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## How do predators generalize warning signals in simple and complex prey communities? Insights from a videogame

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1 **How do predators generalise warning signals in simple and complex prey communities?**

2 **Insights from a videogame**

3

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17

18

19 **Abstract**

20           The persistence of distinct warning signals within and between sympatric mimetic  
21 communities is a puzzling evolutionary question because selection favours convergence of  
22 colour patterns among toxic species. Such convergence is partly shaped by predators' reaction  
23 to similar but not identical stimulus, i.e. generalisation behaviour. Thus, generalisation by  
24 predators is likely to be shaped by the diversity of local prey. However, studying  
25 generalisation behaviour is generally limited to simple variations of prey colour patterns.  
26 Here, we used a computer game played by humans as surrogate predators to investigate  
27 generalisation behaviours in simple (4 morphs) and complex (10 morphs) communities of  
28 unprofitable (associated with a penalty) and profitable butterflies. Colour patterns used in the  
29 game are observed in natural populations of unprofitable butterfly species such as *H. numata*.  
30 Analyses of 449 game participants' behaviours show that players avoided unprofitable prey  
31 more readily in simple than in complex communities. However, generalisation was observed  
32 only in players that faced complex communities, enhancing protection of profitable prey that  
33 looked similar to at least one unprofitable morph. Additionally, similarity among unprofitable  
34 prey also reduced attack rates only in complex communities. These results are consistent with  
35 previous studies using avian predators but artificial colour patterns, and suggest that mimicry  
36 is more likely to evolve in complex communities where increases in similarity are more likely  
37 to be advantageous.

38 **Keywords:** citizen science, imperfect mimicry, Müllerian mimicry, Batesian mimicry,  
39 Heliconius

40

41 **Introduction**

42           Chemically protected prey often sport warning signals advertising their unpalatability  
43 to predators [1]. Predators usually learn to associate prey appearance and distastefulness after  
44 sampling several aposematic prey bearing a common warning signal [2–5]. Therefore, the  
45 larger the number of distasteful prey displaying a common warning signal, the smaller is the  
46 risk to individual prey of suffering predatory attacks [6]. This form of positive frequency-  
47 dependent selection is thought to be the main force promoting evolutionary convergence  
48 between distantly-related toxic species living in sympatry (i.e. Müllerian mimicry) and  
49 underlying the formation of so-called mimicry “rings” of multiple species sharing a similar  
50 appearance [7–9]. Despite the strong selection for resemblance, several mimicry rings can be

51 found in sympatry in the wild [8]. Moreover, visual signals may still vary within a mimicry  
52 ring, among unpalatable co-mimics, as shown in Arctiid moths [10] and Dendrobatidae frogs  
53 [11], but also between protected species and their less or unprotected mimics (i.e. Batesian  
54 mimics) [12]. Such visual diversity found within mimicry rings is puzzling and its  
55 maintenance is partly linked to the extent to which predators generalise their learnt association  
56 between prey quality and prey appearance. Generalisation capacities on a given signal can  
57 range from very narrow, imposing strong selection on resemblance, to very broad, recognising  
58 as unprofitable morphs bearing phenotypes that are more different from initially learned  
59 signals [13]. This generalisation behaviour is not only determined by the cognitive capacities  
60 of the predator, but it is also shaped by prey community composition [12,14–16]. Indoor  
61 experiments have shown that avian predators generalise more broadly when exposed to a  
62 more phenotypically heterogeneous assemblage of prey, rejecting a more visually diverse  
63 mimicry ring [17]. Whether similar predator reactions can explain the maintenance of several  
64 sympatric mimicry rings and the phenotypic diversity found between species sharing each of  
65 those warning signals is yet to be uncovered.

