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

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1 Main Text

1 Summary

1
1 Ever since Alfred R. Wallace suggested brightly coloured, toxic insects warn predators about their
2 unprofitability, evolutionary biologists have searched for an explanation of how these aposematic prey evolve
3 and are maintained in natural populations. Understanding how predators learn about this widespread prey
4 defence is fundamental to addressing the problem, yet individuals differ in their foraging decisions and the
5 predominant application of associative learning theory largely ignores predators' prior experience. Here we
6 revisit the suggestion made almost 15 years ago that signal detection theory (SDT) provides a useful framework
7 to model predator learning by emphasising the integration of prior information into predation decisions. Using
8 multiple experiments where we modified the availability of social information using video playback, we show
9 that personal information (sampling aposematic prey) improves how predators (great tits, *Parus major*)
10 discriminate between novel aposematic and cryptic prey. However, this relationship was not linear and beyond
11 a certain point personal encounters with aposematic prey were no longer informative for prey discrimination.
12 Social information about prey unpalatability reduced attacks on aposematic prey across learning trials, but it
13 did not influence the relationship between personal sampling and discrimination. Our results suggest therefore
14 that acquiring social information does not influence the value of personal information, but more experiments
15 are needed to manipulate pay-offs and disentangle whether information sources affect response thresholds or
16 change discrimination.

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17 1. Introduction

18
19 The idea that conspicuous colouration could function as a warning signal to alert predators about prey toxicity
20 was first described by Wallace over 150 years ago [1]. How conspicuous aposematic prey evolve and persist
21 have puzzled evolutionary biologists ever since, and one of the key questions is to understand how predators
22 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
23 traditionally focused on associative learning by predators. Associative learning theories predict that predators
24 require a fixed amount of experience to acquire avoidance, and the shape of this learning curve depends on
25 characteristics of prey, such as the salience of the warning signal [9,13] and the strength of chemical defence
26 [11,12,14]. While this provides a basic framework for predator behaviour, reality is more complex: the number
27 of unpalatable prey that predators consume during learning varies among individuals [15,16,17,18] and
28 depends on the abundance of different prey types [10,19,20,21]. How, then, do predators learn about aposematic
29 prey?

30

31 (a) Signal detection theory for aposematic prey

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

46

47 More recent theoretical work has used an exploration-exploitation approach to model the uncertainty
48 that a predator experiences when sampling unfamiliar prey [31,32,33,34]. This approach has much in common
49 with SDT, but instead of considering a single decision, it models how predators iteratively revise their
50 expectations about the profitability of prey when sampling them repeatably [31]. This also takes into account
51 that continued sampling might not always be beneficial. If the prey is rare, for example, gaining information
52 about its profitability might have little future value, which could provide an explanation for the positive
53 correlation between the number of aposematic prey sampled and their abundance [31]. In contrast, SDT

54 typically considers a single decision that an individual makes [23,24]. The assumption of a single decision is,
55 however, often unrealistic in nature, and recent theoretical work shows that the classical predictions of SDT can
56 be reversed when the model assumes that an individual makes repeated decisions [35]. In addition to
57 considering iterative sampling [36], recent work has also incorporated speed-accuracy trade-offs and attention
58 allocation into SDT to create more realistic models of a predator's behaviour [37].

59

60 **(b) Integrating social and personal information about prey**

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

73

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

86

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

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

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

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

117

118 2. Methods

119

120 (a) Birds

121 We used wild-caught great tits (N = 79) as predators, using different individuals in each of the three experiments
122 (N = 27 [18]; N = 28, [43]; N = 24, [44]). Birds were sexed and aged according to plumage characteristics [52]
123 (juvenile females: N = 13, juvenile males: N = 26, adult males: N = 22, adult females: N = 18). The experiments
124 were conducted at the University of Jyväskylä Research Station, Konnevesi, Finland (62.6° N, 26.3° E) during
125 three winters (2013-2014, 2016-2017, 2017-2018); the date a bird was involved in an experiment was recorded as
126 days since the Autumn equinox. Birds were caught using feeding traps and housed individually in plywood
127 cages after being weighed to the nearest 0.25g using a Pesola balance. They were provided food (sunflower

128 seeds, tallow and peanuts) and fresh water ad libitum, except before experiments when food was restricted for
129 2 hours to ensure birds' motivation to forage. After the experiments (approximately one week) birds were
130 weighed to measure change in mass, ringed, and released.

