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1 **Title: Social transmission of avoidance among predators**
2 **facilitates the spread of novel prey**

3

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12

13

14 **Introductory paragraph:**

15 Warning signals are an effective defence strategy for aposematic prey, but only if they are
16 recognised by potential predators. If predators must eat prey to associate novel warning
17 signals with unpalatability, how can aposematic prey ever evolve? Using experiments with
18 great tits (*Parus major*) as predators, we show social transmission enhances the acquisition
19 of avoidance by a predator population. Observing another predator's disgust towards tasting
20 one novel conspicuous prey item led fewer aposematic than cryptic prey to be eaten for the
21 predator population to learn. Despite reduced personal encounters with unpalatable prey,
22 avoidance persisted and increased over subsequent trials. We then use a mathematical
23 model to show social transmission can shift the evolutionary trajectory of prey populations
24 from fixation of crypsis to fixation of aposematism more easily than previously thought.
25 Therefore, social information use by predators has the potential to have evolutionary
26 consequences across ecological communities.

27

28 Since the first description of aposematism over 150 years ago¹, explaining how these
29 conspicuous warning signals evolve to protect prey in the face of hungry predators remains
30 a challenge²⁻⁴. Aposematic displays confer little advantage until predator populations
31 associate the prey's display with its unprofitability, and while conspicuous signals are easy to
32 detect and facilitate rapid learning⁵, this feature also means they are often taken much more
33 readily than cryptic prey during predator education^{5,6}. If all predators must consume novel
34 conspicuous prey to learn, then aposematism is unlikely to evolve², and nor can it be
35 maintained easily if immigrants or juvenile predators are naïve^{7,8}. This becomes particularly
36 problematic when prey are lethal, as predators have no opportunity to learn from their
37 foraging mistakes⁹. Nevertheless, aposematism is a widespread defence with multiple
38 evolutionary origins, showing that it can establish across diverse predator-prey systems^{10,11}.

39

40 Many factors might assist aposematic phenotypes overcome this cost of
41 conspicuousness to reach fixation in prey populations¹¹, although experiments in the lab and
42 field suggest the puzzle is yet to be fully resolved⁴. For example, aggregating reduces attack
43 rates endured by unpalatable prey¹², but predators still require repeated encounters with
44 prey aggregations to learn avoidance¹² and aposematic displays are more common among
45 non-aggregating prey³. Wariness of novel food items may confer an initial advantage for
46 aposematic prey¹¹. However experiments demonstrate that dietary conservatism is rarely
47 sufficient to reduce initial predation risk below that of cryptic phenotypes¹³ and social
48 effects during foraging encourage predators to become less conservative about
49 incorporating novel foods into their diet¹⁴. Even innate biases against common warning
50 signals (e.g. black and yellow stripes) are insufficient to protect novel prey completely: novel
51 aposemes suffer higher mortality overall than cryptic phenotypes¹³, perhaps because
52 reinforcement is required for predators' initial biases to become avoidance¹⁵, and juvenile
53 predators can show less aversion to novel prey than adults^{7,15}. Furthermore, when a

54 predator's nutritional state declines they increase their consumption of unpalatable prey⁴
55 meaning aposematic prey in the wild continue to face predation⁸, even when some of the
56 population is educated¹⁶.

57

58 Considering the information ecology of aposematism¹⁷ may help reconcile how it
59 evolves and persists. When encountering novel prey, predators face uncertainty about its
60 palatability and nutritional benefit⁴ so, in theory, they should acquire as much information
61 as possible before risking consumption^{17,18}. Previous work has focussed on predators
62 becoming educated about warning signals through interacting with and consuming prey
63 themselves⁴ (i.e. personal information), perhaps influenced by innate preferences and biases
64 against colours or patterns¹⁵, or wariness of unusual foods in general¹¹. However, paying
65 attention to the foraging behaviour of others (i.e. social information¹⁷) could provide an
66 additional potent source of information¹⁹. Social transmission of food aversions has been
67 demonstrated in a range of taxa: for example vervet monkeys learn to prefer palatable
68 rather than unpalatable foods by observing educated troop members²⁰, juvenile great tits
69 increase their avoidance of aposematic prey if they observe an adult eat an alternative²¹,
70 and tamarin monkeys²², red-winged blackbirds²³, house sparrows²⁴, and domestic chicks²⁵
71 avoid foods after observing a conspecific show distress. Observing another's characteristic
72 response to distasteful food can also increase chickens' wariness of two typical colours used
73 by aposematic prey²⁶. However, whether social transmission facilitates the evolution and
74 spread of novel conspicuous prey compared to an alternative phenotype²⁷ remains
75 untested.

