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

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20 **ABSTRACT**

21 Most research on aposematism has focused on chemically defended prey but

22 signalling difficulty of capture remains poorly explored. Similar to classical

23 Batesian and Müllerian mimicry related to distastefulness, such "evasive

24 aposematism" may also lead to convergence in warning colours, known as

25 evasive mimicry. A prime candidate group for evasive mimicry are *Adelpha*

26 butterflies, which are agile insects and show remarkable colour pattern

convergence. We tested the ability of naïve blue tits to learn to avoid and generalise *Adelpha* wing patterns associated with difficulty of capture, and compared their response to that of birds that learned to associate the same wing patterns with distastefulness. Birds learned to avoid all wing patterns tested, and generalised their aversion to other prey to some extent, but learning was faster with evasive prey compared to distasteful prey. Our results on generalisation agree with longstanding observations of striking convergence in wing colour patterns among *Adelpha* species since, in our experiments, perfect mimics of evasive and distasteful models were always protected during generalisation and suffered the lowest attack rate. Moreover, generalisation on evasive prey was broader compared to that on distasteful prey. Our results suggest that being hard to catch may deter predators at least as effectively as distastefulness. This study provides empirical evidence for evasive mimicry, a potentially widespread but poorly understood form of morphological convergence driven by predator selection.

KEYWORDS

Adelpha - evasive aposematism - predator learning - distastefulness – convergence - prey defence

BACKGROUND

Many organisms with chemical, morphological or behavioural defences often display a conspicuous signal, such as a colour pattern, that warns predators of the potential cost of attacks [1]. Possession of such warning signals is known as aposematism [1,2]. In many cases, the effectiveness of aposematism in terms of

prey avoidance depends on the ability of predators to associate the signal with an unpleasant experience (i.e. learning and lasting memory), and to attribute signal properties to different prey individuals (i.e. generalisation, reviewed in [3]; [4–6]). Aposematic prey are under positive frequency-dependent selection, which can result in convergence of warning signals among co-occurring defended species, known as Müllerian mimicry [7]. Aposematism and Müllerian mimicry associated with distastefulness have been extensively studied in many taxa [8–11], and especially so in Lepidoptera [12–16]. However, there is increasing evidence that aposematism may also be associated with an alternative defence, namely evasiveness ([17,18]; reviewed in [19]). Theoretically, predators should avoid attacking evasive prey since unsuccessful attacks likely represent a significant cost in time and energy [19–21], similar to that described for prey that signal long handling times [22]. Selection exerted by predators is thus expected to drive convergence in signals that they associate with the evasiveness of their prey [18,23–27], in a process known as escape mimicry or evasive mimicry (hereafter we use the latter term).

Previous experiments have shown that bird predators can use visual cues to identify evasive prey [28–30], but more empirical work is needed to test whether outstanding potential examples of evasive mimicry could indeed be the result of selection for such signals related to evasiveness. One such example is the diverse Neotropical butterfly genus *Adelpha*, where repeated convergence of their apparently conspicuous and contrasting wing patterns among distantly related sympatric species has been interpreted as evidence for mimicry [31–33]. Putative aposematic displays occur in *Adelpha* butterflies when they are at rest (not perching) with the wings open, and during flight as well, which involves short

bursts of wing beats and longer periods of gliding i.e., with the wings open and horizontal).

Mimicry in *Adelpha* has been hypothesized to be at least partly driven by chemical defences in some species [34–36], but there is currently limited, conflicting evidence for distastefulness [25,35,37,38]. In contrast to most classic groups of chemically defended butterflies, *Adelpha* butterflies have short and stout thoraxes which are favourable traits for strong flight [37,39], and exhibit an irregular flight with sharp turns and powered dives when pursued by avian predators (K.W., personal observations, [21]), making the genus a prime candidate for evasive mimicry [40]. Moreover, species resembling *Adelpha* exist in distantly related lineages (e.g., females from the genus *Doxocopa*, belonging to a different subfamily [21,31]), whereas closely related, allopatric *Adelpha* species may harbour different wing colour patterns, suggesting convergence rather than inheritance from a shared ancestor [32,33,41].

In this study, we use artificial prey models based on common *Adelpha* wing patterns and wild blue tits as naïve bird predators to address the following questions: 1. Can birds learn to associate wing colours and patterns with evasiveness of prey? 2. Can such a signal be generalised across putative mimetic species? 3. What type of defence drives faster learning by predators, evasiveness or distastefulness?

MATERIALS AND METHODS

We used wild blue tits (*Cyanistes caeruleus*) to examine whether birds learn to avoid *Adelpha* colour patterns associated with evasive (escaping) behaviour, and whether birds generalise the learned avoidance across similar, naturally

occurring wing patterns. In addition, we conducted parallel experiments with distasteful prey having the same colour pattern but not evasiveness. European blue tits were chosen as predators because: 1) they have no previous experience with wing colour patterns displayed by Neotropical *Adelpha* butterflies, 2) they have been used extensively in learning experiments as naïve (and experienced) predators with various types of prey [4,42–44], 3) they are visual foragers and their visual capabilities are well understood [45,46], and 4) they eagerly catch both stationary prey as well as moving prey (e.g., flying butterflies, JM personal observations). Potential unwanted behaviours of naïve predators (e.g., startling, fleeing prey sooner or no motivation to attack) were controlled first during the pre-training phase in their home aviaries the day before the experiment, and then in the experimental aviaries; an approximate 2–3-hour habituation period was needed until startling, or no motivation to attack disappeared (See electronic supplementary material S1).

