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1 **Colour alone matters: no predator generalization among morphs of an aposematic moth**

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14

15 Local warning colour polymorphism, frequently observed in aposematic organisms, is
16 evolutionarily puzzling. This is because variation in aposematic signals is expected to be selected
17 against due to predators' difficulties associating several signals with a given unprofitable prey. One
18 possible explanation for the existence of such variation is predator generalization, which occurs
19 when predators learn to avoid one form and consequently avoid other sufficiently similar forms,
20 relaxing selection for monomorphic signals. We tested this hypothesis by exposing the three
21 different colour morphs of the aposematic wood tiger moth, *Arctia plantaginis*, existing in Finland
22 to local wild-caught predators (blue tits, *Cyanistes caeruleus*). We designed artificial moths that
23 varied only in their hindwing coloration (white, yellow and red) keeping other traits (e.g. wing
24 pattern and size) constant. Thus, if the birds transferred their aversion of one morph to the other two
25 we could infer that their visual appearances are sufficiently similar for predator generalization to

26 take place. We found that, surprisingly, birds showed no preference or aversion for any of the three
27 morphs presented. During the avoidance learning trials, birds learned to avoid the red morph
28 considerably faster than the white or yellow morphs, confirming previous findings on the efficacy
29 of red as a warning signal that facilitates predator learning. Birds did not generalize their learned
30 avoidance of one colour morph to the other two morphs, suggesting that they pay more attention to
31 conspicuous wing coloration than other traits. Our results are in accordance with previous findings
32 that coloration plays a key role during avoidance learning and generalization, which has important
33 implications for the evolution of mimicry. We conclude that, in the case of wood tiger moths,
34 predator generalization is unlikely to explain the unexpected coexistence of different morphs.

35

36 **Keywords.**

37 learning, polymorphism, predator generalization, predator–prey interactions, warning signals, wood
38 tiger moth

39

40 Aposematic organisms display warning signals that predators learn to associate with their
41 unprofitability (Poulton, 1890). The survival of such prey is thus highly dependent on a predator's
42 ability to learn, remember and generalize their learned avoidance to other individuals sharing the
43 same warning signal (reviewed in Ruxton, Sherratt, & Speed, 2004). Signal sharing among
44 aposematic prey benefits both the prey and their potential predators: (1) a given individual has a
45 lower risk of predation when more individuals share the same warning signal, and (2) predators
46 benefit from not having to sample as many unprofitable or toxic prey and can more easily
47 remember one and not multiple signals (Ghirlanda & Enquist, 2003; Guilford & Dawkins, 1991;
48 Müller, 1878; Rowland, Ihalainen, Lindström, Mappes, & Speed, 2007; ten Cate & Rowe, 2007).
49 Therefore, local polymorphism in warning coloration is expected to be selected against (Chouteau,

50 Arias & Joron 2016; Endler 1991; Joron & Mallet, 1998; Lindström, Alatalo, Lyttinen, & Mappes,
51 2001; Mallet & Barton, 1989; Mallet & Joron, 1999; but see also Ihalainen, Lindström, & Mappes,
52 2007 who found no evidence for slower avoidance learning of single versus multiple signals).

53 Despite the predicted disadvantages, warning signal polymorphisms are present in several
54 aposematic taxa, such as frogs (Amézquita, Castro, Arias, González, & Esquivel, 2013; Rojas &
55 Endler, 2013), ladybirds (O'Donald & Majerus, 1984; Průchová et al. 2014) and butterflies (Jiggins
56 & McMillan, 1997). In fact, they seem to be more common than expected considering that warning
57 signals are predicted to be under positive frequency-dependent selection (Müller, 1878; Ruxton,
58 Sherratt, & Speed, 2004). One possible explanation for the co-occurrence of several warning signal
59 forms within the same population is predator generalization. This refers to a predator's ability to
60 transfer its learned avoidance of one signal to other signal(s) that share common characteristics
61 (Gamberale-Stille & Tullberg, 1999; Lindström, Alatalo, Mappes, Riipi, & Vertainen et al. 1999b;
62 Guilford & Dawkins, 1991; Mappes & Alatalo 1997). Generalization can be symmetric, meaning
63 that once one colour is learned it is equally possible to transfer the learned aversion to other similar
64 colours, or asymmetric, implying that transferring a learned avoidance from one colour to other(s)
65 depends on the signal salience (Aronsson & Gamberale-Stille, 2008; Exnerová et al., 2006;
66 Gamberale & Tullberg, 1996; Gamberale-Stille & Tullberg, 1999; Ham, Ihalainen, Lindström &
67 Mappes, 2006; Ruxton, Franks, Balogh, & Leimar, 2008; Waldron et al., 2017).

68 Predator learning involves different cognitive processes that establish the association
69 between warning coloration and unprofitability, and aid the memorization of this association once
70 established. This learning process may vary between predators even at intraspecific levels (e.g.
71 Adamová-Ježová et al., 2016; Endler & Mappes, 2004; Exnerová et al., 2010; 2015; Karlíková et
72 al., 2016; Lindström, Alatalo, & Mappes, 1999a; Sherratt & Macdougall, 1995; Skelhorn, Halpin,
73 & Rowe, 2016). Predators may also vary in their ability to cope with defended prey, due for
74 example to dietary conservatism (Marples & Kelly, 1999; Mettke-Hofmann et al., 2002; Webster &

75 Lefebvre, 2000; Turini, Veselý & Fuchs, 2016). Therefore, investigating how predators learn to
76 associate the appearance of prey with the noxious effects of their unprofitability is crucial to
77 understanding how signal variation can be maintained within a population. During the learning
78 process predators acquire information about the nutrient and toxin content of aposematic prey.
79 Thus, individual predators are expected to make different decisions on how to use the information
80 gathered from an encounter with aposematic prey (Exnerová et al., 2003; Exnerová et al., 2007;
81 Halpin, Skelhorn, & Rowe, 2014; Lynn, 2005; Skelhorn et al., 2016; Trimmer et al., 2011), and
82 modify their ingestion of toxic prey according to their toxic burden (Skelhorn & Rowe, 2007).