76

77 Here we combine experiments with a mathematical model to test if social
78 transmission of avoidance among predators enables novel aposematic prey phenotypes to
79 reach fixation more readily than previously assumed. We used the novel-world method^{5,28}

80 where naïve predators search in an artificial landscape for artificial prey (paper packets
81 containing food) marked with novel signals that are either cryptic (they share the signal
82 printed on the landscape) or conspicuous^{5,28}. The palatability of prey is manipulated by
83 soaking small pieces of almond in chloroquine, a mild toxin that facilitates associative
84 learning²⁹. This method avoids using signals that are found in a predator's current
85 environment, or in its evolutionary past. We used great tits, *Parus major*, as our model
86 predator because they learn from personal encounters to avoid novel artificial^{5,28} and real
87 aposematic prey^{7,30}, and also use social information for foraging: they copy foraging
88 locations³¹ and acquire new foraging skills from observing others in the wild³². Like many
89 bird species³³, great tits respond to distasteful prey items by shaking their head and wiping
90 their beak vigorously on a nearby perch (Supplementary Videos 1,3); using video playback,
91 we provided half of the predators with this potential source of social information about
92 signals and unpalatability before they encountered the prey population. We predicted that
93 socially-informed predators would (i) forage for novel prey more quickly than naïve
94 predators without social information³³, and (ii) consume fewer conspicuous than cryptic
95 prey despite them being almost three times more visible to predators⁵. If social information
96 is to facilitate the evolution of novel aposematic prey, avoidance must persist during
97 multiple encounters with prey populations. Therefore, we repeated our experiment on two
98 subsequent days (but without further video playback) and predicted that socially-informed
99 predators would (iii) continue to avoid unpalatable prey, despite fewer opportunities for
100 personal learning and feedback from toxin ingestion⁴. We then used a mathematical model
101 (Box 1) to investigate the evolutionary consequences of social transmission for a spatial
102 mosaic of prey populations.

103

104 **Results:**

105 Socially-informed predators were quicker than naïve control birds to select their first item
106 from the prey population (effect of social information = -1.13 ± 0.24 , $\chi^2 = 20.06$, d.f. = 1, $p <$
107 0.001 , Fig. 1a, Supplementary Table 1), and 67% ate a cryptic prey item first compared to
108 53% of predators naïve to the unpalatability of the conspicuous symbol (Fig. 1b,
109 Supplementary Table 1). This suggests that socially-informed predators were not foraging
110 more quickly simply because they had observed a conspecific, but that social information
111 encouraged quicker decision-making. Observing another predator consume just one
112 unpalatable prey item subsequently resulted in a 32.1% reduction in predation risk for the
113 novel aposematic phenotype (Fig. 2): focal birds presented with social information
114 consumed fewer aposematic prey items than the alternative cryptic form during the first
115 trial, when compared to birds that needed to learn through trial-and-error only (Fig. 2; effect
116 of social information = -0.65 ± 0.23 , $\chi^2 = 7.98$, d.f. = 1, $p = 0.005$; Supplementary Table 2).
117 Adult male great tits (our demonstrators) are dominant over juveniles and females³⁴, yet
118 conspicuous prey enjoyed similar protection from socially-informed predators regardless of
119 the age of the observer (adult vs. juvenile observers = 0.22 ± 0.47 , $\chi^2 = 2.38$, d.f. = 1, $p = 0.63$)
120 or if they were subordinate to the demonstrator (adult male vs. subordinate observers =
121 0.60 ± 0.45 , $\chi^2 = 2.03$, d.f. = 1, $p = 0.15$).

122

123 During subsequent encounters with prey populations, we found that all birds
124 continued to learn to avoid aposematic prey (effect of trial number = -0.77 ± 0.12 , $\chi^2 = 24.00$,
125 d.f. = 1, $p < 0.001$; Supplementary Table 2). Regardless of information available, birds
126 improved across trials at a similar rate (information*trial number: $\chi^2 = 0.14$, d.f. = 1, $p = 0.71$)
127 despite differences in the amounts of unpalatable prey ingested (effect of social information
128 = -0.58 ± 0.18 , $\chi^2 = 12.13$, d.f. = 1, $p < 0.001$; Supplementary Table 2). Therefore, when
129 experimental prey populations were under selection from socially-educated predators, the

130 aposematic phenotype was more likely to persist than the cryptic form, even across
131 subsequent days (Fig. 2).

132

133 Our experiments provided ample opportunity for socially-informed birds to also
134 learn through personal experiences: the artificial prey population was already 50%
135 aposematic⁵. In nature, however, the proportion of aposematic prey present will vary, which
136 will affect the chances for observers to witness and learn from predation events. We
137 therefore next investigated the expected evolutionary consequences of social transmission
138 using a modelling approach (Box. 1) where we varied (i) the initial proportion of the
139 population that was aposematic, (ii) the cost of conspicuousness, and (iii) the number of
140 predators learning by observing a predation event, relative to the probability of learning
141 from a single personal encounter with distasteful prey. We assumed that the predator was
142 not a specialist on the focal prey species, and our model implicitly assumed the availability
143 of alternative palatable prey.