Experiments were conducted from January to March 2019 at Konnevesi Research Station in Central Finland, which provided the infrastructure, wildlife research and collection permits, and expertise needed to conduct experiments with wild birds in captivity. Blue tits were captured from feeding sites around the station and were maintained in captivity for a maximum of 10 days. During captivity, they were kept singly in illuminated plywood cages (daily light period of 12 h 30 min) with food and fresh water available *ad libitum.* After experiments, each bird's sex and age were determined, birds were ringed and released into the site of capture. Our sample comprised individuals of both sexes (51 males and 36 females) and was composed mainly by juveniles (65 out of 87), which likely reflects natural variation in the composition of blue tit winter flocks (JM

125 personal observations, see [47]). We performed preliminary generalized linear

126 mixed models (GLMMs) to test the effects of sex and age on learning. We did not

127 find any significant effect of sex on learning (Z=0.55; p value= 0.58; CI= 0.82 –

128 1.42), therefore, we excluded the sex factor from further analyses. Although

129 juveniles tended to learn slightly faster than adults (mean±SD number of attacks

130 until learning criterion is achieved: adults 53.1±21.4; juveniles 49.4±20.7), the

131 effect of age on learning was not significant either (Z=1.906; p value= 0.06; CI

132 0.99 – 1.93), in agreement with studies that have not detected a strong age effect

133 in blue tits' learning of novel prey (e.g., [48]). We therefore also excluded the age

134 factor from further analyses.

135 *Artificial prey*

136 Artificial defended prey (4.1 x 2.5 cm) were constructed by printing images (HP

137 Color Laserjet CP2025, regular printer paper) of different wing colour patterns

138 displayed by the species *Adelpha salmoneus* (orange forewing band), *A. cocala*

139 (orange and white transverse band), and *A. epione* (white forewing band; figure

140 1). These species represent three putatively distinct mimicry rings [31,33] and

141 were chosen because they differ in colour and pattern. We used these to test if

142 apparently distinct signals may provide protection from predation in evasive

143 mimicry. An entirely dark brown model of a non-defended prey was constructed

144 as a control. To make prey attractive for birds, a piece of almond (reward) was

145 glued to the underside of prey. For distasteful models (see below), almonds were

146 soaked in chloroquine phosphate solution (7%) to give them a bitter taste

147 (following e.g., [49]).

148 *Experimental procedures*

149   The experiments took place in experimental aviaries of 49 x 48 x 67 cm. To mimic

150   daylight conditions, aviaries were illuminated with a TRUE-LIGHT Daylight 6000

151   20W (960 lm) fluorescent light bulbs (these lamps do not emit enough amount of

152   UV to be reflected by our paper models). Each aviary contained a perch and a

153   water bowl. Birds were observed through a one-way glass situated on the front

154   of the aviary. Two plastic prey holders gliding on aluminium profile rails (fixed on

155   both sides of the aviary's floor) allowed simulation of the artificial prey's escaping

156   (see electronic supplementary material, S1-figure 2 and a video is available in

157   S4).

158   *Avoidance learning*

159   We used 87 birds, trained to attack artificial butterflies (see the electronic

160   supplementary material, S1 for details of the training procedure), divided into 3

161   treatment groups (figure 1). The first two groups were trained to avoid evasive

162   prey and a third group was trained to avoid distasteful prey with the same wing

163   colour pattern as group 2. Before initiating the experiment, birds were habituated

164   to the experimental aviary for at least an hour. In the treatment group where birds

165   were trained to avoid escaping prey, the learning experiments consisted of

166   presenting simultaneously two prey items to the bird, one control and one

167   displaying an *Adelpha* wing colour pattern. Birds had one opportunity of attack

168   per trial. If they approached the control prey, they were allowed to capture and

169   eat the almond of that prey; if they approached the evasive prey, it was rapidly

170   pulled out of reach (i.e., escaping) when the bird was less than 5 cm from the

171   prey and displaying a clear intention to attack (see electronic supplementary

172   material S1 and video S4). In the treatment group where birds were trained to

173   avoid distasteful prey they were allowed to consume the attacked prey (i.e.,

174 distasteful prey and control prey). Training presentations continued for at

175 maximum 80 trials or until the bird attacked an evasive or distasteful prey no more

176 than twice over ten consecutive trials. This learning criterion was important for

177 two reasons: 1) it allowed us to test if some treatments were associated with a

178 faster learning than others; and 2) it ensured that all birds, i.e., "quick" and "slow"

179 learners, reached the same level of knowledge despite encountering different

180 numbers of preys ("quick" learners encountered fewer preys than "slow" learners)

181 which is important for generalisation.

182 Birds that finished the experiment earlier and were able to continue with the

183 generalisation experiment the same day received a break of at least 2 hours with

184 3 sunflower seeds offered every 30 minutes before starting the next experiment.