83 Generalized avoidance should be broad and persist for a relatively long time to offer
84 protection to different warningly coloured prey morphs. On the other hand, naïve predators can also
85 avoid warningly coloured prey due to innate wariness, neophobia or dietary conservatism
86 (Exnerová et al., 2007; Lindström, Alatalo & Mappes, 1999; Marples & Kelly, 1999; Marples &
87 Mappes 2011), which could be further reinforced by the short-term effects of negative experience
88 with other aposematic prey. It has been suggested that multiple modalities of warning signals can
89 help predators discriminate between palatable and unpalatable prey (Siddall & Marples, 2008,
90 Kazemi, Gamberale-Stille & Leimar, 2015). However, generalized avoidance of aposematic prey
91 can also be based on cues of different sensory modalities, such as odour, sound, colour or pattern or
92 combinations of these. Depending on the cognitive processes of predators, they could also associate
93 their negative experience with certain stimuli to any other stimuli encountered simultaneously
94 (Mackintosh, 1975; Pavlov, 1927). These results emphasize the importance of studying how
95 multiple cues and separate signal components influence a predator's decision to attack prey
96 (Kikuchi, Mappes, Sherratt & Valkonen, 2016; Rowe & Halpin, 2013).

97 Here, we tested the hypothesis that the hindwing colour polymorphism of an aposematic
98 moth is enabled by predator generalization, and investigated whether or not that generalization is
99 symmetric. We exposed paper models of the different hindwing colour morphs of the wood tiger

100 moth, *Arctia plantaginis* (formerly known as *Parasemia plantaginis*) to natural predators (blue tits,
101 *Cyanistes caeruleus*), and examined whether, once they learned to avoid one of the colour morphs,
102 they would generalize this aversion to the two unlearned colour morphs, which would allow
103 multiple morphs to coexist. A lack of generalization among colour morphs would mean that birds
104 pay more attention to colours than to other cues of the moth wings.

105

106 <H1>METHODS

107 The wood tiger moth (Rönkä, Mappes, Kaila, & Wahlberg, 2016) is an aposematic diurnal moth
108 with a Holarctic distribution (Hegna, Galarza, & Mappes, 2015). They have two different chemical
109 defences, one of which is secreted from the prothoracic glands. Although the chemical composition
110 is not fully known, these fluids contain two types of methoxypyrazines, which are produced de
111 novo (Burdfield-Steel, Pakkanen, Rojas, Galarza & Mappes 2016) and make them a deterrent to
112 birds. Experiments with bird predators suggest that the fluids of yellow males have a more repulsive
113 odour (Rojas et al. 2017), while those of white males taste worse (Rojas, Burdfield-Steel & Mappes
114 2015). Individuals vary in the degree of melanization and black patterning of the wings, as well as
115 in levels of chemical defence, but the most striking feature of the wood tiger moth is its local
116 hindwing colour polymorphism (Hegna et al., 2015). In Europe, its forewings present a black and
117 white pattern in both males and females, whereas the hindwing colour combined with black pattern
118 differs between the sexes (e.g. Galarza, Nokelainen, Ashrafi, Hegna, & Mappes, 2014; Hegna &
119 Mappes, 2014). The distinct white and yellow male morphs are genetically determined by one
120 autosomal locus and at least three alleles, dominant white, recessive white and intermediate yellow
121 (Galarza, Nokelainen & Mappes 2016), while female hindwing coloration varies continuously from
122 yellow to red (Lindstedt et al. 2017; Fig. 1). In Finland, for example, yellow and white males may
123 occur within one population (Nokelainen, Valkonen, Lindstedt, & Mappes, 2014) whereas female
124 hindwing coloration is mostly red (Hegna et al., 2015).

125 To study the reaction of bird predators (see below for details on procedure) to the different
126 hindwing colour morphs, we used artificial moth models. The usage of artificial prey allows for the
127 controlled manipulation of one or more warning signal components at a time, while accounting for
128 how predators (i.e. birds) would see them (Endler & Mielke 2005). In this way, other components
129 can be kept constant and independent of prey qualities, such as the variation in the level of chemical
130 defence or behaviour (Karlíková et al., 2016; Lindström et al., 1999a; Veselý & Fuchs 2009). Here,
131 our artificial moth models eliminated individual variation in moth size, shape, degree of
132 melanization, wing pattern, wing posture, behaviour, smell or taste. Model wings were constructed
133 with the software GIMP (2.8.16; <http://www.gimp.org/>) from pictures of a real male wood tiger
134 moth specimen collected in Finland. Pictures of one forewing and one hindwing of a typical white
135 moth were duplicated to obtain a symmetric pattern for the whole model. The melanization pattern
136 of the moths used was a representative sample of a wing pattern in Finland (Fig. 1). To control for
137 the amount and shape of melanized (mainly black) pattern of the wings, yellow and red models
138 were created from the same wing picture, changing the hue of the white parts of the hindwing
139 towards yellow or red. Finished models were printed double sided (HP Color LaserJet CP2025) on
140 waterproof (Rite In The Rain, Tacoma, WA, U.S.A.) paper. To ensure that the model colours
141 resembled the real wood tiger moth morphs, colour reflectance was measured with an Ocean Optics
142 Maya2000 Pro spectrometer and average reflectance curves from three spots in the model hindwing
143 coloration were compared to average reflectance curves of white, yellow and red moth hindwings
144 (Fig. 1). Models were then cut out from the paper and completed with a body made of rolled pastry,
145 composed of two parts of lard, six parts of coarse wheat flour and one part of water to make them
146 edible. The total body weight was 0.04 ± 0.005 g. Bodies were dyed on top with black food
147 colouring, to make models resemble the real moths as accurately as possible. Finally, bodies were
148 glued on the paper models with nontoxic glue (UHU stick).

149

150 <H2>*Bird predators*

151 Blue tits were chosen as predators for several reasons: (1) they are visual foragers and their visual
152 capabilities are well known (Hart, Partridge, Cuthill, & Bennett, 2000; Hart & Vorobyev, 2005),
153 ensuring that they are able to distinguish all of the wood tiger moth's colour morphs; (2) they have
154 been used in several experiments on coloration (e.g. Dimitrova & Merilaita, 2010; Exnerová et al.,
155 2007; Kikuchi et al., 2016) and wood tiger moths (Nokelainen, Hegna, Reudler, Lindstedt, &
156 Mappes, 2012), and also with similar moth models (Rojas, Burdfield-Steel & Mappes 2015); (3) tits
157 are likely to be important natural predators of wood tiger moths in Finland (Nokelainen, Valkonen,
158 Lindstedt, & Mappes, 2014); and (4) blue tits are common in central Finland, and easy to capture
159 and keep in captivity for a short period of time.

