

1 **Hard to catch: Experimental evidence supports evasive mimicry**

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19 **ABSTRACT**

20 Most research on aposematism has focused on chemically defended prey, but

21 signalling difficulty of capture remains poorly explored. Similarly to classical

22 Batesian and Müllerian mimicry related to distastefulness, such “evasive  
23 aposematism” may also lead to convergence in warning colours, known as  
24 evasive mimicry. A prime candidate group for evasive mimicry are *Adelpha*  
25 butterflies, which are agile insects and show remarkable colour pattern  
26 convergence. We tested the ability of naïve blue tits to learn to avoid and  
27 generalise *Adelpha* wing patterns associated with difficulty of capture, and  
28 compared their response to that of birds that learned to associate the same wing  
29 patterns with distastefulness. Birds learned to avoid all wing patterns tested, but  
30 learning was faster with evasive prey compared with distasteful prey. Birds  
31 generalised their learned avoidance from evasive models to imperfect mimics if  
32 the mimic shared colours with the model. Despite imperfect mimics gaining  
33 protection from bird’s generalisation, perfect mimics always had the best fitness,  
34 supporting selection for accurate mimicry. Faster avoidance learning and broader  
35 generalisation of evasive prey suggest that being hard to catch may deter  
36 predators at least as effectively as distastefulness. Our results provide empirical  
37 evidence for a potentially widespread alternative scenario, evasive mimicry, for  
38 the evolution of similar aposematic colour patterns.

## 39 **KEYWORDS**

40 *Adelpha* - evasive aposematism - predator learning - distastefulness –  
41 convergence - prey defence

42

## 43 **BACKGROUND**

44 Many organisms with chemical, morphological or behavioural defences often  
45 display a conspicuous signal, such as a colour pattern, that warns predators of

46 the potential cost of attacks. Possession of such warning signals is known as  
47 aposematism (1,2). In many cases, the effectiveness of aposematism depends  
48 on the ability of predators to associate the signal with an unpleasant experience  
49 related with the stimulus, and to attribute signal properties to different prey  
50 individuals (i.e. generalisation) (reviewed in (3)) (4–6), which results in prey  
51 avoidance. Aposematic prey are under positive frequency-dependent selection,  
52 which can result in selection for convergence of warning signals among co-  
53 occurring defended species, known as Müllerian mimicry (7). Aposematism and  
54 Müllerian mimicry associated with distastefulness have been extensively studied  
55 in many taxa (8–11), but especially in Lepidoptera (12–16). However, there is  
56 increasing evidence that aposematism may also be associated with an alternative  
57 defence, namely effective evasiveness (reviewed in (17)). Theoretically,  
58 predators should avoid attacking evasive prey since unsuccessful attacks likely  
59 represent a significant cost in time and energy to the predator (17–19). In this  
60 case, selection exerted by predators is expected to drive convergence in signals  
61 that they associate with the evasiveness of their prey (20–25), in a process known  
62 as escape mimicry or evasive mimicry (hereafter we use the latter term).

63 Previous experiments have shown that bird predators can use visual cues to  
64 identify evasive prey (26–28), but more empirical work is needed to test whether  
65 outstanding potential examples of evasive mimicry could indeed be the result of  
66 selection for such signals related to evasiveness. One such example is the  
67 diverse Neotropical butterfly genus *Adelpha*, where repeated convergence of  
68 their apparently conspicuous and contrasting wing patterns among distantly  
69 related sympatric species has been interpreted as evidence for mimicry (29–31).  
70 Mimicry in *Adelpha* has been hypothesized to be at least partly driven by chemical

71 defences in some species (32–34), but there is currently limited, conflicting  
72 evidence for distastefulness (22,33,35,36). In contrast to most classic groups of  
73 chemically defended butterflies, *Adelpha* butterflies have short and stout thoraxes  
74 and exhibit fast and unpredictable flight (K.W., personal observations) (19), which  
75 are favourable traits for butterflies aiming to escape predators (35,37), making  
76 the genus a prime candidate for evasive mimicry (38).