144

145 The positive effect of social transmission on prey survival we detected in our
146 experiments also made a difference, at suitable parameter settings, between whether
147 crypsis or aposematism was selected to fixation (Fig. 3, the depicted 20% initial
148 aposematism is above the threshold if individuals learn from others, but below it if they do
149 not). Fixation of the aposematic phenotype required crossing a wider invasion barrier: if
150 abandoning crypsis means prey are much more visible (high α , Fig. 4), then warning colours
151 should be common to begin with. However, when conspicuousness (α) was higher, then the
152 benefit conferred by social transmission was also larger (it was able to reduce the width of
153 invasion barriers the most where these were widest, Fig. 4). As a net effect, however, the
154 smaller reduction apparent at low α might matter more for fixation because narrower
155 invasion barriers are as a whole more likely to be crossed.

156

157 Prey and predators occur across a spatial mosaic of meta-populations which could
158 influence the dynamics and effects of social transmission; avoidance learning may not
159 necessarily occur at the same rate at every site³⁵ and educated predators may also migrate
160 among prey populations, reducing predation pressure on local prey populations³⁵. Therefore
161 we next added migration and stochasticity to the model to investigate how social
162 transmission influenced the chance that aposematic phenotypes would reach fixation. We
163 found that immigration from neighbouring sites that have already crossed an invasion
164 barrier can potentially aid a local population to cross it too (red area in Fig. 5). Spread is
165 facilitated because prey subpopulations can now cross the invasion barrier sequentially: the
166 first subpopulation to do so makes aposematism locally fixed, and aposematic individuals
167 thereafter constantly spread to nearby habitats. Social transmission helps the first
168 subpopulation to reach fixation, which then facilitates other subpopulations to also cross the
169 barrier. Conversely, prey populations that do not enjoy social transmission of avoidance
170 among predators have to rely on other processes³⁵ to help aposematism cross the (now
171 higher) threshold to spread towards fixation.

172

173 **Discussion:**

174 If predators have access to social information about prey palatability and signals, our
175 empirical and theoretical results suggest that aposematism can arise more easily: (i) social
176 information reduces the initial frequency of aposematic prey required for predator
177 populations to become educated, (ii) it can also have an effect even when signals are
178 moderately conspicuous, and (iii) migration of predators and spatial assortment of prey
179 types increases the strength of these effects. Using social information during foraging is a
180 widespread phenomenon, from insects³⁶ to fish³⁷, reptiles³⁸ and mammals³⁹. While
181 demonstrating that avoidance is influenced by observing the interactions of others with

182 unpalatable foods is limited thus far to a few species of mammals^{20,22} and birds^{21,23,26}, the
183 cognitive processes involved in acquiring avoidance asocially are unlikely to be different
184 from learning socially⁴⁰. This means that social information has the potential to influence
185 how many species acquire avoidance. While our experiments used great tits as a model
186 predator, the positive effects we detected of social transmission for novel prey phenotypes
187 could therefore occur across a wide range of predators and prey.

188

189 Our experiments and model were conservative; we gave observers in our experiment
190 only one opportunity to gather social information, and naïve predators could only observe
191 others showing a disgust response once they took an aposematic prey item. Social
192 transmission may also occur, however, if animals observe the foraging decisions of already-
193 educated group members^{20,21}, and there is growing evidence that individuals adopt the
194 majority foraging choices of a group^{20,32}. Furthermore, aposematic prey may sometimes
195 survive predator attacks⁴¹. Although we did not consider this ‘taste-rejection’ in our
196 experiments or model, tasting could potentially provide social information as well as
197 enhance the personal learning of predators⁴¹. Rejected prey would also re-join the prey
198 population, and therefore have potential to educate again. Field experiments recording
199 social transmission and prey survival are required to assess if these processes occur among
200 predator populations; if present, social information could have even stronger effects for
201 aposematic prey in nature than what we detected here.

202

203 Is social learning necessary for social transmission of avoidance? Our experiments did
204 not allow us to assess the exact cues used by observers to adjust their foraging decisions, so
205 observers might have been reluctant to eat the demonstrated signal only to avoid perceived
206 competition (all of the demonstrators used were adult males), for example. However,
207 subordinate great tits will readily move towards a food source once a more dominant bird

208 has moved³⁴ and during the testing phase birds foraged alone. Alternatively, observing
209 another encounter something unpalatable might have encouraged predators to avoid the
210 more conspicuous option by simply increasing neophobia²⁶ or fear⁴². Our data suggests that
211 predators did, however, associate social information with the conspicuous prey signal.
212 “Socially-informed” predators consumed fewer aposematic prey than naïve control birds
213 during the first day, meaning they had fewer opportunities to associate prey signals with
214 palatability directly⁴. If social effects were the cause of the initial reduction, then predation
215 risk should have increased during the second day of the experiment to be the same (or
216 higher) than in the control group. We detected the opposite: socially-informed predators
217 continued to avoid the aposematic prey more than the control group across all three days of
218 the experiment. In addition, both cryptic and conspicuous prey signal types were novel to
219 the birds, and during the video validation experiment focal birds chose to eat from a less
220 preferred cup after observing a disgust response (Supplementary Fig. 1). Together this
221 suggests that social learning is the more likely explanation, but further work is needed to
222 pinpoint the units of information.