66 Here we study how the complexity of the prey community and phenotypic similarity  
67 between colour patterns affect the rate of predatory attack on profitable (as Batesian mimics)  
68 and unprofitable prey (as Müllerian mimics) joining several sympatric mimicry rings. To  
69 explore this question, we use a variety of so-called “tiger patterns” made of orange, black and  
70 sometimes yellow patches used by a large number of aposematic butterflies of the Neotropics,  
71 notably defended species in the Ithomiine and Heliconiine (Nymphalidae), day-flying tiger  
72 moths (Arctiidae), and Batesian mimics in the whites (Pieridae) and fritillaries  
73 (Nymphalinae). Tiger patterns are naturally structured into distinct co-existing mimetic  
74 patterns, forming separate mimicry rings involving distinct species (and multiple morphs of  
75 polymorphic species such as *Heliconius numata* [18]). Nevertheless they constitute a family  
76 of patterns which have radiated within clades and which bear some level of phenotypic  
77 continuity, making them a good model to study generalisation by predators. The survival  
78 benefit related to phenotypic similarity among tiger patterns has already been evaluated in  
79 natural populations. Using artificial butterflies displaying (1) two local mimetic forms and (2)  
80 rare natural intermediate patterns, Arias et al. [19] found that intermediate morphs were more  
81 heavily attacked, and that attack rates on intermediate colour patterns were reduced by (1) the  
82 resemblance to a local form, and (2) the level of similarity of the two local forms. These  
83 results suggest that generalisation promotes protection of non-identical but similar Müllerian

84 mimics. However, natural predators may be exposed to more than two distinct warning  
85 signals in natural populations and generalisation is also important to understand Batesian  
86 mimicry. Yet, the low attack rates in experiments using artificial prey placed in the wild limit  
87 the possibility to investigate predator behaviour facing a larger range of visual and chemical  
88 variation (ranging from 2.3% to 12.72% on studies using artificial prey in tropical  
89 communities [19–23]).

90         Although using artificial prey in natural populations allows directly estimating  
91 selection exerted by natural communities of predators such as different bird species, tests with  
92 humans can cover a larger and more detailed range of visual variation associated with  
93 differences in prey protection. Despite difference in brain structure [24,25], primates and birds  
94 share several cognitive skills [26–28]. Using humans as surrogate predators has proven useful  
95 in the study of generalisation of visual cues [29,30] even though birds have a larger sensitivity  
96 spectrum and a higher colour discrimination than humans [31,32]. Experiments with humans  
97 have been used to investigate whether colour patterns cryptic at a distance can involve  
98 signalling at closer range (i.e. distance dependent dual function) [33], to study the evolution of  
99 non-conspicuous traits signalling unprofitability [34], of transparency in conspicuously  
100 coloured and unpalatable butterflies [35], and of slow movement behaviours in protected prey  
101 [36]. Humans produced similar reactions to natural predators of butterflies. For example, both  
102 non-tropical [37] and wild tropical avian predators [22], as well as humans [38] considered  
103 aggregation of conspicuous prey as an unprofitability signal. Moreover, under the same  
104 experimental design, blue tits [39] and humans [30] showed similar abilities to distinguish  
105 profitable from unprofitable prey, focusing more on salient colour cues than on pattern or  
106 shape information. Colour pattern has also been shown to be one of the salient cues used by  
107 tropical predators such as jacamars to differentiate palatable from unpalatable prey [40,41].  
108 All these studies show that human generalisation resembles tropical and non-tropical avian  
109 predator behaviour sufficiently to allow using human predators to investigate specific  
110 questions otherwise difficult to address in other experimental conditions.

111         To investigate the generalisation capacities of vertebrate predators in different  
112 contexts of prey community composition, we used a computer game where human predators  
113 had to sample flying profitable and unprofitable butterflies displaying a variety of wing  
114 patterns. Our results highlight interesting differences in predator generalisation in response to  
115 the warning signal distribution of profitable and unprofitable prey.