77 In this study, we used models of wing patterns of *Adelpha* butterflies and wild  
78 blue tits as naïve bird predators to address the following questions: 1. Can birds  
79 learn to associate naturally occurring wing patterns with evasiveness of prey? 2.  
80 Can such a signal be generalised across putative mimetic species? 3. What type  
81 of secondary defence drives faster learning by predators, evasiveness or  
82 distastefulness?

## 83 **MATERIALS AND METHODS**

84 We used wild blue tits (*Cyanistes caeruleus*) to examine whether birds can learn  
85 to avoid *Adelpha* colour patterns associated with evasive (escaping) behaviour,  
86 and whether birds generalised the learned avoidance across similar, naturally  
87 occurring wing patterns. In addition, we conducted parallel experiments with  
88 distasteful prey having the same colour pattern but not evasiveness.

89 Experiments were conducted from January to March 2019 at Konnevesi  
90 Research Station in Central Finland, which provided the infrastructure, wildlife  
91 research and collection permits, and expertise needed to conduct experiments  
92 with wild birds in captivity. Blue tits were captured from feeding sites around the  
93 station and were maintained in captivity for a maximum of 10 days, during which  
94 time they were kept singly in illuminated plywood cages (daily light period of 12 h

95 30 min) with food and fresh water available *ad libitum*. After experiments birds  
96 were ringed and released into the site of capture.

### 97 ***Artificial prey***

98 Artificial defended prey (4.1 x 2.5 cm) were constructed by printing images (HP  
99 Color Laserjet CP2025, regular printer paper) of different wing colour patterns  
100 displayed by the species *Adelpha salmoneus*, *A. cocala*, and *A. epione* (figure 1).  
101 These species represent three putatively distinct mimicry rings (29,31) and were  
102 chosen because they differ in colour and pattern, to enable us to test if apparently  
103 distinct signals may provide protection from predation in evasive mimicry. An  
104 entirely dark brown model of a non-defended prey was constructed as a control.  
105 To make prey attractive for birds, a piece of almond (reward), was glued to the  
106 underside of prey. For distasteful models, almonds were soaked in chloroquine  
107 phosphate solution (7%), to give them a bitter taste (following e.g., (39)).

### 108 ***Experimental procedures***

109 The experiment took place in experimental aviaries of 49 x 48 x 67 cm illuminated  
110 by light bulbs. Each aviary contained a perch and a water bowl. Birds were  
111 observed through a one-way glass situated on the front of the aviary. Two plastic  
112 prey holders gliding on aluminium profile rails (fixed on both sides of the aviary's  
113 floor) allowed simulation of the artificial prey's escaping (electronic  
114 supplementary material, S1 figure 2).

### 115 ***Avoidance learning***

116 We used 87 birds, trained to attack on artificial butterflies (see the electronic  
117 supplementary material, S1 for details of the training procedure), and divided into

118 3 treatment groups (figure 1). The first two groups were trained to avoid evasive  
119 prey and a third group was trained to avoid distasteful prey with the same colour  
120 wing band pattern as group 2. Before initiating the experiment, birds were  
121 habituated to the experimental aviary for at least an hour. Experiments consisted  
122 of a series of trials where two prey were presented simultaneously to the bird.  
123 Birds learning evasive model prey had one opportunity of attack per trial, and they  
124 were allowed to capture and eat only the control prey, whereas the evasive prey  
125 was always rapidly pulled out of reach (i.e., escaping) when attacked. In the  
126 treatment group where birds were trained to avoid distasteful prey they were  
127 allowed to consume the attacked prey (i.e., distasteful prey and control prey).  
128 Training presentations continued for at maximum 80 trials or until the bird  
129 attacked an evasive or distasteful prey no more than twice over ten consecutive  
130 trials. This learning criterion ensured that all birds reached the same level of  
131 learning, which was important for the following generalisation test.

