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

Mónica Arias[1,2], John W. Davey[3,4], Simon Martin[4], Chris Jiggins[4], Nicola Nadeau[5], Mathieu Joron[2], Violaine Llaurens[1]

[1] Institut de Systématique, Evolution, Biodiversité, UMR 7205 CNRS-École Pratique des Hautes Études, Muséum National d'Histoire Naturelle, Université Pierre-et-Marie-Curie, 75005 Paris, France

[2] Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175 CNRS-Université de Montpellier, École Pratique des Hautes Études, Université Paul Valéry, 34293 Montpellier 5, France

[3] Bioscience Technology Facility, Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK

[4] Department of Zoology, Downing Street, University of Cambridge, Cambridge, CB2 3EJ, UK

[5] Molecular Ecology Lab, Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

Abstract

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

Keywords: citizen science, imperfect mimicry, Müllerian mimicry, Batesian mimicry, Heliconius

Introduction

Chemically protected prey often sport warning signals advertising their unpalatability to predators [1]. Predators usually learn to associate prey appearance and distastefulness after sampling several aposematic prey bearing a common warning signal [2–5]. Therefore, the larger the number of distasteful prey displaying a common warning signal, the smaller is the risk to individual prey of suffering predatory attacks [6]. This form of positive frequency-dependent selection is thought to be the main force promoting evolutionary convergence between distantly-related toxic species living in sympatry (i.e. Müllerian mimicry) and underlying the formation of so-called mimicry "rings" of multiple species sharing a similar appearance [7–9]. Despite the strong selection for resemblance, several mimicry rings can be found in sympatry in the wild [8]. Moreover, visual signals may still vary within a mimicry ring, among unpalatable co-mimics, as shown in Arctiid moths [10] and Dendrobatidae frogs [11], but also between protected species and their less or unprotected mimics (i.e. Batesian mimics) [12]. Such visual diversity found within mimicry rings is puzzling and its maintenance is partly linked to the extent to which predators generalise their learnt association between prey quality and prey appearance. Generalisation capacities on a given signal can range from very narrow, imposing strong selection on resemblance, to very broad, recognising as unprofitable morphs bearing phenotypes that are more different from initially learned signals [13]. This generalisation behaviour is not only determined by the cognitive capacities of the predator, but it is also shaped by prey community composition [12,14–16]. Indoor experiments have shown that avian predators generalise more broadly when exposed to a more phenotypically heterogeneous assemblage of prey, rejecting a more visually diverse mimicry ring [17]. Whether similar predator reactions can explain the maintenance of several sympatric mimicry rings and the phenotypic diversity found between species sharing each of those warning signals is yet to be uncovered.

Here we study how the complexity of the prey community and phenotypic similarity between colour patterns affect the rate of predatory attack on profitable (as Batesian mimics) and unprofitable prey (as Müllerian mimics) joining several sympatric mimicry rings. To explore this question, we use a variety of so-called “tiger patterns” made of orange, black and sometimes yellow patches used by a large number of aposematic butterflies of the Neotropics, notably defended species in the Ithomiine and Heliconiine (Nymphalidae), day-flying tiger moths (Arctiidae), and Batesian mimics in the whites (Pieridae) and fritillaries (Nymphalinae). Tiger patterns are naturally structured into distinct co-existing mimetic patterns, forming separate mimicry rings involving distinct species (and multiple morphs of polymorphic species such as Heliconius numata [18]). Nevertheless they constitute a family of patterns which have radiated within clades and which bear some level of phenotypic continuity, making them a good model to study generalisation by predators. The survival benefit related to phenotypic similarity among tiger patterns has already been evaluated in natural populations. Using artificial butterflies displaying (1) two local mimetic forms and (2) rare natural intermediate patterns, Arias et al. [19] found that intermediate morphs were more heavily attacked, and that attack rates on intermediate colour patterns were reduced by (1) the resemblance to a local form, and (2) the level of similarity of the two local forms. These results suggest that generalisation promotes protection of non-identical but similar Müllerian mimics. However, natural predators may be exposed to more than two distinct warning signals in natural populations and generalisation is also important to understand Batesian mimicry. Yet, the low attack rates in experiments using artificial prey placed in the wild limit the possibility to investigate predator behaviour facing a larger range of visual and chemical variation (ranging from 2.3% to 12.72% on studies using artificial prey in tropical communities [19–23]).