131

132 **(b) The 'Novel world' set-up**

133 We used an established 'novel world' experimental protocol [8,9] to investigate how predators learn about novel
134 aposematic prey. Prey items were small pieces of almond that were glued inside a white paper packet (8 x 8
135 mm). Both sides of the packets were printed with black symbols that indicated prey profitability: palatable prey
136 were printed with a cross symbol and unpalatable 'aposematic' prey (an almond soaked in bitter tasting quinine
137 solution) with a square symbol. The foraging background was made of white paper sheets with printed crosses,
138 which made palatable prey (crosses) cryptic and more difficult to find compared to aposematic prey (squares)
139 [9,43]. The first learning experiment [18] was conducted in a large aviary (3.0 x 3.5 m). The floor of the aviary
140 was covered in background sheets that contained 24 cryptic and 24 aposematic prey, and in each trial birds were
141 allowed to attack 12 prey items. The other two experiments [43, 44] were conducted in a small-scale set-up (a 50
142 x 66 x 50 cm plywood cage) where birds were sequentially presented with A1 sized background sheets. Each
143 sheet contained 8 cryptic and 8 aposematic prey, so the relative abundance of the two prey types was constant
144 (50:50) in all experiments. For each trial, birds were presented with four backgrounds, allowing them to attack
145 in total 16 prey (four from each of the four backgrounds).

146

147 **(c) Experimental protocol**

148 Before the experiments, birds were trained to consume artificial prey items and forage in the experimental arena
149 [18,43]. Birds were then divided into two treatments that (i) received social information about unpalatable prey
150 signal, or (ii) did not receive information about prey profitability before the foraging trials. Social information
151 was provided by presenting birds with video playback of a conspecific's aversive response to the unpalatable
152 prey (a square symbol). This included a demonstrator attacking the prey and performing vigorous beak wiping
153 and head shaking. The video also included an alternative cryptic prey (a cross) in an empty cage to ensure that
154 birds were familiar with both prey items. Control groups were presented with a video of prey items only
155 without a demonstrator bird. Both control and social information videos were 80 or 90 s long (depending on the
156 experiment) and they were presented from an LCD monitor (Dell E198FPPF, 19", resolution 1,280 x 1,024, 75 Hz
157 refresh rate, 300 cd/m²) that was placed against the plexiglass wall of the test cage (50 x 66 x 50 cm). Our previous
158 work with the same set-up shows that blue tits pay attention to video playback of a demonstrator bird [53], and
159 videos therefore provide a good method to manipulate the presented information. Birds were allowed to forage
160 in the novel world immediately after the video, and we recorded the prey types that they attacked. The first
161 experiment consisted of three foraging trials that were conducted over three consecutive days, and in each trial
162 birds were allowed to attack 12 prey [18]. The two other experiments consisted of four trials conducted over
163 two days [44] and five trials conducted over three days [43], and birds were allowed to attack 16 prey in a trial.

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

166

167 **(d) Statistical analysis**

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

176

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

$$179 \quad \Delta d' = \frac{\text{aposematic prey taken in trial}_i}{\text{total prey taken in trial}_i} - \frac{\text{aposematic prey taken in trial}_{i-1}}{\text{total prey taken in trial}_{i-1}}$$

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

189

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

196

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

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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 3a). 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 3a).