160 The birds used for the experiment were caught from Konnevesi Research Station and City of
161 Jyväskylä (central Finland), maintained individually in plywood cages with a perch, water bowl and
162 food ad libitum, and kept on a 12:12 h light:dark cycle. Each bird was weighed before and after the
163 experiment, ringed, and its sex and age were determined before being released to the same place of
164 capture. Birds were used with permission from the Central Finland Centre for Economic
165 Development, Transport and Environment and licensed from the National Animal Experiment
166 Board (ESAVI/9114/04.10.07/2014) and the Central Finland Regional Environment Centre
167 (VARELY/294/2015). All experimental birds were used according to the ASAB/ABS Guidelines
168 for the treatment of animals in behavioural research and teaching.

169

170 <H2>*Experimental procedures*

171 The experiment consisted of three phases: a preference test, a learning test and a generalization test
172 (see details below). Each bird was tested individually and only once for each part of the experiment.
173 The experiment was conducted between November 2015 and March 2016 at Konnevesi Research

174 Station, in central Finland and lasted, on average, 3 days for each individual, depending on how
175 long the bird took to complete the different tests.

176 Trials took place in experimental custom-built plywood cages (50x50 cm and 70 cm high)
177 illuminated with a daylight lamp (Exo Terra Repti Glo 10.0 UVB, <http://exo-terra.com/>). Each
178 aviary had a perch and a water bowl (access ad libitum). Birds were observed through a small
179 mesh-covered window situated on the front of the cage, and filmed with a Canon Powershot S120
180 camera. The experiment took place in a dark room to minimize observers disturbing the birds.

181 Food and experimental models were offered on a green platform through a moveable tray
182 behind a visual barrier, allowing us to estimate the exact time when the bird first saw the model and
183 thus started the trial (see details in Nokelainen et al. 2012). A standard green background was used,
184 because wood tiger moths rest on green leaves in nature (Hegna et al. 2013, Nokelainen et al.,
185 2012). All colours used in the moth models are easily distinguished from the background by birds:
186 Hegna et al. (2013) reported just noticeable difference (JND) values in colour contrast ranging from
187 8.6 to 11.6 for white and yellow artificial moth models and real wood tiger moths against the green
188 background used also in this experiment, and Lindstedt et al. (2011) calculated JND values above
189 27.27 for orange and red females on natural green leaves of *Alnus incana*.

190 During pretraining, birds were allowed to habituate to the experimental cages and learned to
191 eat three sunflower seeds from the green platform. To motivate the birds to attack the moth models
192 during the experiment (see below), they were food deprived for 2 h before the preference test, 1 h
193 before the learning test and 1 h before the generalization test. After food deprivation, bird
194 motivation was tested with a sunflower seed; if eaten, the bird was considered ready to begin the
195 test.

196

197 <H3>Phase 1: Preference test

198 A preference test was included in the experimental protocol for two reasons. As we used wild-
199 caught birds, we first tested whether they had any pre-existing biases towards white, yellow or red
200 moth morphs. Second, by offering palatable morphs several times to birds we ensured that any
201 potential unlearned or learned biases disappeared, allowing us to test the effect of the coloration on
202 learning and generalization (Ghirlanda & Enquist, 2003).

203 All three morphs (white, yellow and red) were offered simultaneously on the green platform
204 for 5 min, starting from when the bird first saw them. If the bird did not attack (i.e. grab or peck)
205 any of the edible model pastry bodies during the 5 min, the models were taken away and presented
206 again after a break. Once the first attack was made, the models were kept in the cage until the bird
207 finished eating all the pastry bodies. To ensure that all birds had an equally rewarding experience
208 with all the colours, we let the birds finish eating the pastry bodies of all models in three
209 consecutive trials during the preference test. Between the trials, the presentation (order) of the
210 models on the platform was always changed (Fig. 2).

211 As birds were hesitant to attack the moth models for the first time (hesitation times varying
212 from 17 s to 2 h consisting of 5 min presentations), we did not use time to attack in analyses.
213 Instead, we recorded the order in which the models were attacked and eaten during the three
214 consecutive trials. We compared the order of attacks between the first and the last preference test to
215 be sure that all the birds got rid of any potential bias in preferences before the learning phase.
216 Preference test presentations were continued for a maximum of 2 days. Eight of 53 birds did not
217 attack or finish eating the artificial moth models offered during the preference test and were,
218 therefore, excluded from further tests.

219

220 <H3>Phase 2: Learning test

221 In the second phase of the experiment we tested whether blue tits learn to avoid white, yellow and

222 red models differently, and established learned avoidance towards one of the colour morphs before
223 the following generalization test. Birds that completed the preference test were divided into three
224 groups for avoidance learning: 15 birds were offered white models, 15 yellow models and 16 red
225 models as unpalatable. Groups of birds were selected as similar as possible (i.e. similar sex, age and
226 size distribution) and birds from all groups were tested simultaneously. All models were made
227 unpalatable by replacing the water in pastry bodies with 15% chloroquine diphosphate solution
228 (Sigma Life Science, St Louis, MO, U.S.A.). As the pastry bodies were coloured with black dye on
229 top, we also added 15% chloroquine diphosphate solution on top of the bodies and let it dry before
230 the following trials. Chloroquine solution was used because it is odourless (Hong 1976) and thus all
231 qualities other than palatability (i.e. taste) of the prey items remained the same throughout the
232 experiment.

233 During the learning test, unpalatable models were presented individually in consecutive
234 trials alternating with sunflower seeds (Fig. 2). Sunflower seeds were offered to monitor the birds'
235 motivation to forage and avoid unnecessary starvation. If the bird did not attack the sunflower seed,
236 it got a 10 min break without food and was then offered a sunflower seed again. If the bird attacked
237 the sunflower seed, the next unpalatable model was offered 2 min after the bird finished eating. As
238 long as the bird attacked the models, trials were continued alternating with sunflower seeds. If the
239 bird did not attack the unpalatable model, but ate the sunflower seed, it was considered to reject the
240 model. After a bird did not attack the moth model the second time in a row, a small live mealworm
241 (< 20 mm *Tenebrio molitor* larva) was offered instead of the sunflower seed to test the bird's
242 motivation to attack insect prey and increase its motivation to forage. If the bird now attacked the
243 unpalatable model offered after the mealworm, trials were continued again alternating with
244 sunflower seeds, but if it rejected the unpalatable model, it got another mealworm (Fig. 2). We
245 considered the bird to have learned to avoid the unpalatable models when it refused to attack three
246 models in a row, but consumed the sunflower seeds and mealworms offered in between and after

247 the rejected models.