223

224 Social transmission of knowledge about warning signals is likely to interact with other
225 mechanisms and conditions suggested necessary for the evolution of aposematism.
226 Wariness of novel foods by predators, for example, could help rare aposematic phenotypes
227 to evolve if it reduces initial attacks^{11,15}, but dietary wariness varies within predator
228 populations¹³ and initial wariness requires negative feedback to persist². Social transmission,
229 however, could resolve this if warier individuals learn avoidance by observing the foraging of
230 less wary predators, instead of eventually consuming prey themselves². Social information
231 may also be more readily available if prey are aggregated, enhancing the proposed positive
232 effects of aggregations for the evolution of aposematism³ (Fig. 5A). Predators also aggregate
233 and flocking among birds facilitates transmission of information about food⁴³. In addition,

234 flocks commonly include heterospecifics⁴⁴ who may have different propensities to try novel
235 prey items⁷. This means that there could be local variation in the social information
236 available to naïve predators, perhaps explaining why aposematic signals vary among
237 predator communities⁴⁵. Furthermore, even educated predators will sometimes taste
238 aposematic prey⁴ (Fig. 2); this too could provide local knowledge about prey signals for any
239 naïve immigrants^{8,16}.

240

241 Our findings indicate that social interactions within species may have broad
242 implications for understanding interactions among species⁴⁶. For example, range expansion
243 of predators or their prey can lead to populations that are naïve to prey defences. This often
244 has disastrous consequences, but sometimes avoidance occurs much more rapidly than
245 expected⁴⁷. Variation in social behaviour and predators' propensity to learn by observing
246 others could help explain why some species have been able to associate toxicity of novel
247 prey rapidly and consequently avoid consuming them⁴⁸. Despite growing awareness that
248 social networks influence how species learn about their environment, the emergent
249 properties of social transmission for interacting species are only beginning to be
250 realised^{46,49,50}. Our study demonstrates that social transmission among predators has the
251 potential to influence the evolutionary trajectories of prey. Understanding the complexity of
252 coevolution therefore requires an appreciation of the social dynamics taking place within, as
253 well as between interacting parties.

254

255 **Methods:**

256 **Predators and housing.** Wild great tits (*Parus major*) were caught from October 2013 till
257 January 2014 using traps at feeding stations (containing peanuts) in forest at the University
258 of Jyväskylä Research Station, Konnevesi, Finland (62°37.7'N 026°17'E). We controlled for
259 variation in observer-demonstrator familiarity by catching birds in groups of five, and always

260 within two hours (immigration and emigration rates are high during Finnish winters⁵¹).
261 Groups always included at least one adult male (who was used as the group's demonstrator
262 during our experiments), but used juveniles (1st year) and adults (older than 1st year), and
263 both sexes in foraging tests. Adult males are more common in this population so we used
264 them as demonstrators to reduce heterogeneity and because subordinate great tits are
265 known to pay attention to the foraging behaviour of more dominant birds (adult male great
266 tits are dominant over juveniles and females)³⁴. All birds were naïve to our experimental
267 treatments (every great tit caught and released at the research station is ringed) and
268 assigned alternately, but not by catching order (experimental data collected by RT).

269

270 Great tits were housed indoors in individual plywood cages (65 x 50 x 80 cm) with a
271 daily light period of 11.5 h (lights on automatically between 8.30 and 20.00 EET). Birds had
272 acoustic contact only. They were provided an *ad libitum* supply of fresh water, sunflower
273 seeds, and tallow, but were food deprived prior to experiments for 2 h to ensure motivation
274 to search for prey. Water was always available. Our experiments were conducted with
275 permission from the Central Finland Centre for Economic Development, Transport and
276 Environment (KESELY/1017/07.01/2010), and license from the National Animal Experiment
277 Board (ESAVI-2010-087517Ym-23). No birds died in captivity and all were released at their
278 site of capture following experiments.

279

280 **The 'novel world' experimental arena.** We used an established protocol^{5,28} to test
281 differences in relative predation risk between cryptic and conspicuous prey signals. The floor
282 of the aviary (3 x 3.5 m) was covered in white paper sheets, printed with 71 x 80 small black
283 crosses and laminated to protect the surface. An additional 100 three-dimensional 'fake
284 prey' (white paper squares with a cross symbol, 8 x 8 mm) were stuck randomly across the
285 surface (using white double-sided adhesive foam tape). This enhanced crypsis of the prey

286 that shared the cross symbol (see below). The floor was divided into 8 rows using wooden
287 planks; this allowed us to assign a grid reference to the floor so we could note where birds
288 selected prey, and provided great tits with positions to inspect prey. Two perches were also
289 provided on the walls of the aviary on which the birds consumed their chosen prey. The
290 foraging choices of the birds were observed via a one-way glass window in the door to the
291 aviary.