185 Otherwise, those birds that finished the experiment late in the afternoon were

186 placed back in their home cages and continued with the generalisation

187 experiment the next day. Birds that finished the experiment but did not achieve

188 the learning criterion were not included in the generalisation test.

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

190 We used only birds that achieved the learning criterion in the previous phase

191 (group 1 n=23 out of 28, group 2 n=25 out of 31, group 3 n=18 out of 28) to test

192 whether and to what extent the previously learned avoidance of warning

193 colouration associated with evasiveness (group 1 and 2) or distastefulness

194 (group 3) can be remembered and generalised to novel wing colour patterns that

195 shared similar features (i.e., either colour or pattern, figure 1). Those novel colour

196 patterns are referred to as imperfect mimics. This phase consisted of a single trial

197 where birds encountered simultaneously four types of prey: a (i) control prey, (ii)

198   the model they have previously learned (which can be regarded as a perfect

199   mimic) and (iii) two imperfect mimics (figure 1). The experiment was finished after

200   the first choice of attack was registered (see electronic supplementary material,

201   S1 for detailed description).

202   Before starting the experiment, each bird received, on average, a 15-minute

203   habituation period to the new mechanism for presenting prey (see electronic

204   supplemental material, S1 for details), during which three pre-training prey with

205   one sunflower seed were offered. When the three pre-training prey and the

206   sunflower seeds were consumed, the bird was considered ready to start the test.
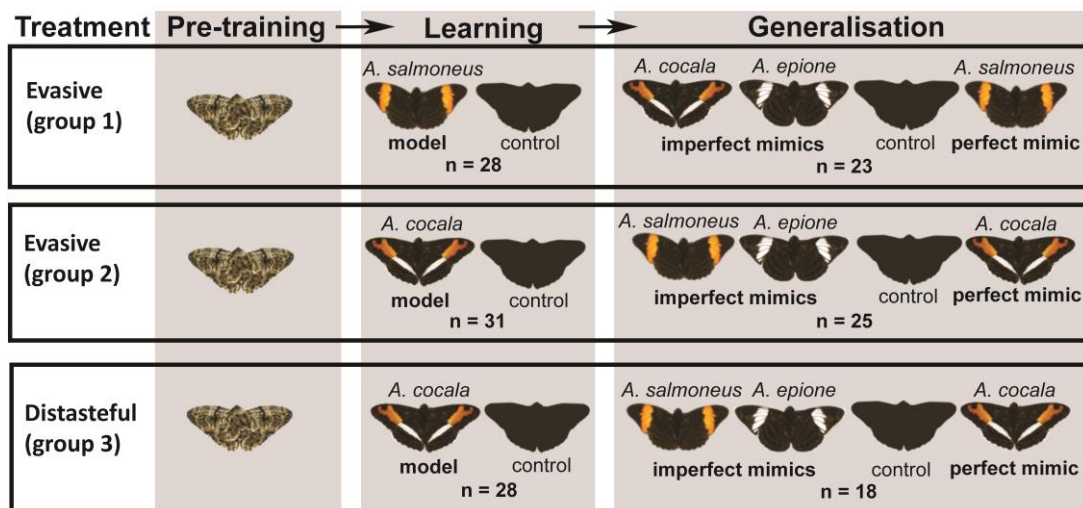
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208   **Figure 1.** Schematic illustration of the experimental design that consisted of 3 phases: pre-
209   training, learning and generalisation. A forewing orange-banded prey (A. *salmoneus*) was
210   presented as a model and perfect mimic for group 1, and as an imperfect mimic during
211   generalisation for group 2 and 3. A transverse forewing orange/hindwing white-banded prey
212   (A. *cocala*) was the model and perfect mimic for group 2 and 3, and an imperfect mimic during
213   generalisation for group 1. The forewing white-banded prey (A. *epione*) was presented as an
214   imperfect mimic during generalisation for all groups.

215   ***Statistical analyses***

216   *Avoidance learning*

217   We examined whether wing colour pattern affected learning of birds from group

218   1 (n=28) and group 2 (n=31) by assessing the probability of prey survival within

219   trials. Learning curves and their confidence intervals (figure 2A) were estimated

220   as a function of the interaction between treatments (i.e., groups) and trial

221   ("*ggeffects*" package version 4.0.3 in RStudio). We performed a generalized

222   linear mixed model (GLMM) ("*lme4*" package v.1.1.23 in RStudio version v.4.0.2)

223   with a logit link function and binomial distribution. Survival probability of prey

224   within trial was explained by the wing colour pattern (explanatory variable). To

225   account for repeated measurements, bird ID nested within trial was added as

226   random factor. Additionally, we calculated the odds ratio (OR) based on GLMM

227   estimates and its confidence interval (CI) to assess the strength of the effect of

228   different wing patterns.