248 Presentation time was set to 5 min from when the bird first saw the model for the first three
249 trials to make sure that each bird had the opportunity to attack and taste the model. To keep the
250 overall duration of the generalization experiment within the permitted 4-day limit, a maximum of
251 30 presentations divided into 2 days was set for the avoidance learning. Furthermore, we reduced
252 the presentation time to 2 min from the fourth to the sixth trial, and to 1 min for the rest of the trials.
253 Based on our observations during a pilot experiment with six birds and fixed durations of trials,
254 birds were unlikely to attack the model and did not consume it within 5 min if they did not attack
255 within the first minute. Sunflower seeds were usually attacked quickly, and hesitation time declined
256 to a few seconds as the trials proceeded, implying that 1 min was sufficient to test the bird's
257 willingness to attack the models. Two of the 46 birds did not stop attacking (white and red) models
258 within 30 presentations and were therefore excluded from the following generalization test.

259

260 <H3>Phase 3: Generalization test

261 In the third phase, we tested whether the 44 birds that had learned one of the colour morphs as
262 unpalatable would avoid attacking the other two colour morphs. When birds had completed the
263 learning test, half of them had a break of at least 2 h with food and 1 h of food deprivation before
264 the last phase of the experiment, and half were tested the following day. The generalization test
265 started after the bird had consumed a sunflower seed offered to test its motivation to attack. Birds
266 were tested for the generalization with the colours that they did not learn as unpalatable: yellow and
267 red for those that learned white as unpalatable, white and red for those that learned yellow, and
268 white and yellow for those that learned red (Fig. 2). The two colours tested were presented
269 simultaneously on the green platform in alternating positions for three trials lasting 5 min each. This
270 allowed us to test the repeatability of bird behaviour. The trials were interspersed with sunflower
271 seed presentations to make sure that birds were not attacking the models due to lack of motivation.

272 Moreover, offering alternative food ensured that birds were not forced to eat the models simply
273 because of hunger. Models used for the generalization test were palatable.

274

275 <H2>*Statistical analysis*

276 <H3>*Phase 1: Preference test*

277 The potential colour bias of blue tits was analysed separately for the first trial (Fig. 2) and all three
278 trials pooled. Colour biases are most likely to be detected reliably by checking the order of attacks
279 on the white, yellow and red models in the first trial ($N=53$), when the birds first encountered the
280 models. The number of moths of each colour taken first, as well as left last, were compared by
281 means of a chi-square test. Additionally, all three trials were pooled in another analysis to find out
282 whether the potential biases disappeared as the birds learned to eat all the models. In the pooled
283 data, each colour was scored based on the order of choice by the bird in each trial; the colour
284 chosen first was scored 1, that chosen second was scored 2 and the colour chosen last was scored 3.
285 Thereby, the minimum score expected for a preferred colour was 3 (i.e. always chosen first), and
286 the maximum score expected for an avoided colour was 9 (i.e. always chosen last). To study the
287 population level bias to all colours, the scores of each colour in each of the three trials were
288 summed and compared to an even distribution by means of a chi-square test. The potential
289 influence of the first colour chosen on the subsequent choice was checked with a binomial exact
290 test.

291

292 <H3>*Phase 2: Learning test*

293 Potential differences in learning rate between the three colour morphs were analysed using a mixed-
294 effect Cox regression model, using the 'coxme' package (version 2.2-5; Therneau, 2015) in RStudio
295 (v. 0.99.902; RStudio, 2015). The response variable was the probability that the presented model

296 was attacked in each trial; time was represented as number of trials. Model colour was added as an
297 explanatory factor and bird individual as a random effect.

298

299 <H3>Phase 3: Generalization test

300 If birds generalized their learned aversion of a given colour to the two nonlearned colours, we
301 would expect them to refrain from attacking models offered during the generalization test but eat
302 the alternative prey offered between trials. Hence, the probability of attack on palatable models is
303 expected to be significantly lower than random (< 0.5). If, in contrast, birds were unable to
304 generalize their learned avoidance, we would expect the attack probability to be significantly higher
305 than 0.5. High attack probability is expected (in the case of no generalization) since the birds had
306 attacked and eaten similar palatable models in the preference test and did attack the models
307 presented first in the learning test within the 5 min presentation. Thus, to test whether the birds
308 generalized and the attack probability on the models was lower (or higher) than random, we built
309 two generalized linear mixed models (GLMM 1 and 2) with a logit link and binomial distribution,
310 including whether the prey was attacked (1) or not (0) as the dependent variable. Bird ID and bird
311 ID nested within trial in GLMM 2 were added as random factors using package lme4 (Bates et al.
312 2015) in R. GLMM 1 was used to test for generalization in the first trial only, and GLMM 2 in all
313 three trials.

314 To test for asymmetric generalization, we divided the birds into six treatment classes by the
315 colours they learned (white, yellow and red) and were offered (yellow and red, white and red, white
316 and yellow, respectively). This classification was then used as the explanatory variable ('colour
317 combination') in two GLMM models separately for the first trial only (Table A1 in the Appendix)
318 and all three trials (Table A2 in the Appendix) of generalization (again with a logit link and
319 binomial distribution, including whether the prey was attacked (1) or not (0) as the dependent
320 variable, and bird ID nested within trial and/or bird ID as random factors). A chi-square test was

321 used to check whether the birds attacked one colour morph first more frequently between the two
322 colour morphs offered, both in the first trial and in the first three trials pooled (Table A3 in the
323 Appendix). Birds tested the same or the following day after avoidance learning were pooled in all
324 analyses, as there were no differences in the number of attacks between birds tested the same or the
325 following day after avoidance learning in the first trial (unpaired two-sample Wilcoxon test:
326 $W=276$, $N=44$, $P=0.21$) or in the three trials pooled ($W=262$, $N=44$, $P=0.59$). We also checked
327 whether the rate of learning correlated with the number of attacks in the generalization test with a
328 Spearman correlation.

329

330 <H1>RESULTS

331 <H2>Preference test

332 At the population level, birds did not show any preferences (Table 1) or aversion (chi-square test:
333 $\chi^2_2=2.577$, $P=0.28$) towards any of the colours (white, yellow or red) during the first trial. Birds
334 chose the second colour to attack with the same probability between the two colours left,
335 irrespective of the first colour chosen (binomial exact test: $P>0.05$ for all comparisons).