132 *Generalisation of learned avoidance to other prey (imperfect mimics)*

133 We used only birds that achieved the learning criteria in previous phase (group 1  
134 n=23, group 2 n=25 [number of birds that learned is 29 out of 31, but data of four  
135 birds that followed a different preliminary protocol for generalisation are not  
136 included], group 3 n=18) to test whether and to what extent the previously learned  
137 avoidance of warning coloration associated with evasiveness (group 1 and 2) or  
138 distastefulness (group 3) was generalised to novel wing colour patterns that  
139 shared some features with the learned colour pattern (i.e., either colour or  
140 pattern). Those novel colour patterns are referred to as imperfect mimics. Birds  
141 were simultaneously presented with four types of prey: a (i) control prey, (ii) the

142 model they had learned and (iii) two imperfect mimics (figure 1; see electronic  
143 supplementary material, S1 for detailed description).

## 144 ***Statistical analyses***

### 145 *Avoidance learning*

146 We examined whether birds from group 1 (n=28) and group 2 (n=31) learned to  
147 avoid wing patterns associated with evasiveness, and whether wing colour  
148 pattern affected learning speed. We used a mixed-effects Cox regression model  
149 (“coxme” package version 2.2.10 in RStudio v.3.5.3; RStudio 2019) where the  
150 response variable was the survival probability of the control prey within trials. The  
151 wing colour pattern that the bird learned to avoid as the evasive model was added  
152 as an explanatory factor, and bird individuals as a random effect.

### 153 *Comparison of avoidance learning between evasive and distasteful prey*

154 To compare avoidance learning among birds facing aposematic prey signalling  
155 for evasiveness, and birds facing aposematic prey signalling for distastefulness  
156 with the same colour pattern (group 2 and 3, respectively; figure 1), we performed  
157 another mixed-effect Cox regression model. The response variable was the  
158 survival probability of the control prey within trials and the explanatory variable  
159 was the type of prey defence (i.e. evasiveness or distastefulness). Bird individual  
160 was defined as a random effect.

### 161 *Generalisation of learned avoidance to other prey (imperfect mimics)*

162 For each experimental group, to test for differences in attack probabilities  
163 between the different types of prey (the control, the model and the two imperfect

164 mimics, figure 1), we calculated the log-likelihood of observing the number of  
165 attacks that were recorded on each prey type across all in the group as follows.

$$166 \quad \log_{10}(L) = \sum_i [a_i \log_{10}(P_i) + (N - a_i) \log_{10}(1 - P_i)] + K$$

167 Where  $i$  is one of the four prey types;  $N$  is the total number of trials;  $a_i$  is the  
168 number of times a butterfly of type  $i$  was attacked;  $P_i$  is the attack rate of butterflies  
169 of type  $i$  and  $K$  is a constant term that disappears in model comparisons.

170 We explored several scenarios where attack rates of different types of prey could  
171 be equal or not (see electronic supplementary material, S3 for a list of all those  
172 scenarios), and calculated the log-likelihood functions of those scenarios. As an  
173 example, a scenario where the attack rate on the control is equal to those on the  
174 imperfect mimics and higher than that on the model means that birds do not  
175 generalise the learned avoidance to the imperfect mimics; a scenario where the  
176 attack rate on the model is equal to those on the imperfect mimics and lower than  
177 that on the control means that birds have fully generalised the learned avoidance  
178 to the imperfect mimics; and a scenario where the attack rate on the imperfect  
179 mimics is lower than that on the control but higher than that on the model means  
180 that birds have partially generalised the learned avoidance to the imperfect  
181 mimics.

182 Models were selected on the basis of their AICc, which accounts for the number  
183 of parameters and the sample size. For each group, the model with the lowest  
184 AICc was considered the best. We considered that models within a 2-unit AICc  
185 interval from the best model could not be rejected.