292

293 **Artificial prey.** Prey were small pieces of almond (approximately 0.1g) glued (with nontoxic
294 UHU glue stick) inside a white paper packet (8 x 8 mm). Packets were printed on both sides
295 with a black symbol to act as a signal of the contents. Cryptic prey were printed with a cross,
296 conspicuous prey were printed with a square that made them 3 x more visible to the birds⁵.
297 Conspicuous prey were made highly unpalatable by soaking the almond slices for 1 h in a
298 solution of 30 ml water and 2 g chloroquine phosphate before air drying; great tits learn to
299 associate signal type with prey distastefulness at this concentration²⁹.

300

301 **Training procedure.** Following a four-step procedure that has been described elsewhere¹³,
302 we trained demonstrators and observers to handle our artificial prey. We used plain white
303 packets during training, and birds could not progress to the next stage until they had opened
304 and consumed five prey. All birds learned to open prey within one day. We next trained the
305 birds to forage in the novel world. First, each catch-group was housed together overnight in
306 the aviary to accustom them to the room and encourage them to forage from the floor.
307 Sunflower seeds and peanuts were available on the floor to encourage them to forage (fresh
308 water was always available), but plastic sheeting obscured the floor. This also ensured that
309 observers were familiar with the demonstrator of their catch-group. The second stage of
310 training introduced birds to the novel landscape and the presence of cryptic prey. We
311 placed nine plain white prey in three groups, and one group of three cross-symbol prey, in

312 random locations. For each group, one prey item was on the wooden plank and so was
313 highly visible, the others were on the paper background and consequently harder to find.
314 Using three cross-type prey ensured that all birds knew how to forage in the novel world,
315 but minimized experience with the signal. All birds were trained individually and in an
316 identical fashion, so there were no differences among experimental treatments in their
317 experience with artificial prey before video playback. Training was complete once birds had
318 found and consumed all 12 prey.

319

320 **Using video playback to provide social information.** Video playback minimizes variation in
321 demonstrator behaviour across replicates³³, alters foraging behavior of blue tits³³, and has
322 been used successfully to manipulate social conditions in great tits⁵². Nevertheless, before
323 our main experiment we validated that video playbacks lead to changes in great tits'
324 foraging behaviour (Supplementary methods, Supplementary Fig. 1).

325

326 Before filming, demonstrators were habituated to the test chamber: a wooden box
327 (50 cm w x 50 cm d x 67 cm h) with a tinted plexiglass front that contained one horizontal
328 perch and fresh water at all times. The box was illuminated by a single energy-saving
329 fluorescent light, and was placed in a dark room with no other lighting. This ensured that
330 the demonstrator was easily observable, and could be filmed, but that the birds could not
331 see us. Videos were recorded using an HD camcorder (Canon Legria HF R37) positioned 1 m
332 away and centered in front of the box. After filming, demonstrators were returned to their
333 home cages (with *ad libitum* food and water), monitored overnight, and then released back
334 into the wild.

335

336 Demonstrators were provided with a square-symbol prey item for filming. This was
337 placed at a ca.45° angle on the floor of the test box (by leaning it against a small piece of

338 adhesive putty (Blu-tack®), and was 15 x 15 mm (to enhance visibility in the video). To
339 ensure a highly visible disgust response, and to minimize heterogeneity among
340 demonstrators⁵³, we made the prey item as distasteful as possible by soaking the almond
341 piece in a saturated solution of 4 g chloroquine phosphate and 30 ml of water for 1 h before
342 being left to dry. Videos consisted of the demonstrator perching next to the prey item,
343 before taking it in its beak to the box's perch. Here the prey was held between the perch
344 and the bird's foot while the packet was opened, allowing a good view of the prey and its
345 symbol. Upon tasting the almond piece, most birds dropped it before wiping their beaks
346 vigorously (Supplementary Video 3). We then edited the videos (using iMovie version 10.0)
347 to include 1 min 30 s of the demonstrator investigating the prey, attempting to consume it,
348 and beak wiping (median beak wipes = 39.5, range = 17 – 59); the beginning and end of the
349 video was spliced with a 30 s clip of the cross-symbol prey (but with no demonstrator
350 present). This ensured that any avoidance or attraction to the cryptic prey was not because
351 of either neophobia or neophilia. See Supplementary Videos 3 and 4 for examples.