229   *Comparison of avoidance learning between evasive and distasteful prey*

230   To compare avoidance learning among birds facing aposematic prey signalling

231   for evasiveness and birds facing aposematic prey signalling for distastefulness

232   with the same colour pattern (group 2 and 3, respectively; figure 1), we performed

233   another GLMM following the method above. Survival of prey within trial was

234   explained by the type of prey defence (i.e. evasiveness or distastefulness). Bird

235   ID nested within trial was defined as random factor. Odds ratio based on GLMM

236   estimates and confidence intervals were calculated as well to assess the strength

237   of the effect of type of defence.
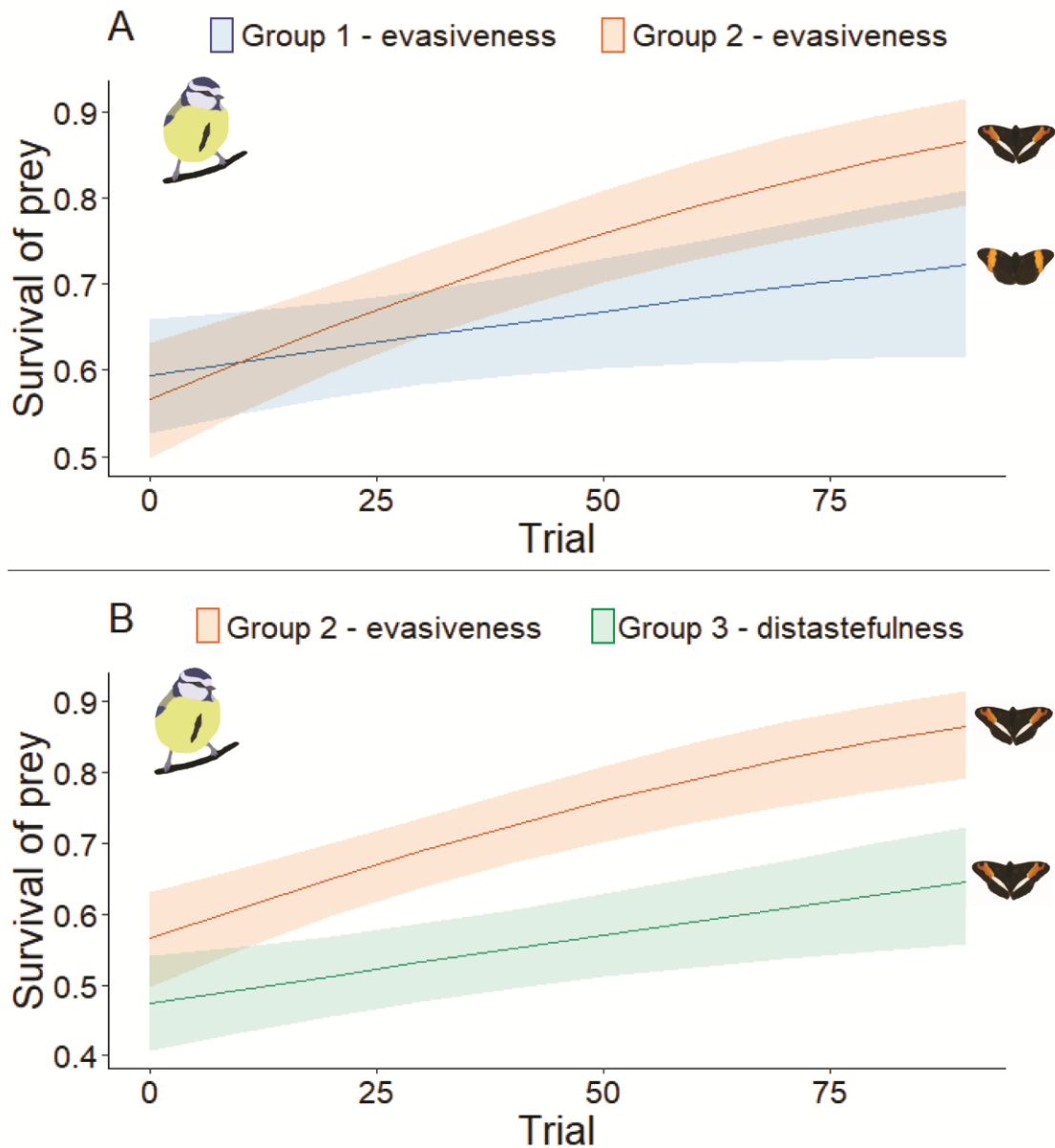
Figure 2. Predicted probability of prey survival among trials. Each curve illustrates predicted values with their 95% confidence intervals (bands) for birds attacks on prey per group and among trials. Each plot shows the comparison between (A) group 1 versus group 2; and (B) group 2 (evasiveness) versus group 3 (distastefulness). The plotted data were derived from the generalized linear mixed models.

Generalisation of learned avoidance to other prey (imperfect mimics)