116 **Materials and methods**

117 Butterfly images

118 We used a computer game (see below) where human predators had to sample flying  
119 butterflies displaying a variety of wing patterns. The wing patterns were built using individual  
120 butterfly photographs from our specimen databases collected from a butterfly fauna in  
121 Northern Peru. In those communities, tiger-patterned butterflies compose up to 7 distinct  
122 warning signals categories, or mimicry rings, although complexity of communities varies  
123 among localities. In the computer game, we used two levels of community complexity. First  
124 (1) we used a complex prey community including five natural mimetic phenotypes displayed  
125 by cohorts of species in natural tiger-patterned communities, and five intermediate  
126 phenotypes rarely found in nature, and used in the field experiment by Arias et al. [19]  
127 (Figure 1a). In total the complex community had 10 possible distinct phenotypes. (2) Second,  
128 we used a subset of four phenotypes to form a simple prey community, used in the field  
129 experiment by Chouteau et al [18]. Because the simple community was composed of the  
130 “mimetic” and non-intermediate phenotypes used in the complex community, the simple  
131 community has fewer morphs which are also more distinct in morphometric space [19,42]. In  
132 nature, phenotypic diversity such as that found in natural populations of *Heliconius numata*  
133 and their *Melinaea* co-mimics seems closer to the simple than to the complex community, as  
134 intermediate forms are rare [18,43]. These butterflies were photographed under standard light  
135 conditions and their photos were directly used in the game.

136

137 Computer game

138 The computer game Hungry birds v2 was developed from a previous version designed for  
139 evolution outreach (Hungry birds v1 was displayed on the *Heliconius* stand of the Royal  
140 Society Exhibition 2014 in London and is available from  
141 [http://heliconius.org/evolving\\_butterflies/](http://heliconius.org/evolving_butterflies/)). Both computer game versions were developed by  
142 FoAM Kernow. Players were asked to catch moving butterflies by touching them on the  
143 screen, simulating hungry predators from a tropical forest. In each trial, two morphs were  
144 randomly assigned as unprofitable, and players had to discover which they were by playing  
145 the game. When a unprofitable morph was touched by a player, a warning message was  
146 displayed on the screen stating ‘Ugh! That butterfly tasted disgusting’. Players were then  
147 prevented from catching any more butterflies for the next 1.3 seconds as a penalty. At the

148 screen top, players could see their constantly decreasing life bar that lasted 13.2 seconds if  
149 players ate no butterfly. The life bar was increased by 1.3 seconds after catching a profitable  
150 butterfly (benefit), and decreased by 1.8 seconds after touching a unprofitable butterfly (cost),  
151 so that players needed to learn and avoid unprofitable prey and to focus their attacks on  
152 profitable prey in order to stay alive for longer. These time parameters were optimised for  
153 human playing on the Hungry birds v1 before the exhibition. To mimic natural conditions, a  
154 maximum of five butterflies appeared simultaneously in the screen, limiting direct  
155 comparison between morphs. Player's motivation stemmed from preventing the life bar from  
156 getting too low (mimicking hunger level) and getting a high score (based on the time each  
157 player stayed alive in the game). Morphs had varying resemblance, allowing us to estimate  
158 how players generalized across morphs while learning and then playing.

159

#### 160 Volunteer players

161 In June 2015 and March 2017, we invited the visitors of the Evolution Gallery (Grande  
162 Galerie de l'Evolution) at the National Museum of Natural History in Paris (France), to play  
163 the game. Hungry Birds v2 was loaded on a Raspberry Pi and accessed by a tablet through  
164 Wi-Fi. We invited people of all ages and we tried to sample both sexes evenly. First, we  
165 informed players that their game results were going to be part of an academic research study,  
166 and made sure they provide an informed verbal consent to participate. We then gave them a  
167 short explanation of the rules of the game. Players were invited to play two or more times,  
168 taking the first time as a familiarization experience. Only players' age (recorded by class:  
169 younger than 10, 10 to 15, 16 to 35, 36 to 50 and older than 50) and number of trials played  
170 were recorded to correct for potential bias. We followed the recommendations from General  
171 Data Protection Regulation (GDPR) for data obtained in the EU, by only collecting volunteer  
172 data needed for the study (player's age, gender and game scores) (1- Relevance criterion), and  
173 by informing volunteers of the use of their results (2- Transparency criterion). Only the trial  
174 where the player scored highest, usually the second one, was included in the analyses.