352

353 **Predation experiment protocol.** Each bird was tested once per day, over three consecutive
354 days (see Supplementary Fig. 2 for set up). Prior to our experiment, individual birds were
355 housed for 2 h in a test box in the corner of the room, identical to that used during filming of
356 the demonstrator, and provided with water only. The LCD monitor was positioned in front of
357 the Perspex screen, so birds were habituated. Immediately before the first test, observers
358 were shown a video; 15 birds in the 'socially-informed' group (4 females, 11 males; 8 adults,
359 7 juveniles) observed the demonstrator responding to the square prey, 15 birds in the
360 'naïve' control group (6 females, 9 males; 6 adults, 9 juveniles) observed a video of identical
361 length, but with 1.5 min of each prey type without a demonstrator present (Supplementary
362 Video 4). Our control videos included the prey to ensure that naïve and socially-informed
363 birds were similarly experienced with the prey symbols, but did not include a demonstrator

364 because a bird ignoring prey may also have provided social information about
365 unpalatability²¹.

366

367 Birds were then allowed to move into the aviary by removing the Perspex screen
368 and controlling the lighting in the test box and in the aviary room (like most birds, great tits
369 are immobile in the dark but move quickly towards light). We recorded when each bird left
370 its box to explore the aviary as the start time for the experiment (there was no difference
371 between experimental groups in their motivation to begin the experiment; $\chi^2 = 0.13$, d.f. = 1,
372 $p = 0.72$). The novel landscape was divided into four quadrants, and 6 of each prey type
373 were scattered randomly across each (24 cryptic prey, and 24 conspicuous prey in total, for
374 each trial). The type of prey and its location were noted so we could ensure that we
375 recorded the foraging choices accurately. Birds were allowed to eat 25% of prey in each trial
376 (12 of 48 prey), and we noted the time (s), and identity of each prey item taken. A predation
377 event was recorded if a package was opened.

378

379 **Statistical analyses.** We used generalized linear models with error distributions appropriate
380 to the data structure, and included a random intercept term to account for potential
381 variation among catch groups. There were twice as many males as females in our
382 experiment, which precluded analyzing sex-differences in response to treatment. Analysis of
383 the predation experiment used a binomial error distribution to model a response term
384 where the number of aposematic prey and cryptic prey consumed were bound, and also
385 included a random intercept and slope for each individual over the three trials. Differences
386 in motivation and latency to take the first prey item used a negative binomial error
387 distribution to account for skew. We ran each analysis by using Akaike's information
388 criterion (AICc, corrected for small sample sizes) to rank a model containing the
389 experimental treatment (in interaction with trial number where appropriate) against

390 candidate models that each included an additional variable of interest (date during
391 experiment, adult vs. juvenile, latency to enter aviary, and whether individual had been used
392 in validation experiment, Supplementary Tables 1,2) and a null model. The model with the
393 lowest ranked AICc was retained and the significance of its terms assessed using likelihood
394 ratio tests compared to a χ^2 distribution (model outputs in Supplementary Tables 1,2). All
395 analyses were conducted in R version 3.4.0⁵⁴ using the lme4 package⁵⁵, and we plotted
396 predicted values to account for effects of random terms. Supplementary Fig. 3 presents the
397 raw data from our experiment.

398 **Data availability:**

399 The datasets generated during the study are available from the NERC Environmental Data
400 Centre (<https://doi.org/10.5285/db55406b-c9a1-4a9e-88c2-2abbcb4bcad3>).

401

402

403 **Box 1. Modelling evolutionary consequences of social transmission for prey phenotypes**

404 We consider a population of predators and prey that inhabit either a single habitat
405 patch (site) or several, in the latter case linked by migration of both predators and prey (see
406 4 below). The focal prey species has two possible morphs, palatable cryptic (C) and
407 unpalatable aposematic (A), which are inherited from parent to offspring. We denote the
408 population density of cryptic prey at site i at time t as $C_i(t)$ and aposematic prey as $A_i(t)$ (i and
409 t are dropped from notation where it improves clarity). Being aposematic increases the
410 attack rate, denoted a , by a factor α , which means that in a starting population of N
411 predators, C cryptic prey and A aposematic prey, attacks occur at a rate $aNC + \alpha aNA$. The
412 population dynamics are governed by the interaction of each of the following processes:

413

414 1. *Naïve predators can become educated via personal experience with distasteful prey.*

415 Predators are born naïve ($N_i(t)$) before becoming educated ($E_i(t)$); a single encounter with
416 an aposematic prey item makes the predator educated with a probability p , and an
417 educated predator will not touch aposematic prey again (thus it takes on average $1/p$
418 encounters for the transition to happen). When a proportion p of encounters with
419 aposematic prey lead to predators leaving the state 'naïve' and arriving at the state
420 'educated', the total rate of individuals experiencing this transition, measured at time t ,
421 equals $p\alpha aN(t)A(t)$. If there are no naïve predators left, or if there are no aposematic prey
422 to be encountered, no predator can become educated.