## 186 **RESULTS**



187 *Avoidance learning*

188 According to the learning criterion, most birds learned to avoid their evasive prey  
189 model: 23 out of 28 birds from group 1 (i.e., orange forewing band) and 29 out of  
190 31 birds from group 2 (i.e., transverse orange/white band). Additionally, 18 out of  
191 28 birds (group 3) learned to avoid the distasteful prey model.

192 The mixed-effects Cox regression model detected no significant differences  
193 ( $Z=0.05$ ;  $P=0.96$ ) between birds that learned to avoid different wing patterns of  
194 evasive prey (i.e. group 1 and group 2), but showed that birds learned to avoid  
195 evasive prey (group 2) significantly faster than distasteful prey with the same wing  
196 pattern (group 3) ( $Z=-3.21$ ;  $P=0.001$ ) (figure 2).

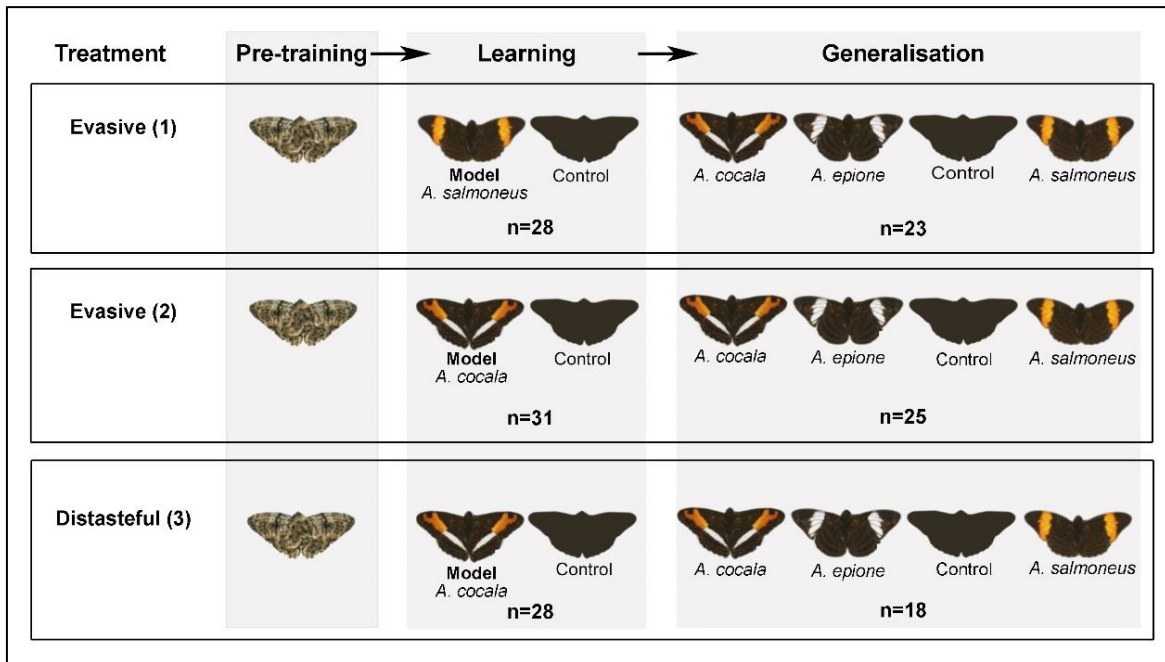
197 *Generalisation of learned avoidance to other prey (imperfect mimics)*

198 Bird's attack frequencies on mimics differed within and among groups (figure 3;  
199 electronic supplementary material S2). For group 1 (prey with orange forewing  
200 band as evasive model), in the best scenario learned avoidance was fully  
201 generalised to the imperfect mimic that shared a colour (orange) with the model,  
202 while the other imperfect mimic (white forewing band) was attacked as much as  
203 the control (estimated attack rates on the model and the orange/white mimic:  
204 0.109; estimated attack rates on the control and the white mimic: 0.391; AICc =  
205 45.079, electronic supplementary material S3). Two additional scenarios could  
206 be considered as similarly plausible, based on their AICc. One was similar to the  
207 previous, except that the orange/white mimic was attacked more often than the  
208 model (but still less than the control; estimated attack rate on the model: 0.043;  
209 on the orange/white mimic: 0.174; on the control and white mimic: 0.391; AICc =  
210 46.809, electronic supplementary material S3), indicating partial generalisation.