For each experimental group, to test for differences in attack probabilities between the different types of prey (the control, the model and the two imperfect mimics, figure 1), we calculated the log-likelihood of observing the number of
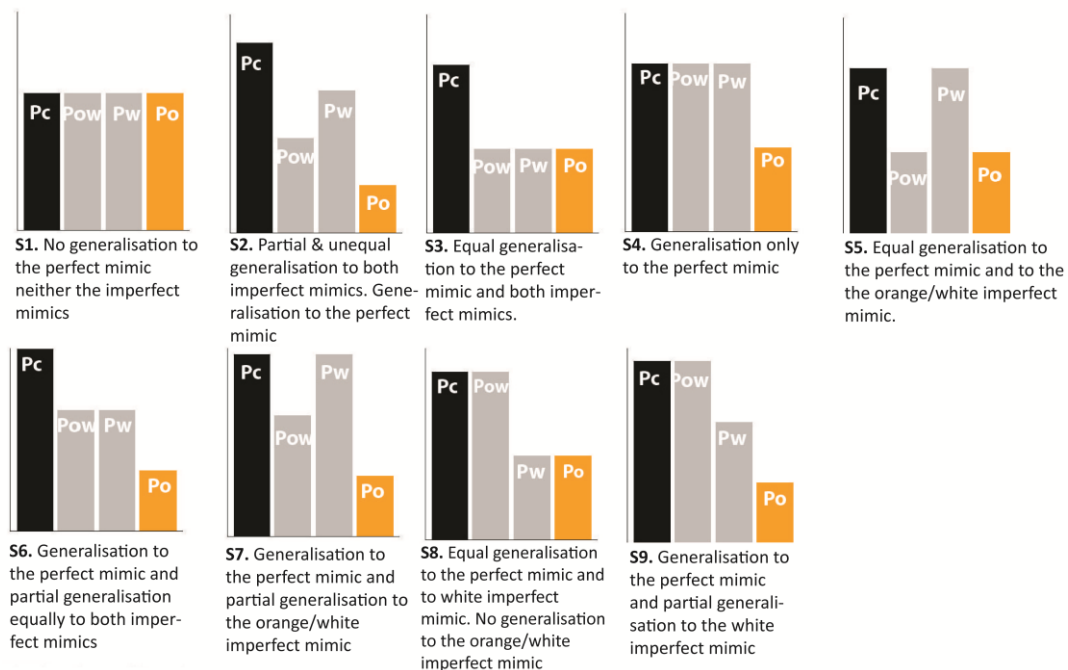
248 attacks that were recorded on each prey type compared to others in the group as

249 follows (calculation details are in electronic supplementary material, S3.1).

250 $$\log_{10}(L) = \Sigma_i[a_i \log_{10}(P_i) + (N - a_i) \log_{10}(1 - P_i)] + K$$

251 Where i is one of the four prey types; N is the total number of trials; a_i is the

252 number of times a butterfly of type i was attacked; P_i is the attack rate of butterflies

253 of type i and K is a constant term that disappears in model comparisons. This

254 maximum-likelihood method has been used in previous studies to estimate

255 differences in probabilities of attack [16] and to investigate mate preference [50].

256 We explored several scenarios where attack rates of different types of prey could

257 be equal or not (see figure 3 and electronic supplementary material S3.2 for a list

258 of all those scenarios) and calculated the log-likelihood functions of those

259 scenarios. As an example, a scenario where the attack rate on the control is equal

260 to those on the imperfect mimics and higher than that on the perfect mimic means

261 that birds only generalises the learned avoidance to the perfect mimic, and not to

262 the imperfect mimics; a scenario where the attack rate on the perfect mimic is

263 equal to those on the imperfect mimics and lower than that on the control means

264 that birds have fully generalised the learned avoidance to the perfect and

265 imperfect mimics; and a scenario where the attack rate on the imperfect mimics

266 is lower than that on the control but higher than that on the perfect mimic means

267 that birds have partially generalised the learned avoidance to the imperfect

268 mimics, compared to the perfect mimic.

269 Models were selected on the basis of their AICc, which accounts for the number

270 of parameters and the sample size. For each group, the model with the lowest

271 AICc was considered the best. We considered that models within a 2-unit AICc

272 interval from the best model could not be rejected.

S1. No generalisation to the perfect mimic neither the imperfect mimics

S2. Partial & unequal generalisation to both imperfect mimics. Generalisation to the perfect mimic

S3. Equal generalisation to the perfect mimic and both imperfect mimics.

S4. Generalisation only to the perfect mimic

S5. Equal generalisation to the perfect mimic and to the the orange/white imperfect mimic.

S6. Generalisation to the perfect mimic and partial generalisation equally to both imperfect mimics

S7. Generalisation to the perfect mimic and partial generalisation to the orange/white imperfect mimic

S8. Equal generalisation to the perfect mimic and to white imperfect mimic. No generalisation to the orange/white imperfect mimic

S9. Generalisation to the perfect mimic and partial generalisation to the white imperfect mimic

Here we present the case of group 1 where the model learned (and the perfect mimic) in the previous phase was the orange forewing band pattern *Po*. Bars illustrate the probability of attack of the control prey *Pc* (black coloured bar), imperfect mimics (grey coloured bars) such as the orange/white transverse band pattern *Pow* for group 1 or orange forewing band pattern *Po* for group 2 and group 3; and the white forewing band pattern *Pw* for all groups. For groups 2 and 3, the model (and the perfect mimic [orange coloured bar]) *Pow* is the orange/white transverse band pattern.

274 **Figure 3.** Scenarios investigated based on attack rates from the generalisation experiment
275 (group 1 is used as an example).

276

277 **RESULTS**

278 *Avoidance learning*

279 According to the learning criterion, most birds learned to avoid their evasive prey

280 model: 23 out of 28 birds from group 1 (i.e., orange forewing band) and 29 out of

281 31 birds from group 2 (i.e., orange/white transverse band). Additionally, 18 out of

282 28 birds (group 3) learned to avoid the distasteful prey model.