175

#### 176 Estimation of phenotypic distances and rates of attack

177 Müllerian and Batesian mimicry are promoted by the advantage gained from sharing a  
178 common warning signal. However, this advantage depends on the level of resemblance  
179 between co-mimics. Therefore, we estimated phenotypic similarities between all morph pairs

180 by computing Euclidian distance between the ten morphs on the first 15 components of the  
181 binary PCA. In the game, the two unprofitable morphs were randomly chosen among  
182 available morphs for each trail (four in the simple community, ten in the complex  
183 community), so resemblance between colour patterns of the two unprofitable prey differed  
184 among trials. This allowed us to test if profitable and unprofitable butterflies benefit from  
185 greater protection when they display more similar colour patterns to those exhibited by  
186 protected butterflies. We thus computed the phenotypic distance 1) between the two  
187 unprofitable morphs in the trial, and 2) between each profitable butterfly attacked and the  
188 most similar unprofitable morph. The most similar morph was identified based on the  
189 phenotypic distance computed from binary PCA as described hereafter.

190 Phenotypic distances among morphs were computed using the Colour Pattern Modelling  
191 (CPM) method described in Le Poul et al. [42] and implemented in Matlab [44]. In CPM,  
192 pictures of the butterfly wings used in the game were aligned (using rotation, translation and  
193 rescaling) to a colour pattern model built recursively, minimizing colour pattern differences  
194 between each real wing and the model wing. After alignment, the position of each pixel of the  
195 wing image was considered homologous among all individuals. Phenotypic variations were  
196 then described by Principal Component Analysis (PCA, as shown on Figure 1b), using binary  
197 values for presence/absence of each of the four colour classes (black, orange, yellow, white)  
198 as values for each pixel of the wing image (referred to as binary PCA hereafter).

199 Player variables (ID number associated with the single best trial included for each player,  
200 player age and trial score measured as trial duration) and trial variables (ID of the two  
201 unprofitable morphs, total number and ID of butterflies consumed, as well as order of  
202 sampled butterflies) were recorded. Trials with less than 4 or 10 butterflies sampled, for the  
203 simple and complex community game respectively, were discarded, in order to analyse only  
204 trials where players are likely to have encountered most of the community diversity.

## 205 Statistical analyses

206 Comparing unprofitable attack rate in differently complex prey communities. To explore  
207 whether players learnt to distinguish and avoided unprofitable morphs differently according to  
208 community diversity level, we compared expected vs. observed attack rate per morph. Our  
209 null hypothesis is that protected morphs will be more attacked in the simple than in the  
210 complex community, only because players had 0.5 chance to find an unprofitable morph in  
211 the simple community, while this chance was 0.2 in the complex community. To calculate the



212 expected attack rate under the null hypothesis, we assumed that players had no information  
213 about the profitability of each morph, and all morphs had equal chance to be attacked.  
214 Therefore, we divided the overall number of attacks per game by 4 in the simple community  
215 and by 10 in the complex one, and then we calculated the expected attack rate per morph.  
216 Then, we subtracted the observed attack rate to this expected attack rate. We then fitted a  
217 linear mixed model (LMM), using the deviation from expected attack rates at random as  
218 response variable. We used morph profitability, community type, player age, morph ID and  
219 score as explanatory variables, and game ID as random effect.

220 Generalisation behaviour. To explore differences in profitable morph attack proportion, we  
221 fitted independent generalized linear mixed models (GLMMs), one for each community type,  
222 considering the proportion of attack on each profitable morph on each game (attacks on the  
223 profitable morph M divided by attacks on the closest unprofitable morph, as in Arias et al  
224 2016) as the response variable. We included phenotypic distance to its closest unprofitable  
225 morph, distance between toxic morphs, whether it shared colours (either an orange/black or an  
226 orange/black/yellow combination) with none, one or both toxic morphs of the game, morph  
227 ID and players age and score as explanatory variables. We log-transformed the proportion of  
228 attacks to fit the Normal distribution of the response variable and we included Game ID as a  
229 random factor. Morph ID was included to test for differences in attack between morphs, and  
230 whether differences were related to phenotypic distance. Therefore, we built a morph contrast  
231 matrix according to the average phenotypic distance between the morph and the entire  
232 community, with the first morphs having a high general resemblance to the entire community,  
233 and the last being more different.