211 In the other, only the model was attacked less than the control, implying no  
212 generalisation (attack rate on the model: 0.043, attack rates on the control and  
213 mimics: 0.319; AICc = 45.690, electronic supplementary material S3).

214 Regarding group 2, (orange/white as evasive model), in the best scenario  
215 avoidance was fully generalised to both imperfect mimics, which both shared a  
216 colour with the model (estimated attack rate on the model and mimics: 0.188,  
217 estimated attack rate on the control, 0.435, AICc = 47.732, electronic  
218 supplementary material S3). Two additional scenarios were within a 2-unit AICc  
219 interval with that of the model. One of those scenarios was similar to the previous,  
220 except that generalisation to the mimics was partial (estimated attack rate on the  
221 model: 0.080, estimated attack rate on the mimics: 0.261, estimated attack rate  
222 on the control: 0.560, AICc = 49.481, electronic supplementary material S3). In  
223 the other, generalisation only applied to the orange mimic, which suffered an  
224 attack rate similar to that of the model (estimated attack rates on the model and  
225 orange mimic: 0.109; estimated attack rates on the control and white mimic:  
226 0.391, AICc = 49.415, electronic supplementary material S3).

227 In group 3 (orange/white as distasteful model), a single scenario stood out as  
228 best, in which avoidance was fully generalised to the orange mimic only  
229 (estimated attack rates on the model and orange mimic: 0.109; estimated attack  
230 rates on the control and white mimic: 0.391, AICc = 33.517, electronic  
231 supplementary material S3).



232

233 **Figure 1.** Schematic illustration of the experimental design that consisted of 3  
234 phases: pre-training, learning and generalisation. A forewing orange-banded prey  
235 (*A. salmoneus*) was presented as a model for group 1, and as an imperfect mimic  
236 during generalisation for group 2 and 3. A transverse forewing orange/hindwing  
237 white-banded prey (*A. cocala*) was the model for group 2 and 3, and an imperfect  
238 mimic during generalisation for group 1. The forewing white-banded prey (*A.*  
239 *epione*) was presented as an imperfect mimic during generalisation for all groups.