283 The generalized linear mixed model detected no significant effect of treatments

284 on predicted survival probabilities within trials (Z=0.01; P=0.992) (OR=1.002; CI

285 0.736 – 1.362) for group 1 and group 2, i.e., birds that learned to avoid different

286 wing patterns of evasive prey. For group 2 and 3, (birds that learned to avoid

287 evasive or distasteful prey that harboured the same pattern) a significant effect

288 of treatment on predicted survival probabilities within trials was detected (Z=3.60;

289 P=0.0003). Birds were 1.6 times more likely to attack distasteful prey than

290 evasive prey (OR=1.640; CI=1.248 – 2.159) (figure 2B).

291 *Generalisation of learned avoidance to other prey (perfect and imperfect mimics)*

292 Bird attack frequencies on mimics differed within and among groups (figure 4,

293 electronic supplementary material S2). For group 1 (prey with orange forewing

294 band as evasive model, figure 4A, table 1), in the best scenario (s5) learned

295 avoidance was fully generalised to the imperfect mimic that shared the orange

296 colour with the model (orange/white transverse band), while the other imperfect

297 mimic (white forewing band, which shares the pattern but no colour with the

298 model) was attacked as much as the control. Two additional scenarios could be

299 considered as similarly plausible based on their AICc. One scenario (s7) was

300 similar to the previous, except that the orange/white imperfect mimic was

301 attacked more often than the perfect mimic (but still less than the control),

302 indicating partial generalisation. In the other scenario (s4), only the perfect mimic

303 was attacked less than the control, implying generalisation only to the perfect

304 mimic.

305 Regarding group 2, (orange/white as evasive model) (figure 4B, table 1), in the

306 best scenario (s3) avoidance was fully generalised to both imperfect mimics,

307 which both shared a colour with the model. Another scenario (s6), where

308 generalisation to the mimics was partial, was within a 2-unit AICc interval with

309 that of the best scenario. In group 3 (orange/white as distasteful model) (figure

310 4C, table 1), a single scenario stood out as best, in which avoidance was fully

311 generalised to the orange imperfect mimic (s5). See results from all the explored

312 scenarios in electronic supplementary material S3.3.

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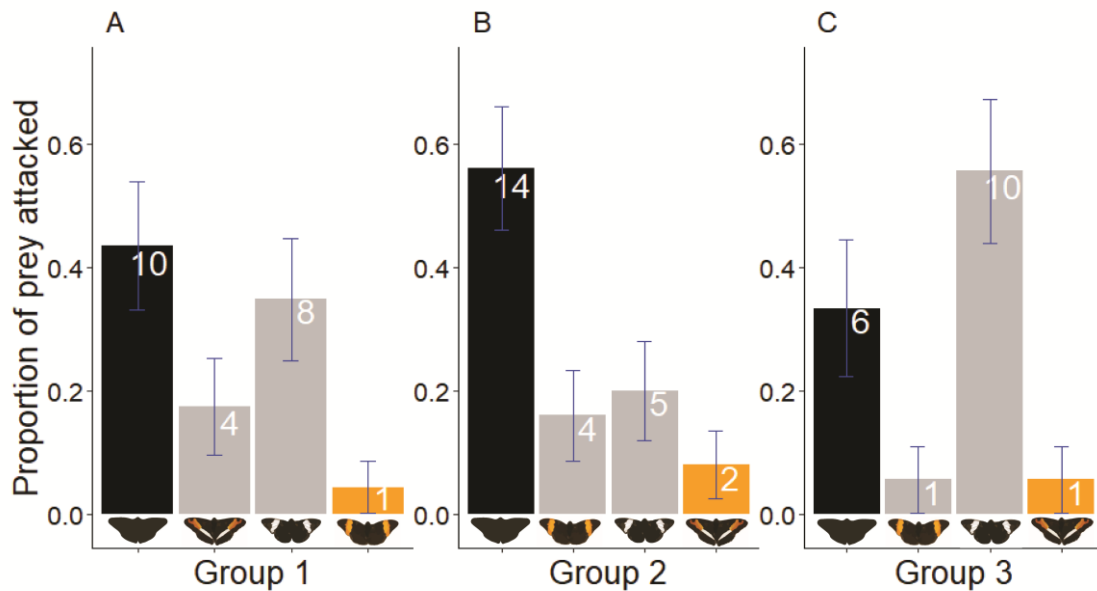
Figure 4. Comparison among observed attack rates during generalisation tests. Bars illustrate proportion of attacks within groups on the control (black coloured bar), different putative mimics (grey coloured bars) and the perfect mimic (orange coloured bar) after birds learned to avoid the model pattern. Number of attacks are indicated inside the bars (at the top of the bars), as well as standard error bars. Birds from group 1 (A) learned evasive orange prey as the model; group 2 (B) learned orange/white as the model; and group 3 (C) learned distasteful orange/white as the model.