234 Mimicry between unprofitable morphs. We also explored whether phenotypic proximity  
235 enhanced protection (decreased attack rate) on unprofitable morphs. For each locality type,  
236 we fitted a GLMM including attack rate (number of attacks on a toxic morph divided by total  
237 number of attacks in the trial) as response variable and phenotypic distance between toxic  
238 morphs, whether unprofitable morphs shared colours, morph ID and player age and score as  
239 explanatory variables.

240

241 Players' behaviour. General player behaviour was studied by including player characteristics  
242 (age and score) on each of the models above described. We found similar behaviours among  
243 players that scored higher. To further explore the best players behaviour, we fitted the same

244 GLMMs described above, to the 5%, 10% and 20% of players with the highest scores.  
245 Additionally, we explored whether players show a learning behaviour similar to the one  
246 reported by experiments on avian predators, where unprofitable prey are sampled at the  
247 beginning of the trial (while predators are acquiring knowledge about the prey community)  
248 and scarcely or not at all afterwards. To explore this, we checked how many players attacked  
249 more unprofitable prey during the first half of the trial. All statistics were computed using R  
250 [45].

251

## 252 **Results**

253 Unprofitable prey are more readily avoided in simple communities

254 Unprofitable prey were avoided in both communities ( $t = 24.237$ ,  $p < 0.001$ ). However, in the  
255 simple community, attack rates on unprofitable prey showed a greater deviation from random  
256 expectation than in the complex community (Figure 2,  $t = 6.442$ ,  $p < 0.001$ , Table S1). This  
257 suggests that players were more successful at avoiding the two unprofitable morphs in the  
258 simple than in the complex community.

259 Profitable morphs were protected by resemblance to unprofitable morphs in complex  
260 communities

261 In the complex community, profitable morphs that looked more similar to an unprofitable  
262 morph suffered fewer attacks by players ( $t = 3.07$ ,  $p < 0.001$ , Table S2). However, sharing  
263 colours with unprofitable morphs was not sufficient to reduce attack rates ( $t = -0.44$ ,  $p = 0.66$ ,  
264 Table S3). By contrast, in the simple community, morphs that resembled an unprofitable  
265 morph were not protected by generalisation ( $t = -0.27$ ,  $p = 0.79$ , Table S3).

266 Do unprofitable morphs benefit from resembling each other?

267 Phenotypic distance between unprofitable morphs had an effect on the attack rate suffered by  
268 unprofitable morphs in both communities. As expected when generalisation behaviour is  
269 involved, the two unprofitable morphs benefited from increased mutual resemblance, and this  
270 was the case in the complex community ( $t = 2.83$ ,  $p = 0.005$ , Table S6). By contrast,  
271 phenotypically distant unprofitable morphs were less attacked in the simple community ( $t = -$   
272  $2.04$ ,  $p = 0.04$ , Table S7), consistent with a specialized identification of each of the four  
273 morphs by players when facing the simple community. This identification could thus be  
274 facilitated by unprofitable morphs that were more phenotypically different. Certain specific

275 morphs were attacked by players at higher rates than others (Tables S1 and S6). These  
276 differences are likely related to the number of games where those morphs were randomly  
277 selected as unprofitable (Figure S1). Trends reported were similar when analysing only the  
278 players with the best performances (Tables S8 and S9).

#### 279 Predator behaviour

280 Players that achieved higher scores avoided more unprofitable morphs in both community  
281 types (simple  $t = -11.9$ ,  $p < 0.001$ ; complex  $t = -9.23$ ,  $p < 0.001$ , Figure 2, Tables S4 & S5).  
282 However, when studying players' learning behaviour, we noticed that just 20 out of 449  
283 players attacked more unprofitable butterflies on the first than on the second half of the  
284 experimental trial, in contrast to avian predators that learn prey unprofitability during the first  
285 sampling events and then avoid them. Player age had no effect on their performance on the  
286 experiment (Tables S1-S9).