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

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

Materials and methods

Butterfly images

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

Computer game

The computer game Hungry birds v2 was developed from a previous version designed for evolution outreach (Hungry birds v1 was displayed on the Heliconius stand of the Royal Society Exhibition 2014 in London and is available from http://heliconius.org/evolving_butterflies/). Both computer game versions were developed by FoAM Kernow. Players were asked to catch moving butterflies by touching them on the screen, simulating hungry predators from a tropical forest. In each trial, two morphs were randomly assigned as unprofitable, and players had to discover which they were by playing the game. When a unprofitable morph was touched by a player, a warning message was displayed on the screen stating 'Ugh! That butterfly tasted disgusting'. Players were then prevented from catching any more butterflies for the next 1.3 seconds as a penalty. At the screen top, players could see their constantly decreasing life bar that lasted 13.2 seconds if players ate no butterfly. The life bar was increased by 1.3 seconds after catching a profitable butterfly (benefit), and decreased by 1.8 seconds after touching a unprofitable butterfly (cost), so that players needed to learn and avoid unprofitable prey and to focus their attacks on profitable prey in order to stay alive for longer. These time parameters were optimised for human playing on the Hungry birds v1 before the exhibition. To mimic natural conditions, a maximum of five butterflies appeared simultaneously in the screen, limiting direct comparison between morphs. Player's motivation stemmed from preventing the life bar from getting too low (mimicking hunger level) and getting a high score (based on the time each player stayed alive in the game). Morphs had varying resemblance, allowing us to estimate how players generalized across morphs while learning and then playing.

Volunteer players

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

Estimation of phenotypic distances and rates of attack

Müllerian and Batesian mimicry are promoted by the advantage gained from sharing a common warning signal. However, this advantage depends on the level of resemblance between co-mimics. Therefore, we estimated phenotypic similarities between all morph pairs by computing Euclidian distance between the ten morphs on the first 15 components of the binary PCA. In the game, the two unprofitable morphs were randomly chosen among available morphs for each trail (four in the simple community, ten in the complex community), so resemblance between colour patterns of the two unprofitable prey differed among trials. This allowed us to test if profitable and unprofitable butterflies benefit from greater protection when they display more similar colour patterns to those exhibited by protected butterflies. We thus computed the phenotypic distance 1) between the two unprofitable morphs in the trial, and 2) between each profitable butterfly attacked and the most similar unprofitable morph. The most similar morph was identified based on the phenotypic distance computed from binary PCA as described hereafter.

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

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

Statistical analyses

Comparing unprofitable attack rate in differently complex prey communities. To explore whether players learnt to distinguish and avoided unprofitable morphs differently according to community diversity level, we compared expected vs. observed attack rate per morph. Our null hypothesis is that protected morphs will be more attacked in the simple than in the complex community, only because players had 0.5 chance to find an unprofitable morph in the simple community, while this chance was 0.2 in the complex community. To calculate the expected attack rate under the null hypothesis, we assumed that players had no information about the profitability of each morph, and all morphs had equal chance to be attacked. Therefore, we divided the overall number of attacks per game by 4 in the simple community and by 10 in the complex one, and then we calculated the expected attack rate per morph. Then, we subtracted the observed attack rate to this expected attack rate. We then fitted a linear mixed model (LMM), using the deviation from expected attack rates at random as response variable. We used morph profitability, community type, player age, morph ID and score as explanatory variables, and game ID as random effect.

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

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

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

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

Results

Unprofitable prey are more readily avoided in simple communities

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

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

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

Do unprofitable morphs benefit from resembling each other?

Phenotypic distance between unprofitable morphs had an effect on the attack rate suffered by unprofitable morphs in both communities. As expected when generalisation behaviour is involved, the two unprofitable morphs benefited from increased mutual resemblance, ant his was the case in the complex community (t = 2.83, p = 0.005, Table S6). By contrast, phenotypically distant unprofitable morphs were less attacked in the simple community (t = -2.04, p = 0.04, Table S7), consistent with a specialized identification of each of the four morphs by players when facing the simple community. This identification could thus be facilitated by unprofitable morphs that were more phenotypically different. Certain specific morphs were attacked by players at higher rates than others (Tables S1 and S6). These differences are likely related to the number of games where those morphs where randomly selected as unprofitable (Figure S1). Trends reported were similar when analysing only the players with the best performances (Tables S8 and S9).