(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

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

251

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

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

268

269 Receiving social information about prey unpalatability did not influence the relationship between
270 personal information and prey discrimination. We have previously demonstrated that observing a negative
271 feeding experience of a conspecific reduces the number of novel aposematic prey that great tits attack [18,43,44],
272 and here we confirm that this effect is consistent across three different experiments, providing a rare example
273 of replication [60] across years (experiments were conducted in 3 different years between 2014 and 2018), time
274 (experiments varied in duration from 3 to 5 trials over 3 days to 4 trials over 2 days), and foraging space

275 (experimental arenas varied from 0.25 m² to 10.5 m²). Our previous work also indicated that even though socially
276 educated birds initially sample fewer aposematic prey, their learning rate across foraging trials is similar to
277 control birds. Here we extend this idea to show that social information does not interact with personal
278 information in prey discrimination, which suggests that acquiring social information does not alter the value of
279 personal encounters with prey. Indeed, even though social information can be cheaper to gather, it comes at a
280 risk that it may be less accurate than personal information [38,61,62]. Observing foraging behaviour of others
281 can therefore provide predators information about prey quality, but learning about more accurate toxin and
282 nutrient quantity requires personal sampling, which could explain the similar effect of personal information in
283 socially educated birds. Furthermore, our results suggest that personal and social information influence
284 predator decision-making independently. However, the cognitive processes involved in learning about
285 physiological effects of prey toxins and nutrients [49], as well as the mechanisms involved in social learning
286 about prey defences are still poorly understood.

287

288 **(b) Individual differences in signal detection**

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

307

308 External and internal factors have potential to influence shifts in both prey discrimination and the
309 response threshold, and determining to what extent avoidance learning is attributed to improved
310 discrimination, shifting response thresholds, or their combination is often difficult [36]. In our experiment, we
311 defined discrimination between prey types as a change in foraging choices from trial to trial, however, this

312 change might also depend on the birds' response threshold. Recent mathematical work suggests that
313 disentangling these could be critical for explaining inconsistencies in iterative responses to repeated encounters
314 [35]. This would require us to quantify four types of foraging decisions: i) correct detections (attacks on cryptic
315 prey), ii) false alarms (attacks on aposematic prey), iii) missed detections (rejections of cryptic prey) and iv)
316 correct rejections (rejections of aposematic prey, [22]). However, in our experiments we could only be certain
317 about the prey that birds attacked as we could not assess whether a prey item was seen but ignored (correct
318 rejection). Future studies should therefore aim to quantify the rejections of both prey types, which would enable
319 us to better estimate the cost-benefit ratios for making different types of mistakes, as well as to investigate
320 variation in response thresholds.

321

322 5. Conclusions

323

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

344

345

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347

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542 Additional Information

543 **Ethics**

544 Wild birds were used with permission from the Central Finland Centre for Economic Development, Transport
545 and Environment and license from the National Animal Experiment Board (ESAVI/9114/ 04.10.07/2014) and the
546 Central Finland Regional Environmental Centre (VARELY/294/2015).

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548 **Data Accessibility**

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

550

551 **Authors' Contributions**

552 L.H. and R.T. conceived and designed the study, collected and analysed the data, and wrote the manuscript.

553 Both authors approved the final version of the manuscript.

554

555 **Competing Interests**

556 We have no competing interests.

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559 **Tables**

560 **Table 1:** The effects of personal and social information on changes in discrimination towards aposematic versus
 561 cryptic prey. Social information was provided before the first foraging trial to half of the birds (N = 39, N = 79
 562 in total) and personal information (number of aposematic prey eaten previously) was modelled as a 2nd order
 563 polynomial. Interactions between these terms did not improve model fit and were removed. Number of trials
 564 varied from 3 to 5 across three experiments (trial and experiment were included as random effects with bird
 565 identity, N = 236 trials in total). Significance was determined via a simple approximation based on the *t*-statistic,
 566 significant terms are shown in bold. Conditional R² indicates model fit given the random effects [58].
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Predictors	Estimate ± standard error	<i>t</i> -statistic	<i>p</i>
(Intercept – no social information)	-0.08 ± 0.06	-1.40	0.16
Personal information, 1 st -order	-1.55 ± 0.23	-6.82	<0.001
Personal information, 2 nd -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		