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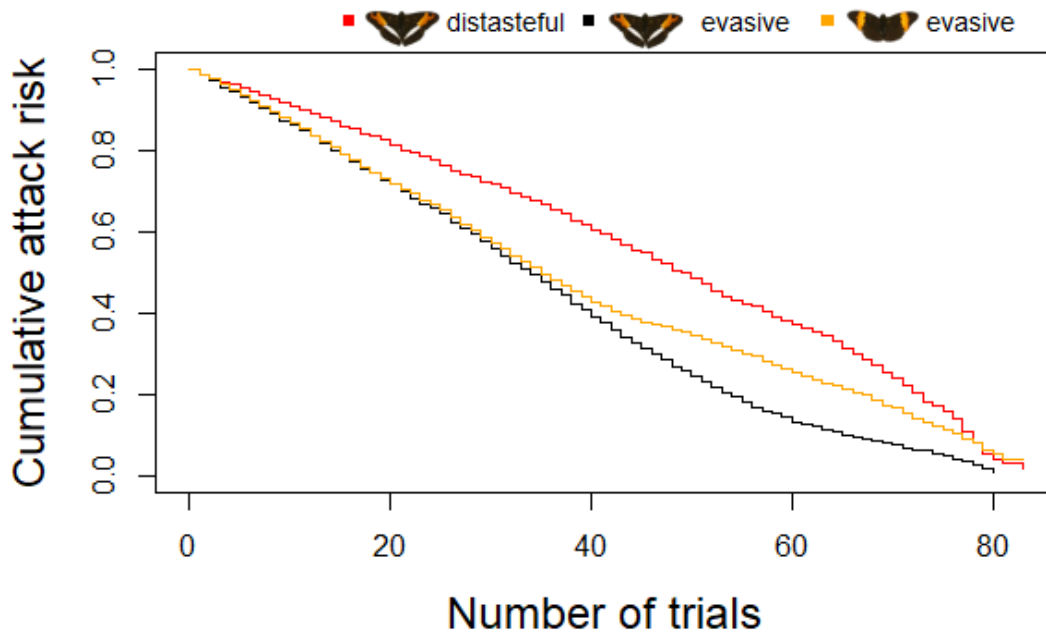
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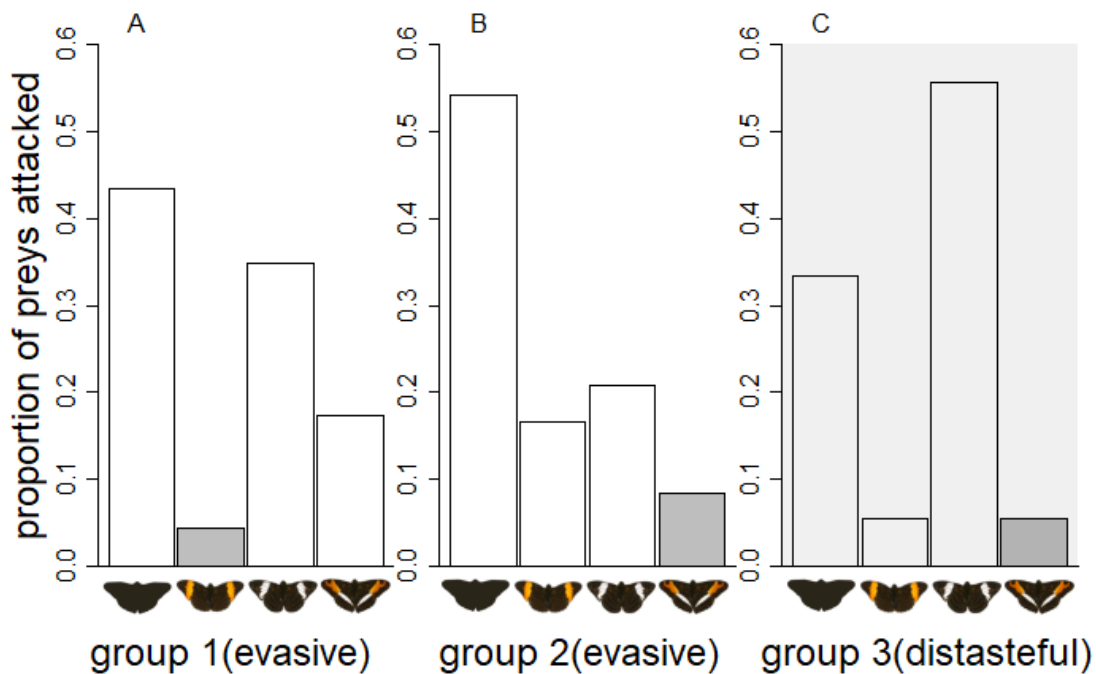
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254 **Figure 2.** Cumulative attack risk curves of the model during learning trials. Each  
255 line represents a type of prey model presented to each group of birds (group 1  
256 yellow line, group 2 black line, and group 3 red line.

257



258

259 **Figure 3.** Comparison among observed attack rates on the model, control and  
260 imperfect mimics during generalisation tests. Bars illustrate the attack proportion  
261 within groups on different wing colour patterns after birds learned to avoid the  
262 model pattern (group 1: n=23, group 2: n=25, group 3: n=18). The grey bar  
263 indicates the model.