Predator behaviour

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

Discussion

Generalisation behaviour observed in humans

Here we used a videogame to investigate the generalisation behaviour of predators toward warning signals naturally displayed by mimetic butterflies in tropical forests. Players, especially those with the highest scores in the game, managed to recognize and avoid wing colour patterns associated with a cost, in a similar way to birds learning to avoid a warning signal associated with a repulsive taste [9,46]. This learnt aversion towards unprofitable forms was higher in the simple communities (composed of four distinct morphs), where players were able to discriminate specifically the two unprofitable morphs from the two unprofitable morphs. Our results may be expected if humans facing a less diverse prey community identify warning signals more easily, as seen in birds [17]. However, the simple community also lacks the butterflies with intermediate phenotypes included in the complex community. Therefore, by definition, morphs in the single community were on average more distinct from their nearest neighbour in phenotypic space than in the complex community, which may contribute to making identification easier. Indeed, when playing the complex community version, players were faced with a large diversity of more similar patterns and the interplay of higher diversity and higher resemblance could hamper or slow down predators' discrimination learning. Predator confusion while foraging on communities composed of multiple warning signals may therefore trigger players (receivers) to generalise more widely, as has been suggested for complex communities of velvet ants [47], benefiting Batesian "imperfect" mimics that resembled protected prey. Finally, the generalisation behaviour shown by players could also be influenced by the availability of alternative prey: if profitable prey are rarer, as in the simple community, the gain in identifying profitable prey that look like unprofitable ones is higher. By contrast, when profitable alternative prey are more frequent, as the 80% of prey composing the complex community, ignoring certain profitable prey generates lower opportunity costs, lowering the incentive in discriminating prey resembling unprofitable models. Models investigating condition-dependent predator behaviour show that imperfect mimicry (i.e. wide generalisation) can be favoured when alternative profitable prey are abundant [48]. However, the frequency at which each morph is presented is higher in the simple community, increasing players' familiarity with each morph. Therefore, the simple community gives players more opportunity to learn the value of each morph (i.e. whether each morph is palatable or not). Therefore, although predators have more pressure to learn to identify unpalatable morphs at lower abundances of alternative prey, they also have better knowledge per prey type, and both processes can lead to a better discrimination in the simple community. In our study, and as is probably the case in some natural communities, we cannot disentangle the effects of diversity of colour pattern in the community from abundance of palatable prey. However, generalisation seems stronger in complex than in simple communities, although explaining the mechanism behind this goes beyond our study, and will hopefully be the aim of future investigations.

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

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

Humans as a relevant proxy for investigating predation behaviours

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

Conclusions

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

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

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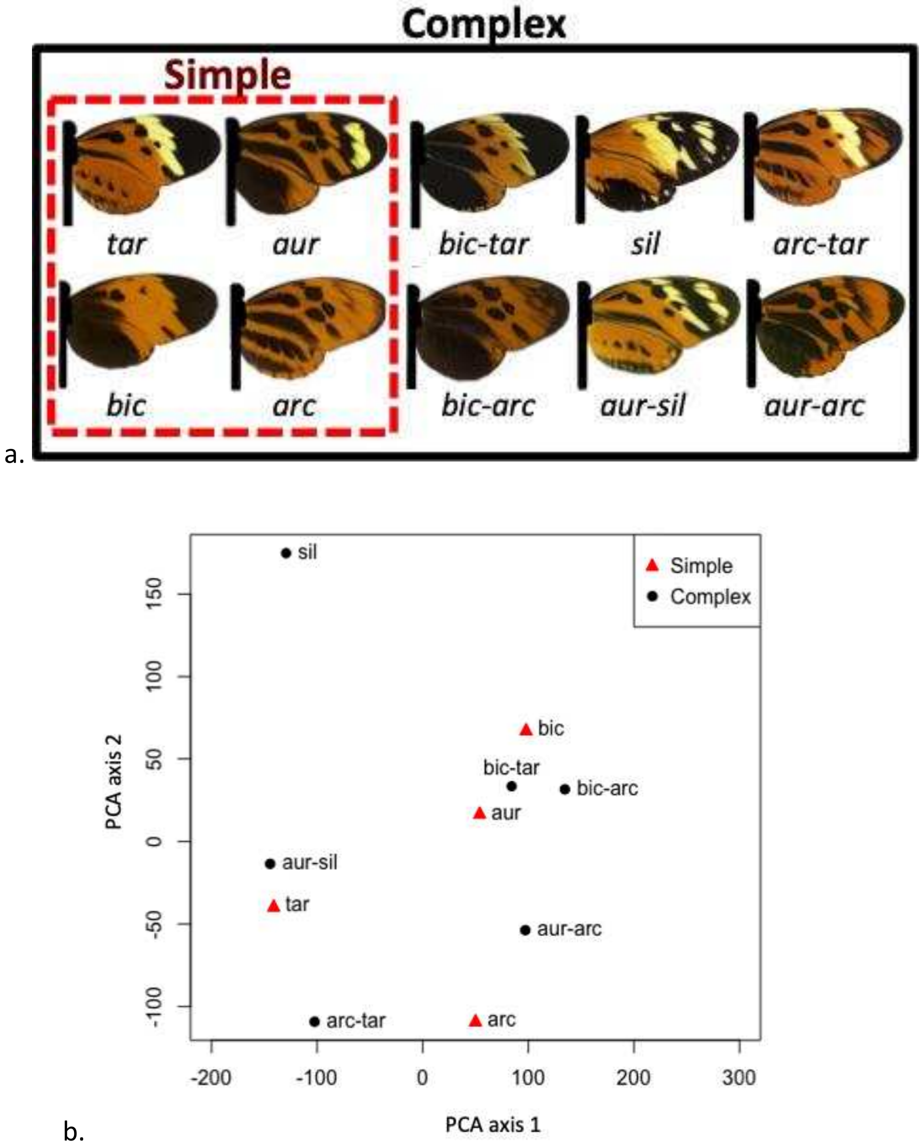