336 At the individual level, 35 birds (85.4%, $N=41$) chose at least one colour in the same order
337 for two different trials (for instance, the same bird chose the yellow morph as last choice in two
338 trials out of three). Two birds showed a strong preference for one of the colour morphs, choosing
339 the same colour (yellow and red, respectively) first for all three trials. Three birds showed
340 avoidance for one colour morph (one for white, two for red), leaving the same colour as last in all
341 the trials. All other birds changed their order of choice during the three trials, showing that they got
342 rid of potential biases towards the colours during training. When we tested the overall scores for
343 each colour morph during the three trials, birds did not show differences between the colour morphs
344 (chi-square test: $\chi^2_2=0.789$, $P=0.67$).

345

346 <H2>*Learning test*

347 Apart from two individuals, all birds ($N=44$) learned to avoid their moth model according to the
348 criterion of no attack over three subsequent trials. The number of trials needed to learn to avoid the
349 unpalatable model varied between 2 and 23 among the birds (mean=7). The Cox regression model
350 (Fig. 3) showed that birds learned to avoid the red colour morph significantly faster than the yellow
351 ($Z=2.17$, $P=0.03$), but showed no significant differences between the yellow and white morphs
352 ($Z=0.87$, $P=0.38$).

353

354 <H2>*Generalization test*

355 Overall, blue tits did not generalize their learned avoidance from one colour morph to the other two,
356 as the attack probabilities were significantly higher than 0.5 in the first trial (GLMM 1: $Z=4.33$,
357 $P<0.001$; Fig. 4) and the three trials pooled (GLMM 2: $Z=6.42$, $P<0.001$). Only three of 44
358 individuals did not attack any of the palatable models during the generalization test, showing
359 generalized avoidance.

360 We did not find clear evidence of asymmetric generalization. The estimated attack
361 probabilities did not differ significantly between the combinations of colour learned and colour
362 offered in generalization trials (Tables A1 and A2 in the Appendix), and no differences were found
363 in which colour the birds attacked first during the first trial of the generalization test (chi-square
364 test: $P>0.05$ in all cases; Table A3 in the Appendix). In the first trial, however, birds that learned
365 yellow attacked fewer white models compared to the other colour combinations, and the effect is
366 near the 0.05 significance level (Table A1 in the Appendix). Also, when the three trials were
367 pooled, we found that birds that learned to avoid the white morph attacked the red morph first
368 significantly more often than the yellow one (chi-square test: $\chi^2_1=5.9$, $P=0.02$).

369 The rate of learning did not correlate significantly with the proportion of attacked models in
370 the first generalization trial (Spearman correlation $r_s=0.12$, $N=44$, $P=0.45$) or the total number of
371 attacks in the three generalization trials (Spearman correlation: $r_s=0.27$, $N=44$, $P=0.07$), thus
372 allowing us to compare the effect of the colour learned on generalization despite different learning
373 rates of red versus the other colours.

374

375 <H1>DISCUSSION

376 <H2>*No generalization based on hindwing colour*

377 Generalized avoidance by local predators from one warning signal to another has been proposed to
378 contribute to the maintenance of local warning signal polymorphism in aposematic species
379 (Amézquita et al., 2013; Exnerová et al., 2006; Gamberale & Tullberg, 1996; Gamberale-Stille &
380 Tullberg, 1999; Ham et al., 2006; Hegna & Mappes, 2014; Rojas, Rautiala, & Mappes, 2014;
381 Ruxton et al., 2008; Waldron et al., 2017). Here we studied in more detail how bird predators learn
382 and generalize the warning colours of a polymorphic (red, yellow, white) wood tiger moth
383 population using artificial moth models. Attack rates during the generalization test were in general
384 very high. Indeed, the birds did not generalize their learned avoidance among the wood tiger moth
385 morphs, but instead treated them as different prey types based on the differing hindwing colour
386 alone, as the morph models used did not differ in size, shape, pattern, taste or smell.

387

388 <H2>*The importance of colour*

389 Our findings are in line with previous experiments showing that colour is of foremost importance in
390 avian predator learning, contributing especially to the discrimination between palatable and
391 unpalatable prey (Aronsson & Gamberale-Stille, 2008, Kazemi, Gamberale-Stille, Tullberg, &
392 Leimar, 2014). A large body of research has demonstrated birds' ability to learn to avoid

393 conspicuous, unpalatable prey (Aronsson & Gamberale-Stille, 2008; Rowe, Lindström, & Lyytinen,
394 2004; Svádová et al., 2009). This is because conspicuous warning coloration enhances prey
395 recognition (Guilford, 1986; Sherratt & Beatty, 2003), speed of avoidance learning and
396 memorability (e.g. Roper & Redston, 1987). Different predators may use different components of
397 the warning signal as a primary cue depending on their sensory systems (Aronsson & Gamberale-
398 Stille, 2012; Endler, 1992; Guilford & Dawkins, 1991) and disregard others. Studies done with
399 birds have demonstrated that colour seems to be a more important feature in warning signals than
400 size or pattern (Aronsson & Gamberale-Stille, 2008; Exnerová et al., 2006; Sillén-Tullberg, 1985;
401 Terhune, 1977).

402 As predators can associate palatability or unpalatability with several different kinds of prey
403 traits, it is convenient to compare the relative importance of those traits with how much they
404 facilitate associative learning. The expectation is that more salient signals are learned faster
405 (Kazemi et al. 2014). Our results indicate that red was the most salient warning colour: birds
406 learned to avoid the red morph faster than the other morphs. This is in accordance with Lindstedt et
407 al. (2011), who found that the red female morph of the wood tiger moth was better protected against
408 bird predators, suffering fewer attacks than its orange or yellow counterparts. Indeed, red has been
409 shown to be a very efficient warning signal compared to other warning colours such as orange,
410 yellow or white, and other colours such as violet, blue, green and brown, at least for some bird
411 predators (Cibulková, Veselý, & Fuchs, 2014; Exnerová et al., 2006; Gamberale-Stille & Tullberg,
412 1999; Lindstedt et al., 2011; Svádová et al., 2009).