287

## 288 **Discussion**

### 289 Generalisation behaviour observed in humans

290 Here we used a videogame to investigate the generalisation behaviour of predators  
291 toward warning signals naturally displayed by mimetic butterflies in tropical forests. Players,  
292 especially those with the highest scores in the game, managed to recognize and avoid wing  
293 colour patterns associated with a cost, in a similar way to birds learning to avoid a warning  
294 signal associated with a repulsive taste [9,46]. This learnt aversion towards unprofitable forms  
295 was higher in the simple communities (composed of four distinct morphs), where players  
296 were able to discriminate specifically the two unprofitable morphs from the two unprofitable  
297 morphs. Our results may be expected if humans facing a less diverse prey community identify  
298 warning signals more easily, as seen in birds [17]. However, the simple community also lacks  
299 the butterflies with intermediate phenotypes included in the complex community. Therefore,  
300 by definition, morphs in the single community were on average more distinct from their  
301 nearest neighbour in phenotypic space than in the complex community, which may contribute  
302 to making identification easier. Indeed, when playing the complex community version,  
303 players were faced with a large diversity of more similar patterns and the interplay of higher  
304 diversity and higher resemblance could hamper or slow down predators' discrimination  
305 learning. Predator confusion while foraging on communities composed of multiple warning

306 signals may therefore trigger players (receivers) to generalise more widely, as has been  
307 suggested for complex communities of velvet ants [47], benefiting Batesian “imperfect”  
308 mimics that resembled protected prey. Finally, the generalisation behaviour shown by players  
309 could also be influenced by the availability of alternative prey: if profitable prey are rarer, as  
310 in the simple community, the gain in identifying profitable prey that look like unprofitable  
311 ones is higher. By contrast, when profitable alternative prey are more frequent, as the 80% of  
312 prey composing the complex community, ignoring certain profitable prey generates lower  
313 opportunity costs, lowering the incentive in discriminating prey resembling unprofitable  
314 models. Models investigating condition-dependent predator behaviour show that imperfect  
315 mimicry (i.e. wide generalisation) can be favoured when alternative profitable prey are  
316 abundant [48]. However, the frequency at which each morph is presented is higher in the  
317 simple community, increasing players’ familiarity with each morph. Therefore, the simple  
318 community gives players more opportunity to learn the value of each morph (i.e. whether  
319 each morph is palatable or not). Therefore, although predators have more pressure to learn to  
320 identify unpalatable morphs at lower abundances of alternative prey, they also have better  
321 knowledge per prey type, and both processes can lead to a better discrimination in the simple  
322 community. In our study, and as is probably the case in some natural communities, we cannot  
323 disentangle the effects of diversity of colour pattern in the community from abundance of  
324 palatable prey. However, generalisation seems stronger in complex than in simple  
325 communities, although explaining the mechanism behind **this** goes beyond our study, and will  
326 hopefully be the aim of future investigations.

327         The generalisation behaviour detected in humans is consistent with evidence from  
328 field experiments on the same colour patterns, showing that avian predators tend to avoid  
329 butterflies looking similar to the locally defended morphs [19]. Similar studies using  
330 strikingly different prey phenotypes shown to humans as surrogate predators [29,30], and  
331 avian predators [49,50], report colour sharing as the salient signal used by observers to  
332 generalise among morphs or discriminate profitable from unprofitable prey. Our contrasting  
333 results suggest that overall similarity rather than just colour sharing might be at play when  
334 generalising and discriminating in complex communities of resembling prey. In natural  
335 populations of jacamars, body shape and, to a lower extent, flight behaviour and colour  
336 pattern, were all used to discriminate palatable and unpalatable butterflies [41]. This suggests  
337 that signal salience of colour is context dependent and that diverse visual cues can be involved  
338 in discrimination and generalisation.

339           Smaller phenotypic distances between unprofitable prey enhanced morph protection in  
340 the complex community. This follows the Müllerian mimicry expectations, as the similarity  
341 among protected prey favours generalisation of warning signal and thus, protection of all prey  
342 sharing it [6,51]. Generalisation also enhanced survival of imperfect Batesian mimics in the  
343 complex community in our videogame. By contrast, when facing a lower diversity of  
344 unprofitable forms, players recognised each form independently, without looking for common  
345 elements among them, suggesting that resemblance was not conferring additional advantages  
346 to either profitable or unprofitable mimics. Whether predators would react similarly in a  
347 simple community where morphs resemble each other and that offers more alternative prey,  
348 remains an open question.