264

## 265 **DISCUSSION**

### 266 ***Learning and generalisation of signals associated with an effective*** 267 ***escaping ability***

268 The idea that some butterflies have evolved signalling of evasiveness as an anti-  
269 predator defence has a long history (19,21,40–42). Still, surprisingly few  
270 experiments to date have tested the idea (22,26–28), and nobody has so far  
271 tested whether predators can remember and generalise their learned avoidance  
272 to other species with signals that are similar to some extent, which is crucial for  
273 the evolution of mimicry. Gibson (26,27) and Hancox & Allen (28) presented wild  
274 avian predators with artificial prey (i.e. dyed millet seeds, coloured mealworms or  
275 pastry models) that disappeared from sight when attacked. After extensive  
276 training (approx. 20 days), it was observed that birds reduced their attacks on  
277 such hard-to-catch prey. We showed that wild birds, with no experience of  
278 *Adelpha* butterflies, were able to associate both orange and orange/white  
279 patterns with evasiveness within a day of training. Unlike previous experiments  
280 (26–28), our birds faced a “simpler” prey scenario (39), with a warningly coloured  
281 prey that could be easily discriminated from the non-defended prey, which may  
282 explain the faster avoidance learning we observed.

283 Our results also showed that birds were able to generalise their learned  
284 avoidance to novel, somewhat similar prey (i.e., that shared either a colour or the  
285 pattern with the learned model), even though perfect mimics were always the  
286 most strongly avoided. Previous work on distasteful prey found that avian  
287 predators primarily focus on colour, rather than pattern (43–47) or wing shape  
288 (48), when learning and generalising aposematic visual signals. Our findings  
289 seem to be consistent with these studies, because all three groups of birds  
290 generalised their avoidance to evasive prey that presented a colour in common  
291 with the formerly learned model, despite harbouring different patterns, and in  
292 group 1, where one imperfect mimic shared the pattern but no colour with the  
293 model, birds did not generalise to that mimic. Moreover, although we did not  
294 formally test whether some colours or patterns are more efficient as a visual cue  
295 for learning or generalisation, we sometimes observed an asymmetrical  
296 generalisation (e.g., higher attack rate on the white than the orange mimic in  
297 group 3). Further experiments comparing models with different colours could  
298 shed light on whether some colours are better learned than others.

299 The three *Adelpha* species we studied are not regarded as strongly co-mimetic,  
300 since a number of other species show much more similar (practically identical)  
301 colour patterns, concordant geographic variation and broader sympatry (29).  
302 Preliminary trials in our experiment suggested that our predator was incapable of  
303 distinguishing among the most perfect co-mimics of *A. cocala*, so we expanded  
304 our experiment to include more dissimilar species to examine the significance of  
305 mimetic accuracy. Although imperfect mimics gained varying levels of protection,  
306 the perfect mimic appeared to mostly be the best protected. Those results

307 suggest strong selection on mimetic fidelity and could explain the extremely close  
308 similarity within some putative *Adelpha* mimicry rings.

### 309 ***Evasiveness versus distastefulness as deterrents to predators***

310 Learning about distastefulness is thought to be generally quicker and easier than  
311 evasiveness because prey unprofitability can be determined, unambiguously,  
312 from a single experience when prey is ingested. By contrast, a prey individual  
313 might escape capture because of better escaping ability, or just because of  
314 chance (17). There is thus some disagreement about the circumstances under  
315 which evasive aposematism and mimicry might occur and the extent to which its  
316 evolution might be different from that of aposematism and mimicry based on  
317 distastefulness (6).

318 In our experiments, in contrast to expectations (17), birds learned to avoid  
319 evasive prey faster than distasteful prey, and learning seemed to be easier as a  
320 higher proportion of birds achieved the learning criterion with evasive prey (94%)  
321 compared to distasteful prey (63%). The close spatio-temporal association  
322 between the unrewarding experience (loss of prey) and the received signal could  
323 help predators to learn faster about evasiveness, which might not always be the  
324 case for distasteful prey (e.g., delayed emetic effect when ingesting a toxic prey,  
325 (49)). There is also the possibility of significant variation in distastefulness even  
326 within the population of a single mimicry ring as a result of differences in larval  
327 host plants and access to adult resources (50,51), or intra and interspecific  
328 variation in a predator's tolerance to distastefulness (49,52–55). Therefore,  
329 signals associated with prey evasiveness may actually provide a more reliable

330 message to birds about unprofitability than does aposematic signalling related to  
331 toxicity.