413 In the present study prey items were made to resemble real wood tiger moth morphs as
414 closely as possible, keeping all traits other than hindwing colour constant. This allowed us to
415 compare the effects of warning coloration of hindwings only. Changing the warning colour hue
416 altered not only the internal contrast on model hindwings, but also the contrast between the model
417 and the green background. Although all colours in our experiment were clearly conspicuous to the

418 birds, red had the highest colour contrast against the green background whereas white had the
419 lowest. This might explain why red seems to be the most salient signal. Aronsson and Gamberale-
420 Stille (2009) found similar results using domestic chicks, *Gallus gallus domesticus*, which learned
421 to avoid red prey faster if presented on a contrasting background compared to a background of
422 similar hue. In another experiment, however, red prey colour was found to influence predator
423 avoidance independent of background colour (Sillén-Tullberg, 1985). Thus, it seems that both prey
424 coloration per se and its contrast against the background can contribute to predator avoidance, but it
425 is still relatively unclear which properties of prey coloration, chromatic or achromatic, play the
426 most important role. Previous work with wood tiger moths has shown that the achromatic contrast
427 against a green background is highest for white morphs, which are the most luminous of the three
428 (Lindstedt et al. 2011; Henze, Lind, Mappes, Rojas & Kelber 2017). Luminance has not been found
429 to affect predator responses towards the wood tiger moth, while the chromatic contrast in hue seems
430 to be very important (Nokelainen et al., 2012).

431 Generalization has been suggested to stabilize selection towards aposematic signals via a
432 peak shift phenomenon (Leimar, Enquist, & Sillen-Tullberg, 1986; Lindström et al. 1999b). The
433 minimum (and maximum) responses of predators (i.e. peaks of the generalization gradient) have
434 been found to be displaced from the negative (and positive) stimulus (Gamberale & Tullberg, 1996;
435 Hanson, 1959), such as yellow, towards a similar, but more salient novel stimulus, such as red.
436 Overall, we did not find strong evidence of asymmetric generalization, but there were some trends
437 between the colours tested. Birds that learned to avoid red models attacked almost all the white and
438 yellow models in the generalization trials, whereas birds that learned the less salient colours yellow
439 and white generalized more, hinting at a tendency to generalize from the less salient signals towards
440 the more salient signal.

441 Svádová et al. (2009) found asymmetric generalization using great tits, *Parus major*, which
442 did not generalize from red firebugs, *Pyrrhocoris apterus*, to white or yellow mutants, but did

443 generalize from yellow mutants to red firebugs. Interestingly, in our experiment, four blue tits that
444 learned to avoid the yellow morph ($N=15$) refrained from attacking white models, while only two
445 did so for the red ones. Birds that learned to avoid the white morph attacked both unlearned morphs
446 equally, but chose red models first more often than yellow ones. This indicates that birds tended to
447 generalize more between the white and yellow than between white and red. The yellow morph
448 seems to benefit least from the other colours, since only between 7 and 34% of yellow models were
449 left unattacked (Table 2, Fig. 4).

450

451 <H2>Limitations of testing generalization in the laboratory

452 Despite the majority of birds showing no generalization in our experiment, the possibility remains
453 that predators might generalize among morphs of the wood tiger moth under different
454 circumstances. Studying generalization in the wild is practically impossible due to the rareness of
455 predation events on aposematic prey as well as difficulties in observing the choices of individual
456 predators in natural conditions. A previous study aiming to explain the variability in the warning
457 signals of the harlequin poison frog, *Dendrobates histrionicus*, showed that predators avoided
458 attacking aposematic frog models but not cryptic ones in areas where aposematic frogs occur,
459 exhibiting some generalization among different frog colour morphs in the field. However, the same
460 study found no generalization by naïve chicks tested in the laboratory (Amézquita et al., 2013). This
461 might imply that naïve and experienced predators in the wild can use different generalization
462 strategies (see also Ihalainen, Lindström, Mappes & Puolakkainen, 2008). Birds might also be
463 prone to generalize more or less widely under different circumstances (Aronsson & Gamberale-
464 Stille, 2012), for example under physiological stress during winter months (Barnett, Bateson &
465 Rowe 2007; Chatelain et al. 2013; Veselý et al. 2017), limited food availability (Lindström, Alatalo,
466 Lyytinen & Mappes, 2004; Ihalainen, Rowland, Speed, Ruxton, & Mappes, 2012), limited time to
467 make decisions (Ings & Chittka, 2008), when the prey is dangerously toxic (Lindström, Alatalo, &

468 Mappes, 1997; Sherratt, 2002), when the prey community is complex versus simple (Ihalainen et
469 al., 2007), or when the prey population has palatable Batesian mimics in addition to the unprofitable
470 prey (Plowright & Owen, 1980).

471 Avoidance learning has been suggested to happen in two steps: first, the birds learn simple
472 rules based on certain cues, and once the basic rules are formed, they then learn in more detail about
473 prey quality (Chittka & Osorio, 2007). Recent studies indicate that birds are able to assess the
474 nutritional benefits of unprofitable prey and use this information in subsequent encounters (Halpin
475 et al., 2014). This ability could have affected not only bird learning rates, but also their decision to
476 attack in the generalization phase of our experiment. As our models' pastry bodies were of high
477 nutritional value and the birds were hungry, it is possible that the birds were willing to take more
478 risks and thus took more trials to learn to avoid the models than it would take them to learn to avoid
479 defended prey in the wild. In addition, the 5 min presentations gave the birds plenty of time to
480 decide whether to attack or not, and to make more sophisticated assessments of prey quality than
481 might be possible in the wild. Birds were given alternative food between the presentations, but not
482 enough for saturation, and would thus have benefited energetically from discriminating between the
483 unprofitable and profitable models. Nevertheless, the cost–benefit relationship was exactly the same
484 for all morphs in our experiment and, thus, we can safely compare the relative differences between
485 morphs in their salience.

486 The avoidance learning was based on counterconditioning, where the colour signal was first
487 associated with a positive reinforcement (i.e. palatability) and then with a negative reinforcement
488 (i.e. unpalatability). Previous research has shown that in cases of single counterconditioning the
489 associations learned second are forgotten at higher rates than those learned first (Speed, 2000 and
490 references therein). Therefore, it is possible that the birds' experience and learned association with
491 palatability in the preference test exceeded the effect of generalized avoidance among the morphs
492 for most of the birds, which could partly explain the low level of generalization observed. Offering

493 the models as palatable at the beginning of the experiment was necessary to get rid of any pre-
494 existing biases or neophobia prior to learning and testing generalization effects of the birds; this was
495 also necessary to motivate the birds to attack and taste the unpalatable models during the first
496 learning trials.