423

424 2. *Naïve predators can become educated predators via social transmission.*

425 Focal predators can observe the foraging of b other individuals who reside in the same
426 habitat patch (cases with $b > 0$ are called social transmission scenarios). Parameter q ($0 \leq$
427 $q \leq 1$) specifies the efficiency of social transmission, relative to personal experience (p). If,
428 for example, $p = 0.5$ and $q = 0.1$, then personal experience with a distasteful item leads to

429 future avoidance with probability 50%, but watching another individual react the same
 430 way only leads to $qp = 0.05$ probability (i.e. 5%) that this transition happens for the
 431 observer. If $q = 1$, then watching is equally efficient as personal experiences: $qp = p$ in this
 432 case.

433

434 We make the conservative assumption that social transmission occurs only after
 435 observing others transition from naïve to educated, and observation effort is not
 436 specifically directed towards naïve individuals. The computations necessary are thus that
 437 each of these b other individuals is currently naïve with probability $N/(N+E)$, therefore
 438 each focal predator is offered ‘social transmission opportunities’ at rate $q\alpha pbN/(N+E)$,
 439 and the total number of transitions happening through social transmission is obtained by
 440 multiplying by N , the density of naïve observers capable of following this route.

441

442 3. *Prey die because of predation, and predators may also die. Both experience logistic*
 443 *population growth towards their carrying capacity (K_{prey} , K_{pred}).*

444 All attacks are assumed fatal for the prey, whether or not a predator becomes educated.

445 Because only naïve predators attack aposematic prey, the per capita deaths of

446 aposematic prey equal αaN , leading to density changes $(-\alpha aN + r_{prey}(1 - (A +$
 447 $C)/K_{prey}))A$ for aposematic prey. The corresponding change for cryptic prey is

448 $(-a(N + E) + r_{prey}(1 - (A + C)/K_{prey}))C$. Here r_{prey} denotes the intrinsic growth

449 rate of the prey population and the term $(1 - (A + C)/K_{prey})$ describes density

450 dependence leading to logistic growth where aposematic and cryptic prey are assumed

451 to contribute identically to density dependence.

452

453 The mortality rate of predators, μ_{pred} for all predators, is assumed to be independent of
 454 whether predators are educated or not. Predator mortality may occur due to other
 455 causes than encounters with the focal prey species; and we allow for the density of naïve
 456 individuals to increase when there is turnover in the predator population (all individuals
 457 being naïve at birth). Population growth towards carrying capacity is therefore added to
 458 naïve predator density, leading to a population growth term $-\mu_{pred}N + r_{pred}(1 - (N +$
 459 $E)/K_{pred})) (N + E)$ for naïve predators and $-\mu_{pred}E$ for educated predators.

460

461 4. Migration.

462 Per capita migration rates equal m_{pred} and m_{prey} for predators and prey, respectively.

463 Migration is assumed to lead to individuals emigrating their natal patch and landing in
 464 any other patch, which means that the net immigration for patch i , exemplified for naïve

465 predators, is $-m_{pred}N_i + \frac{m_{pred} \sum_{i=1}^k N_i}{k}$ if there are k patches in total.

466

467 When all the processes (1)...(4) occur simultaneously, the system as a whole obeys the

468 following equations:

$$\frac{dN_i}{dt} = -p\alpha a N_i(t) A_i(t) - \frac{q\alpha a p b N_i(t)^2}{N_i(t) + E_i(t)} - \mu_{pred} N_i(t) + r_{pred} \left(1 - \frac{N_i(t) + E_i(t)}{K_{pred}} \right) (N_i(t) + E_i(t)) - m_{pred} N_i(t) + \frac{m_{pred} \sum_{i=1}^k N_i(t)}{k}$$

469

$$\frac{dE_i}{dt} = p\alpha a N_i(t) A_i(t) + \frac{q\alpha a p b N_i(t)^2}{N_i(t) + E_i(t)} - \mu_{pred} E_i(t) - m_{pred} E_i(t) + \frac{m_{pred} \sum_{i=1}^k E_i(t)}{k}$$

470

$$\frac{dC_i}{dt} = -a(N_i(t) + E_i(t)) C_i(t) + r_{prey} \left(1 - \frac{A_i(t) + C_i(t)}{K_{prey}} \right) C_i(t) - m_{prey} C_i(t) + \frac{m_{prey} \sum_{i=1}^k C_i(t)}{k}$$

$$\frac{dA}{dt} = -\alpha a N_i(t) A_i(t) + r_{prey} \left(1 - \frac{A_i(t) + C_i(t)}{K_{prey}} \right) A_i(t) + r_{prey} \left(1 - \frac{A_i(t) + C_i(t)}{K_{prey}} \right) C_i(t) - m_{prey} C_i(t) + \frac{m_{prey} \sum_{i=1}^k C_i(t)}{k}$$

471

472

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597

598

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609

610 **Author contributions:**

611 RT conceived the project, and designed and conducted experiments and analyses; JM
612 designed experiments and assisted with analyses; HK conceived and conducted modelling.
613 All authors wrote the manuscript.