321 **Table 1**. Best scenarios from generalisation based on the AICc value. Scenarios within a 2-unit AICc interval with that of the best scenario are considered

322 plausible as well.

group	best scenario	alternative scenarios	
(1) orange as evasive model	**s5 [$P_c=P_w\neq P_o=P_{ow}$]** Equal generalisation to the perfect mimic and to the orange/white imperfect mimic	**s4 [$P_o\neq P_c=P_{ow}=P_w$]** Generalisation only to the perfect mimic	**s7 [$P_c=P_w\neq P_o\neq P_{ow}$]** Generalisation to the perfect mimic and partial generalisation to the orange/white imperfect mimic
ln(L) - K	-20.239	-20.545	-19.773
AICc	**45.079**	45.690	46.809
(2) orange/white as the evasive model	**s3 [Pc≠Pow=Po=Pw]** Equal generalisation to the perfect mimic and both imperfect mimics	**s6 [$P_c\neq P_{ow}\neq P_o=P_w$]** Generalisation to the perfect mimic and partial generalisation equally to both imperfect mimics	
ln(L) - K	-21.026	-20.710	
AICc	**46.598**	48.563	
(3) orange/white as the distasteful model	**S5 [$P_c=P_w\neq P_o=P_{ow}$]** Equal generalisation to the perfect mimic and to the orange imperfect mimic		
ln(L) - K	-14.095		
AICc	**32.990**		

323

DISCUSSION

Learning and generalisation of signals associated with an effective escaping ability

The idea that some butterflies have evolved signalling of evasiveness as an anti-predator defence has a long history [21,24,51–53]. Still, surprisingly few experiments to date have tested the idea of evasive mimicry [25,28–30]. It is therefore unclear whether predators can learn, memorize and generalise naturally occurring signals associated with evasiveness, which is crucial for the evolution of evasive mimicry. Gibson [28,29] and Hancox & Allen [30] presented wild avian predators with artificial prey (i.e. dyed millet seeds, coloured mealworms or pastry models) that disappeared from sight when attacked. After extensive training (approx. 20 days), they observed that birds reduced their attacks on such hard-to-catch prey. We showed that wild birds, with no experience of *Adelpha* butterflies, were able to associate both orange and orange/white patterns with evasiveness within a day of training. Unlike previous experiments [28–30], our birds faced a "simpler" prey scenario [49], with a warningly coloured prey that could be easily discriminated from the non-defended prey, which may explain the reported faster avoidance learning compared to previous studies. In our experiment, birds were more likely to attack the control prey than the aposematic prey in the first trial of the learning phase. This is not surprising since wild birds often avoid colourful prey [54] and part of this bias seems to have a genetic basis [55]. However, our data provide evidence for additional learning on the top of this initial preference since our learning criterion (no more than two attacks in ten consecutive trials) implies that birds that fulfilled this criterion were at least four times more likely to attack control over aposematic

349 butterflies, which is much more than the initial bias (see electronic supplementary

350 material S5).

351 Our results showed that birds were often able to generalise their learned

352 avoidance to somewhat similar prey that shared either a colour or the pattern with

353 the learned model. Perfect mimics were always strongly avoided but often at a

354 level that could not be distinguished from those of the imperfect mimics. Previous

355 work on distasteful prey found that learning and generalisation of aposematic

356 visual signals by avian predators are primarily driven by colour rather than pattern

357 [43,56–59] and wing shape [60]. Our findings are consistent with these studies

358 for group 2 and partially for group 3 because birds generalised their avoidance to

359 prey that presented a colour in common with the formerly learned model (orange

360 imperfect mimic and white imperfect mimic for group 2; only to orange imperfect

361 mimic for group 3), despite harbouring different wing patterns. Generalisation to

362 imperfect mimics is supported with prey models from groups 2 and 3

363 (generalisation to only one imperfect mimic in the latter case). Generalisation to

364 imperfect mimics was unclear for group 1 as results were mixed, possibly due to

365 relatively low sample size and reduced statistical power. The different plausible

366 scenarios for group 1 showed that avoidance was always generalised to the

367 perfect mimic, was never generalised to the white imperfect mimic, and was

368 sometimes generalised to the orange/white imperfect mimic, depending on the

369 scenario. Overall, we showed that birds generalised their learnt association to

370 evasive preys, although the cues used in generalisation remain unclear. Further

371 experiments comparing models with different colours could shed light on whether

372 some colours are better learned and/or generalised than others. The three

373 *Adelpha* species we studied are not regarded as strongly co-mimetic, since a

374 number of other species show much more similar (practically identical) colour

375 patterns, concordant geographic variation and broader sympatry [31]. Preliminary

376 trials from a pilot test suggested that our predators were incapable of

377 distinguishing among the most closely resembling co-mimics of *Adelpha cocala*

378 (e.g., *Adelpha thesprotia*, see electronic supplementary material S1-figure 4), so

379 we expanded our experiment to include more dissimilar species to examine the

380 significance of mimetic accuracy. Our mixed generalisation results do not allow

381 us to assess the extent of selection on mimetic fidelity in *Adelpha*. However, we

382 show that perfect mimicry is at least as good as imperfect mimicry when providing

383 protection to co-mimics since the model (perfect mimic) was always less attacked

384 than the other mimics, although not always significantly so. Future work might

385 include other aspects such as prey community structure, or the predator's level

386 of hunger, that might affect prey mimetic fidelity, as has been studied in classical

387 aposematism based on chemically defended prey [49,61–63].

388 In the case of *Adelpha*, it would be especially insightful to assess avoidance

389 learning associated with evasiveness in the wild by their natural predators.