497 In the preference and generalization tests, simultaneous prey choice was used to decrease
498 the numbers of birds needed to accomplish the experiment. Simultaneous prey choice is also a very
499 powerful set-up to detect any potential predator biases but, obviously, this approach has
500 disadvantages too (Fig. 2). For example, it is possible that long hesitation delays during the first
501 presentation of the preference test were partly due to an aggregation effect, as aggregations of
502 conspicuous prey have been found to be aversive to predators (Gamberale-Stille, 2000; Riipi,
503 Alatalo, Lindstrom, & Mappes, 2001). On the other hand, Nokelainen et al. (2012) presented wood
504 tiger moths singly to birds, several of which also hesitated for a long time before attacking them.
505 Thus, it is difficult to say how much the simultaneous presentation influenced our results, but
506 during the flying season wood tiger moth morphs typically aggregate at the same sites. Males of
507 both morphs are often found near calling females, and thus all morphs can be visible and vulnerable
508 to predators simultaneously.

509 Lastly, if the wood tiger moths are able to survive bird attacks, the use of artificial models
510 does not necessarily give an accurate estimate of selection. A considerable proportion of attacks in
511 the generalization test were just a single peck, leaving the models uneaten, and thus not necessarily
512 'killed'. The birds' willingness to attack but reluctance to consume the models could stem from the
513 psychology of birds' decision making (Marples & Kelly, 1999). Adamová-Ježová et al. (2016)
514 showed that for great tits and coal tits, *Parus ater*, neophobia (i.e. the avoidance of novel prey
515 affecting the decision to attack), but not dietary conservatism (i.e. restriction of diet to certain prey
516 types affecting the decision to consume the prey), was deactivated during pretraining with a
517 palatable prey, but the initial hesitation of blue tits was not affected by earlier experience. Blue tits

518 have been found to show higher general aversion even towards palatable prey than, for example,
519 great tits, probably because of higher dietary conservatism (Veselý et al. 2006, 2013, Prokopová et
520 al. 2010, Turini et al. 2016). This indicates that predators' decisions of whether to attack or not after
521 avoidance learning might be species specific and, thus, not generalizable from blue tits to other
522 predators. In our experiment, 45 of 53 blue tits overcame their initial avoidance during the
523 preference test and attacked and consumed the models readily in the following avoidance trial. As
524 those birds that did not overcome their hesitation during the preference test were not included in the
525 following phases of the experiment, our results describe the generalization tendency of the less
526 hesitant individuals, which are more likely to attack aposematic prey in the wild in the first place.
527 Many of these less hesitant individuals, however, seemed to regain their dietary conservatism after
528 they had learned avoidance, as they no longer consumed the palatable models attacked. In
529 conclusion, whereas no generalization was found regarding the attack probabilities, we did find
530 individual variation in avoidance learning and dietary conservatism, which could affect selection in
531 the wild.

532

533 <H2>*The importance of other cues*

534 Somewhat surprisingly, the blue tits had no initial biases towards any of the hindwing colours.
535 Earlier studies on the wood tiger moth have found differential predation pressure in the field
536 (Lindstedt et al., 2011; Nokelainen et al., 2012; Nokelainen et al., 2014) and different hesitation
537 times by local predators (Lindstedt et al., 2011; Nokelainen et al., 2012) towards the different
538 colour morphs. As the differences in hesitation times were found using living moths (Nokelainen et
539 al., 2012), it is possible that other cues, such as odour, influenced the results. In nature, the wood
540 tiger moth relies on multiple signal components (i.e. odour, taste) in addition to the visual cues
541 when exposed to potential predators (Rojas, Burdfield-Steel & Mappes 2015). Its chemical defence
542 contains pyrazines (Rojas et al. 2017; Burdfield-Steel, Pakkanen, Rojas, Galarza & Mappes 2016),

543 a group of compounds with a characteristic aversive smell, which is effective against birds
544 (Guilford, Nicol, Rothschild, & Moore, 1987; Rowe & Guilford, 1996). In fact, pyrazine is known
545 to trigger hidden aversions to red and yellow colours (Rowe & Guilford, 1996) and conspicuous
546 prey (Lindström, Rowe, & Guilford, 2001), and enhance both learning and memorability of yellow
547 (Siddall & Marples, 2008) or red coloured prey (Barnea, Gvoryahu, & Rothschild, 2004) at least in
548 domestic chicks (Siddall & Marples, 2008). Pyrazine odour has been associated with Müllerian
549 mimicry rings of insects and suggested to function as a warning signal (Rothschild, 1961). On the
550 other hand, pyrazine odour has also been shown to assist in discriminating prey and thus reduce
551 avoidance generalization between differently coloured prey if the odour is present on only some of
552 them (Siddall & Marples, 2008; Rowe & Guilford, 1996). The specific roles of different cues in
553 predator–prey interactions are uncertain. It might be that odour is easy to associate with palatability,
554 but only functions close up, whereas conspicuous colours aid in memorizing which prey to avoid
555 even from a distance. Here we were interested in colour only. However, it has been shown that
556 when colour is kept constant, predators can discriminate prey based on pattern (e.g. Prokopová et al.
557 2010; Veselý et al. 2013), and when both colour and pattern are equal, other visual and/or chemical
558 features of the prey are used for prey recognition (Karlíková et al. 2016).

559

560 <H2>Conclusions

561 Overall, the colour polymorphism of the wood tiger moth in Finland seems unlikely to be
562 maintained by generalized avoidance based on its warning coloration only. However, predators
563 were hesitant to attack any of the aposematic morphs in the first place, and if they were to encounter
564 them in the wild sharing other warning cues such as pyrazine odour, general aversion seems likely
565 to occur. More knowledge on how predators acquire and use information on prey qualities in
566 different contexts is needed to conclude whether predator generalization contributes to the
567 maintenance of multiple aposematic morphs (see also Skelhorn et al. 2016). The possibility that

568 wild predators can generalize on the basis of the pyrazine odour or the combination of colour and
569 odour requires further investigation. Alternative explanations for the occurrence of local warning
570 signal polymorphism include negative frequency-dependent natural selection, sexual selection,
571 frequency-dependent flight activity (Rojas, Gordon, & Mappes, 2015), signal efficacy trade-offs
572 with other life history traits (Hegna, Nokelainen, Hegna, & Mappes, 2013; Nokelainen et al., 2012),
573 predator species-specific mortality differences between morphs (Nokelainen et al., 2014) or
574 combinations of these mechanisms (Gordon, Kokko, Rojas, Nokelainen, & Mappes, 2015). Colour
575 polymorphism could also be explained by multiple-model mimicry (Edmunds, 2000), if the
576 different morphs share warning colours with other defended prey species, and predators generalize
577 their avoidance from one species to the other based on similar coloration. Thus, generalization of
578 learned avoidance remains as a possible contributor to the maintenance of local polymorphism in
579 wood tiger moth populations. In conclusion, we argue based on our results that although predator
580 generalization could well contribute to the maintenance of different aposematic morphs under
581 certain circumstances, it is unlikely to occur among distinct colour morphs of otherwise similar
582 prey of visually oriented avian predators.