614

615 **Competing financial interests:**

616 The authors declare no competing financial interests.

617 **Figure legends:**

618 **Figure 1. Latency to forage and initial prey choices.** **a**, Socially-informed predators foraged
619 more quickly for **b**, their first prey item than naïve control predators. **(a)** Filled symbols
620 show means (\pm S.E.) from a negative-binomial mixed effects GLM including a random
621 intercept for cohort. One socially-informed predator was excluded (latency = 644 s, effect of
622 social information with outlier included = -0.71 ± 0.36 , $\chi^2 = 3.81$, d.f. = 1, $p = 0.05$,
623 Supplementary Table 1). **(b)** The difference in initial prey symbol taken was not significant
624 (effect of social information on odds of predator taking cryptic prey first = 0.91 ± 0.82 , $\chi^2 =$
625 1.34, d.f. = 1, $p = 0.25$, Supplementary Table 1).

626

627 **Figure 2. Relative predation risk for novel conspicuous prey versus the cryptic phenotype.**

628 Mean (\pm S.E.) number of aposematic prey consumed / number expected by chance during
629 three learning trials over consecutive days (1 trial/day). Great tits with social information
630 about prey signals (circles, $n = 15$) consumed relatively fewer aposematic than cryptic prey,
631 compared to birds with no social information (triangles, $n = 15$). Light-coloured symbols
632 show individual variation in foraging choices, and the solid reference line indicates equal
633 predation of the cryptic and aposematic prey types. Plotted data are derived from a mixed-
634 effects binomial GLM including a random intercept for cohort, and slopes for each
635 individual.

636

637 **Figure 3. An example of the temporal dynamics predicted if social information is available.**

638 We assume all predators are naïve at $t = 0$, aposematic prey are four times ($\alpha = 4$) easier to
639 detect than cryptic prey, and comprise 20% of the initial prey population. When **(a)** social
640 information is not used ($b = 0$), the proportion of naïve predators (green line) becomes less
641 than that of educated predators (blue line), however aposematism vanishes because the
642 former are still present and detect aposematic prey (red line) more easily than cryptic prey

643 (solid grey line). Conversely, **(b)** social transmission ($b > 0$) leads to a faster decline in naïve
644 predators. Once a sufficient proportion of predators are educated, the net growth rate of
645 the aposematic population is faster than that of their cryptic competitors, and aposematism
646 fixes (dashed grey line). Any new naïve predators become educated almost instantly (by
647 personal learning) because aposematic prey are now very common. Here we use $b = 5$ to
648 demonstrate the effect (only threshold frequency varies with this value). Other parameter
649 values: $a = 0.1$, $p = 0.2$, $q = 0.1$, $\mu_{pred} = 0.001$, $r_{prey} = 5$, $r_{pred} = 1$, $K_{prey} = 100$, $K_{pred} = 10$.

650

651 **Figure 4. The threshold frequency of aposematic prey necessary for the phenotype to**
652 **reach fixation.** Social transmission (black circles) reduces the threshold frequency of
653 occurrence that aposematic prey must be present for the phenotype to invade the prey
654 population (compared to personal information only (open circles). Starting populations are
655 created from different initial frequencies for the aposematic type (between 0 and 30%) to
656 seek the threshold frequency that is necessary for subsequent fixation. From Fig. 3 we know
657 that the threshold for $\alpha = 4$ must be located higher than 0.2 if there is no social transmission,
658 and lower than 0.2 if there is; here we seek the exact threshold. Parameter values, except
659 for α (which is now varied), are from Fig. 3.

660

661 **Figure 5. The effect of social transmission on the initial population size required for**
662 **aposematic prey to reach fixation.** Whenever there is migration (all cases with $m > 0$), there
663 is a range of initial population sizes (marked red) where aposematism only fixes if social
664 transmission is possible ($b > 0$). This range of initial frequencies is higher in **(a)**, where we
665 have ‘seeded’ five subpopulations with 100 individuals binomially chosen to be aposematic
666 or not, than in **(b)**, where the 500 individuals ($K_{prey} = 100$ at 5 sites) were additionally
667 grouped to form subpopulations with maximum local association of aposematic prey. Thus
668 if, for example, an initial frequency of 0.2 led to 104 aposematic individuals, subpopulation 1

669 was assumed to be 100% aposematic, subpopulation 2 had 4 aposematic individuals (4%),
670 and the remaining subpopulations had none. Initial frequencies of aposematism ranged
671 from 0.01 to 1 but we do not show values above 0.5 as they always led to fixation,
672 regardless of the scenario. Parameter values: $\alpha = 2.5$, other parameters as in Fig. 4.