Figure 1. a. *Heliconius numata* morphs displayed on the simple (red/dashed) and complex (red/dashed and black/solid) and b. their phenotypic distances (red triangles for morphs used on the simple community and red triangles and black dots for morphs on the complex community). Notice that the complex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

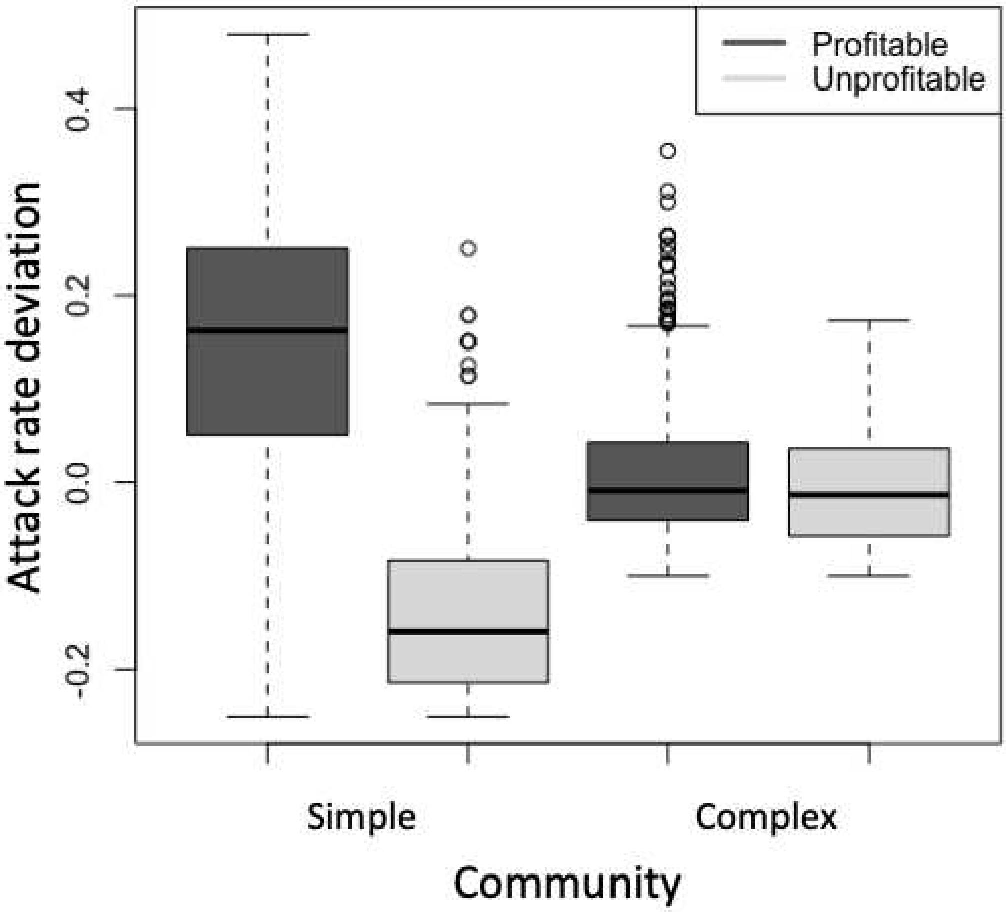

Figure 2. Deviation of observed vs expected attack rate per morph per community according to their protection level (profitable in dark grey and unprofitable in light grey).