332 Another potential explanation for faster learning is that the decision to attack  
333 presumably reflects a trade-off between costs and benefits. All toxic prey also  
334 contain nutrients (56) and many birds handle such prey by removing the most  
335 toxic body parts (57) or simply make a strategic decision to eat a certain amount  
336 of toxin to simultaneously acquire nutrients (58). When a bird predator is hungry,  
337 the cost of eating something distasteful might be lower than the benefits of  
338 achieving their nutritional needs from a defended prey (59), and the cost of  
339 pursuing a prey that is impossible to catch will be increased. In other words,  
340 hungry birds may prefer to pursue a somewhat distasteful prey providing at least  
341 limited nutrients rather than an evasive prey providing no nutrients.

342 We also observed dissimilar generalisation patterns between evasive and  
343 distasteful treatments, suggesting wider generalisation among colour morphs  
344 when the prey defence is evasiveness. Groups 2 (evasive treatment) and 3  
345 (distasteful treatment) had the same model (orange/white transverse band). In  
346 group 2 (evasive treatment), in two out of three best scenarios birds generalised  
347 to some extent their learned avoidance toward the prey sharing any wing colour  
348 with the model, and both imperfect mimics were attacked less than the control.  
349 By contrast, in group 3 (distasteful treatment), birds only avoided the orange  
350 imperfect mimic, as the white imperfect mimic was highly attacked, despite the  
351 fact that the white colour was also present in the model. It has been suggested  
352 that selection for accurate mimicry can be affected by different factors (6) such  
353 as level of prey distastefulness or unpleasantness (56,57). Broad generalisation



354 to imperfect mimics was observed in previous studies when the model was highly  
355 distasteful or unpleasant (see in (60)). Our results, along with those showing  
356 faster avoidance learning with evasive prey, suggest that evasiveness is another  
357 powerful dimension of defence that affects a predator's decision whether to attack  
358 warningly coloured prey. More experiments with different types of predators and  
359 signals are nevertheless needed to examine whether generalisation tends to be  
360 broader across mimics where the model is defended by evasiveness rather than  
361 distastefulness or toxicity.

## 362 **CONCLUSION**

363 Although distastefulness has been considered as a prime adaptive defence  
364 mechanism against predation in aposematic butterflies, evasiveness is also likely  
365 to be important in a number of other groups. Our results give a strong  
366 experimental support for the hypothesis, previously mostly based on field  
367 observations, that predators can learn and generalise naturally occurring colour  
368 pattern signals that are associated with the escaping ability of prey. We therefore  
369 argue that evasive mimicry is a plausible explanation for colour pattern  
370 convergence in fast moving prey, such as the *Adelpha* butterflies that are the  
371 subject of this study.

372 **Ethics.** The Southwest Finland Centre for Economic Development, Transport  
373 and Environment (VARELY/294/2015) and National Animal Experimental Board  
374 (ESAVI/9114/04.10.07/2014) provided permission to capture and keep wild blue  
375 tits (*Cyanistes caeruleus*) in captivity and to use them in behavioural studies.

## 376 **Data accessibility**

377 **Author's contribution.** JM, KRW, ME and PMM conceived the project. JM, EPV,  
378 JV, designed the experimental setup, with input from KRW and ME. EPV, JV,  
379 PMM and JM ran the experiments. EPV, JV and ME performed statistical  
380 analyses. All authors discussed the protocol and results throughout the study.  
381 EPV wrote the paper with contributions from all authors. All authors gave final  
382 approval for publication and agree to be held accountable for the work performed  
383 therein.

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402 **Footnotes.** Electronic supplementary material is available online at

403

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