349

350   Humans as a relevant proxy for investigating predation behaviours

351           Here we found relevant similarities in the generalisation of humans as compared to the  
352 output of natural communities of predators, despite differences in their visual systems and  
353 decision-making processes. Although players that scored highest indeed avoided more  
354 unprofitable morphs, attacks on protected morphs were not concentrated at the beginning of  
355 the trial as has been reported for avian predators exposed to unpalatable prey for the first time  
356 [39,52–54]. Probably, the cost of feeding on a protected morph in the game, was similar to  
357 eating slightly unprofitable prey by a bird, and related to predator behaviour that may  
358 continue to attack some defended prey because they can tolerate a certain toxin burden [55].  
359 The relatively limited cost linked to eating unpalatable prey, in comparison to the benefit  
360 associated with profitable morphs is probably shaping the learning behaviour of players in the  
361 game, and could be investigated in the future by changing these penalties in the game.

362

363   Conclusions

364           Our videogame played by humans reproduced natural predator generalisation  
365 behaviours when responding to colour pattern variations similar to those naturally found in  
366 Neotropical butterfly communities. Prey appearance was generalised more in complex  
367 community, perhaps facilitating the evolution of imperfect Batesian mimicry in those  
368 communities. Moreover, Müllerian mimicry was also found to be more beneficial in complex  
369 communities, perhaps revealing certain community conditions that can promote its evolution.

370 Generalisation differences found in our study are likely to reflect generalisation carried on by  
371 actual predators facing complex prey communities in nature. Our study opens questions  
372 regarding the precise effect of colour pattern diversity and abundance of palatable prey in the  
373 increased generalisation in complex communities. Our results therefore shed new light on the  
374 potential role of communities as ecological filters of mimicry evolution and of mimetic  
375 resemblance.