583

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592

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908

909 Appendix

910

911 **Table 1.** Distribution of colours chosen first in the preference test trials (phase 1)

	White first	Yellow first	Red first	<i>N</i>	<i>df</i>	χ^2	<i>P</i>
Trial 1	34	32	34	53	2	0.04	0.98
Trial 2	44	22%	34	41	2	2.98	0.23
Trial 3	29	27%	44	41	2	2.10	0.35

912

913 The percentages of birds that chose white, yellow or red models first in the three trials of
 914 the preference test, and the corresponding chi-square comparison for preference for each
 915 trial, are shown.

916

917

918 **Table 2.** Proportions (\pm SE) of tested colour morphs attacked in the generalization test
919 trials (phase 3) in relation to the colour learned

Colour learned	Colour tested	First trial	Second trial	Third trial
White	Yellow	0.85 \pm 0.09	0.92 \pm 0.07	0.64 \pm 0.13
White	Red	0.85 \pm 0.09	0.78 \pm 0.11	0.78 \pm 0.11
Yellow	White	0.73 \pm 0.11	0.73 \pm 0.11	0.73 \pm 0.11
Yellow	Red	0.86 \pm 0.09	0.73 \pm 0.11	0.60 \pm 0.13
Red	White	0.93 \pm 0.06	0.86 \pm 0.09	0.73 \pm 0.11
Red	Yellow	0.93 \pm 0.06	0.86 \pm 0.09	0.86 \pm 0.09

920

921 **Table A1.** Test for asymmetric generalization in the first generalization trial

Model	<i>df</i>	LRT	Pr(Chi)	Model AIC
(Intercept) + colour combination	5	10.70	0.058	37.4
(Intercept)				38.1

Random effects	Variance	SD		
Bird ID	4808	69.34		

Fixed effects	Estimate	SE	Z	P
(Intercept: colour combination: yw)	12.48	3.32	3.75	<0.001
Colour combination: yr	14.85	5.22	2.85	0.0044
Colour combination: rw	2.27	8.04	0.28	0.78
Colour combination: ry	2.27	8.19	0.28	0.78
Colour combination: wr	1.38	6.16	0.22	0.82
Colour combination: wy	1.38	6.15	0.22	0.82

923 LRT: likelihood ratio test; y: yellow; w: white; r: red. Model selection was based on model
 924 fit, i.e. the model chosen was the one with the lowest Akaike information criterion (AIC)

925 value. The significance level of χ^2 (Chi) indicates a change from the model with colour
926 combination as an explanatory variable to the model below, with intercept only. Estimates
927 of the best-fitting model (in bold) are shown below. Of the colour combinations, the
928 combination of yellow learned and white offered had least attacks, and was thus set to the
929 intercept.

930

931

932 **Table A2.** Test for asymmetric generalization in all three generalization trials

Model	<i>df</i>	LRT	Pr(Chi)	model AIC
(Intercept) + colour combination	5	4.32	0.50	161.9
(Intercept)				156.2

933

Random effects	Variance	SD
Trial: Bird ID	167.82	12.96
Bird ID	58.01	7.62

Fixed effects	Estimate	SE	Z	P
(Intercept)	10.05	1.57	6.42	< 0.001

934 LRT: likelihood ratio test. Model selection was based on model fit, i.e. the model chosen
 935 was the one with the lowest Akaike information criterion (AIC) value. The significance level
 936 of χ^2 (Chi) indicates a change from the model with colour combination as an explanatory
 937 variable to the model below, with intercept only. Estimates of the best-fitting model (in
 938 bold) are shown below.

939

940

941 **Table A3.** Comparisons of colours attacked first in the generalization trials

	Colour learned	Colour tested	Attacked first	<i>df</i>	χ^2	<i>P</i>
First trial	White	Yellow	6/14	1	0	1
		Red	6/14			
	Yellow	White	6/15	1	0	1
		Red	7/15			
	Red	White	8/15	1	0.13	0.71
		Yellow	6/15			
White		12/42	1			
Red	24/42					
Three trials pooled	Yellow	White	20/45	1	0.75	0.39
		Red	15/45			
	Red	White	22/45	1	0.41	0.52
		Yellow	18/45			

942 Chi-square comparisons of how many times each tested colour morph was attacked first in
 943 the generalization trials, by the colour morph learned. Models that were not
 944 attacked or attacked second are included in the total number of models offered.
 945 Bold indicates significant difference.

946 Figure captions

947 **Figure 1.** (a) Typical wood tiger moth colour morphs from central Finland (leg. Kari
948 Kulmala), (b) artificial white, yellow and red moth wings used in the experiment and (c)
949 reflectance curves of the white, yellow and red hindwings of real moths (darker colours)
950 compared to reflectance curves from white, yellow and red model hindwings (lighter
951 colours). Spectral measurements were taken from three wild-caught individuals of each
952 colour from the spots marked with blue circles on the white moth. The same spots were
953 used to measure the model hindwing colours. Model wings were set in a more natural
954 posture, less spread than the spread collection samples, but unfolded to show the
955 hindwing colour.

956

957 **Figure 2.** Schematic illustration of the experimental design. Each green circle represents a
958 platform presented to a bird in one trial. Moth models as presented to a bird that learned to
959 avoid the red morph are illustrated on the platforms and alternative food offered between
960 the trials is shown above the platforms. For details of the experimental protocol see
961 Methods (Experimental procedures; phases 1-3).

962

963 **Figure 3.** Proportion of models attacked during the learning trials for each colour model.
964 The lines represent the cumulative attacks on unpalatable moth models of white (black
965 line), yellow (yellow line) or red (red line) hindwing colour.

966

967 **Figure 4.** Proportions (\pm SE) of models that were attacked in the first trial of the
968 generalization test. Symbol styles refer to white (black circle), yellow (yellow square) and
969 red (red triangle) models offered in the test.