390 Neotropical passerine birds tend to live longer than higher-latitude birds [64],

391 which potentially means that they can learn more effectively and pay attention to

392 finer signal details, and thus generalise less broadly to other similar prey. It is

393 also important to keep in mind that not only the community structure of predators

394 (see e.g., [65]), but also prey communities influence the outcome of avoidance

395 learning and generalisation of distasteful prey [49].

396 ***Evasiveness versus distastefulness as deterrents to predators***

397 Learning about distastefulness is thought to be generally quicker and easier than

398 evasiveness because prey unprofitability can be determined, unambiguously,

399 from a single experience when prey is ingested. By contrast, a prey individual

400 might escape capture because of better escaping ability, or just because of

401 chance [19]. There is thus some disagreement about the circumstances under

402 which evasive aposematism and mimicry might occur and the extent to which its

403 evolution might be different from that of aposematism and mimicry based on

404 distastefulness [6].

405 In our experiments, in contrast to expectations [19], birds learned to avoid evasive

406 prey faster than distasteful prey, and learning seemed to be easier as a higher

407 proportion of birds achieved the learning criterion with evasive prey (94%)

408 compared to distasteful prey (63%). It is well known that distastefulness of

409 aposematic prey widely varies within and between populations [66,67], and that

410 there is intra- and interspecific variation in predator's tolerance to distastefulness

411 [63,68–71]. Signals associated with prey evasiveness may actually provide a

412 more reliable message to birds about unprofitability than does aposematic

413 signalling related to distastefulness. Moreover, catching a prey, even if

414 distasteful, can be more rewarding for a predator than missing a prey completely.

415 It is thus possible that the learning curve for avoiding evasive prey also depends

416 on the physiological needs of a predator (e.g. its hungriness), the costs of

417 pursuing and consuming a prey (i.e., the likelihood to catch, toxicity) and the

418 nutritional benefits associated with a consumed prey. Although capturing an

419 evasive butterfly prey might represent a rich source of nutrients compared to a

420 distasteful prey (i.e., larger thoracic muscles that allow a powerful flight), there

421 might also be a palatability spectrum, which likely affects the cost-benefit ratio.

422   Future experiments should simulate different scenarios to assess the importance

423   of nutritional value of evasive versus a non-evasive prey in learning to avoid prey.

424   We also found a wider generalisation to imperfect mimics of the evasive prey

425   when it was compared to that of the distasteful prey (i.e., group 2 versus group

426   3, where blue tits were trained on the same wing colour pattern). In group 2

427   (evasive treatment), in two out of three best scenarios birds generalised to some

428   extent their learned avoidance toward the prey sharing any of the wing colours

429   with the model, and both imperfect mimics were attacked less than the control.

430   By contrast, in group 3 (distasteful treatment), birds only avoided the orange

431   imperfect mimic, as the white imperfect mimic was highly attacked, despite the

432   fact that the white colour was also present in the model. It has been suggested

433   that selection for accurate mimicry can be affected by different factors [6] such

434   as level of prey distastefulness or unpleasantness [72,73]. Although broad

435   generalisation to imperfect mimics probably occurs when the model is highly

436   distasteful or unpleasant (see in [74]), our results suggest that evasiveness is

437   another powerful dimension of defence that affects a predator's decision whether

438   to attack warningly coloured prey. Given that a wider generalisation was

439   supported with some prey models, more experiments with different types of

440   predators and signals are needed to examine whether generalisation tends to be

441   broader across mimics where the model is defended by evasiveness rather than

442   distastefulness or toxicity. In addition, a follow-up study to assess the

443   memorability of naturally occurring signals of evasive prey (see [75]) and

444   compare it to that associated to distasteful prey would be very insightful.

445   **CONCLUSION**

446 Although distastefulness has been considered a prime adaptive defence

447 mechanism against predation in aposematic butterflies, evasiveness is also likely

448 to be important in many groups. Our results give a strong experimental support

449 for the hypothesis, mostly based on field observations, that predators can learn

450 and generalise to some extent naturally occurring colour pattern signals that are

451 associated with the escaping ability of prey. We therefore suggest that evasive

452 mimicry could be a plausible explanation for colour pattern convergence in fast

453 moving prey, such as *Adelpha* butterflies.

454 **Ethics.** The Southwest Finland Centre for Economic Development, Transport

455 and Environment (VARELY/294/2015) and National Animal Experimental Board

456 (ESAVI/9114/04.10.07/2014) provided permission to capture and keep wild blue

457 tits (*Cyanistes caeruleus*) in captivity and to use them in behavioural studies.

458 **Data accessibility** The dataset and coding necessary to reproduce the results

459 of this study are available in the Dryad Digital Repository

460 (doi:10.5061/dryad.vq83bk3rj).

461 **Author's contribution**. JM, KRW, ME and PMM conceived the project. JM, EPV,

462 JV, designed the experimental setup, with input from KRW and ME. EPV, JV,

463 PMM and JM ran the experiments. EPV, JV and ME performed statistical

464 analyses. All authors discussed the protocol and results throughout the study.

465 EPV wrote the paper with contributions from all authors. All authors gave final

466 approval for publication and agree to be held accountable for the work performed

467 therein.

468 **Competing interests.** We declare we have no competing interests

Footnotes. Electronic supplementary material is available online in Figshare:

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