376

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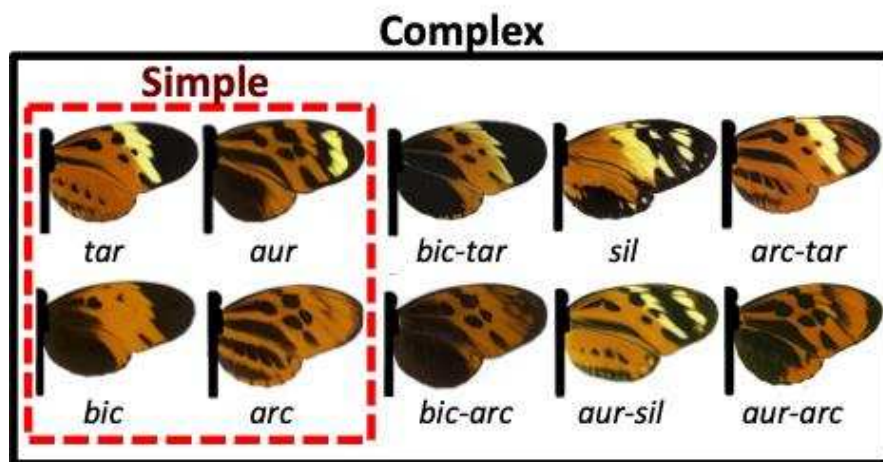
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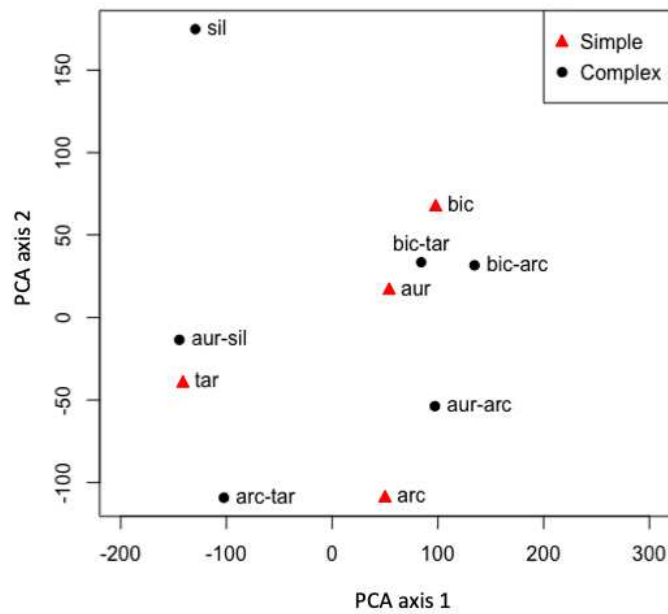
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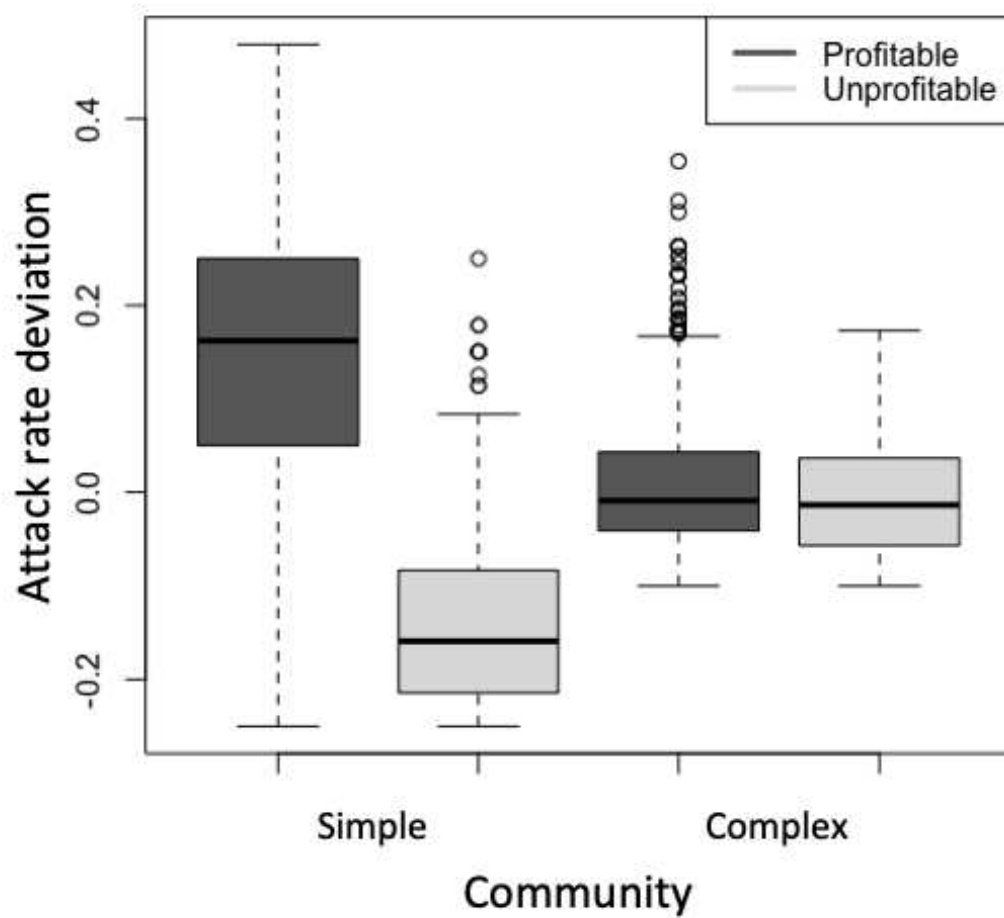
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542 Figure 1. a. *Heliconius numata* morphs displayed on the simple (red/dashed) and complex  
543 (red/dashed and black/solid) and b. their phenotypic distances (red triangles for morphs used on the  
544 simple community and red triangles and black dots for morphs on the complex community). Notice  
545 that the complex community covers a larger morphospace and includes morphs that are very similar  
546 and also distant to others (as the morph *sil*), resulting in a higher diversity (with 10 instead of 4  
547 morphs) that bears and overall higher variance in phenotypic distance.

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549

550 Figure 2. Deviation of observed vs expected attack rate per morph per community according to their  
 551 protection level (profitable in dark grey and unprofitable in light grey).

552