fit, and shaded areas show standard error around these estimates (in (*a*), only the significant overall fit is shown). Sample sizes are the same as in Figure 2.