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570 **Table 2:** Likelihood ratio statistics for GLMM models testing how (a) individual-level covariates of age (adult
571 $N = 40$ vs. juvenile $N = 39$), sex (male $N = 48$ vs. female $N = 31$), seasonality (days since Autumn equinox when
572 tested, $N = 79$), mass at capture from the wild ($N = 74$), and percent change in mass during captivity ($N = 74$)
573 influenced great tits' discrimination of aposematic prey from a cryptic alternative (proportion of prey taken that
574 were aposematic, d'), and (b) depending on whether individuals had been provided social information before
575 their first foraging trial versus a control. All models contained a fixed effect for trial and random slopes and
576 intercepts for individual bird identity (model estimates are in Supplementary tables 1 and 2). Significance was
577 determined via a Likelihood Ratio Test statistic (LRT, χ^2 distribution) compared to a reduced model without the
578 variable of interest (df, degrees of freedom of both models shown), and then adjusted for multiple comparisons
579 (p_{FDR}). The estimated effect size (\pm S.E.) of each covariate and its interaction with social information treatment
580 are provided. Only models with the same sample sizes were compared using LRT.

	Effect size	LRT χ^2 (df)	p	p_{FDR}
<i>(a) Covariates</i>				
Age	-0.226 \pm 0.135	2.767 (6,7)	0.096	0.56
Sex	-0.069 \pm 0.140	0.248 (6,7)	0.62	0.88
Seasonality	0.045 \pm 0.070	0.400 (6,7)	0.53	0.88
Mass at capture	-0.099 \pm 0.070	1.998 (6,7)	0.16	0.56
Percent mass change	1.067 \pm 1.502	0.504 (6,7)	0.48	0.88
<i>(b) Depending on social information</i>				
Social information [§] * Age	0.370 \pm 0.267	1.898 (7,8)	0.17	0.56
Social information [§] * Sex	-0.070 \pm 0.281	0.062 (7,8)	0.80	0.89
Social information [§] * Seasonality	-0.051 \pm 0.141	0.132 (7,8)	0.72	0.89
Social information ⁺ * Mass at capture	-0.163 \pm 0.141	1.338 (7,8)	0.25	0.62
Social information ⁺ * Percent mass change	-0.229 \pm 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, $N = 37$

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

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

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602 Figures

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

614
615 **Figure 2:** The mean (\pm s.e.) number of aposematic prey sampled, relative to a cryptic alternative (discrimination,
616 d'), by great tits during learning trials in three experiments designed to test the effects of social information
617 (triangle, [18]; square, [43]; circle, [44]). Half of the individuals in each experiment received social information
618 about prey signals via video playback (filled symbols, $N = 39$) and half were presented a control video (open
619 symbols, $N = 40$). Grey symbols represent individual data points within each experiment and treatment.

620
621 **Figure 3:** The effect of personal information (sampling of aposematic prey) on the change in predators'
622 discrimination of novel aposematic prey during repeated encounters, depending on whether they (a) received
623 social information about signal unpalatability before encountering prey (filled circles, dashed line; controls =
624 open circles, dotted line), or (b) whether they are male (filled diamonds, solid line) or female (open diamonds,
625 dotted dashed line). Only the interaction shown in (b) is marginally significant (see table 3). The horizontal
626 grey line indicates 0.0 change in discrimination, polynomial fit lines indicate the estimated lines of best fit, and
627 shaded areas show standard error around these estimates (in (a), only the significant overall fit is shown).
628 Sample sizes are the same as in Figure 2.

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