Mimicry among Unequally Defended Prey Should Be Mutualistic When Predators Sample Optimally

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Abstract: Understanding the conditions under which moderately defended prey evolve to resemble better-defended prey and whether this mimicry is parasitic (quasi-Batesian) or mutualistic (Müllerian) is central to our understanding of warning signals. Models of predator learning generally predict quasi-Batesian relationships. However, predators’ attack decisions are based not only on learning alone but also on the potential future rewards. We identify the optimal sampling strategy of predators capable of classifying prey into different profitability categories and contrast the implications of these rules for mimicry evolution with a classical Pavlovian model based on conditioning. In both cases, the presence of moderately unprofitable mimics causes an increase in overall consumption. However, in the case of the optimal sampling strategy, this increase in consumption is typically outweighed by the increase in overall density of prey sharing the model appearance (a dilution effect), causing a decrease in mortality. It suggests that if predators forage efficiently to maximize their long-term payoff, genuine quasi-Batesian mimicry should be rare, which may explain the scarcity of evidence for it in nature. Nevertheless, we show that when moderately defended mimics are profitable to attack by hungry predators, then they can be parasitic on their models, just as classical Batesian mimics are.

Keywords: Pavlovian conditioning, dynamic programming, Bayesian inference, optimal foraging, quasi-Batesian mimicry, Müllerian mimicry.

Introduction

Warning signal mimicry is widespread and may play a considerable role in structuring ecological communities (Gross 2008). For decades, researchers have attempted to understand the evolution of mimicry between defended prey by elucidating the consequences of simple heuristic rules of associative learning by predators. Indeed, in the seminal article on this subject, Müller (1879) conjectured that predators will sample a fixed number of specimens of each distinct unpalatable prey type before avoiding them altogether and proposed that this would lead to selection for a common appearance among defended species (Müllerian mimicry). However, it has long been appreciated that there is wide intra- and interspecific variation in the nature of prey defenses, as well as the nutrients individual prey items provide. Dixey (1909, p. 564), for example, asserted that “distastefulness is relative; that it exists, like other means of defense, in degrees that may vary indefinitely from species to species.” Likewise, Nicholson (1927, p. 34) noted that “every intergrade appears to exist between the most distasteful species and those which are palatable to all predators.” Even within a species, individuals frequently show wide variation in their levels of defense (for review, see Speed et al. 2012). Thus, if we are to fully understand warning signal mimicry among defended species, we need to elucidate the selection pressures on species when they vary in their defense.

Following Müller’s seminal contribution, a wide range of models of predator sampling behavior have been explored to determine the nature of mimicry between prey with unequal defenses. For example, Huheey (1964, 1976) proposed that a predator will avoid attacking a prey type it has just found unpalatable for a fixed number of subsequent encounters and showed that this rule would result in an increase in the attack rates on more unpalatable models as the frequency of less unpalatable mimics increased. Similarly, Speed (1993) assumed a learning algorithm based on a Pavlovian model of conditioning in which the attack probabilities of a predator on a given novel type of prey start at 0.5 and move toward a characteristic asymptotic attack probability for that prey type. Just as Huheey (1976) had reported, he showed that one consequence of this form of aversion learning is that an increase in the density of moderately unpalatable mimics
can cause an increase in the probability of attack on the more unpalatable models. Speed (1990, 1993) dubbed this parasitic form of mimicry “quasi-Batesian mimicry,” and it appears a widespread feature of many models of aversion learning. Indeed, in a systematic evaluation of the consequences of 29 different models of predator learning, 27 of them were found to be capable of generating quasi-Batesian mimicry—although not all of them predict it for a wide range of parameters (Speed and Turner 1999; Turner and Speed 1999). Recent studies based on related models have likewise reported the potential for quasi-Batesian mimicry (Balogh et al. 2008; Honma et al. 2008).

The possibility that aversion learning by predators could generate quasi-Batesian mimicry has far-reaching consequences. In particular, if the attack rates on both highly unpalatable models and their moderately unpalatable mimics increase as the frequency of mimics rises, then it may benefit some of the mimics to resemble an alternative model. This negative frequency dependence could in theory explain certain puzzling cases of polymorphism in unpalatable prey, such as that seen in the chemically defended ladybird Adalia bipunctata and the butterfly Heliconius doris (Speed 1993). However, so far the experimental evidence for quasi-Batesian mimicry has been somewhat mixed (Speed et al. 2000; Rowland et al. 2007, 2010), and quasi-Batesian mimicry has never been clearly demonstrated in nature.

Today, our understanding of predator behavior goes beyond associative learning. In particular, learning is simply a means to an end (maximizing payoff), and so predators may decide not to sample further if the future rewards, including the information value, are estimated to be low (Skelhorn et al. 2016). Moreover, the type of associative learning that has been generally assumed in mathematical models of mimicry tends to produce nonadaptive behaviors. For instance, as argued by Mallet and Joron (1999), the probabilistic decision rules (partial preferences; Pulliam 1974) for attacking models/mimics that have been widely assumed are maladaptive in the long term; predators should eventually learn to avoid attacking a given prey type entirely if such prey are on average unprofitable or always attack such prey if they are on average profitable. Given that it is not adaptive, then focusing exclusively on such models is likely to lead to inconsistent conclusions.

Here we lift this important limitation and thereby move toward a better understanding of how predator behaviors shape mimetic relationships. Our approach recognizes that a predator’s decision to attack an unfamiliar prey item is essentially an exploration-exploitation trade-off (Cohen et al. 2007). Thus, if a predator attacks many prey items of a given type and they turn out to be largely unprofitable, then it will have gained considerable information about the nature of the prey type, but it would not have exploited the knowledge to its best possible advantage. Conversely, if the predator exploits its current belief too soon by avoiding a prey type after limited bad experiences, then it may ultimately be missing out on a prey type that is largely profitable. Sherratt (2011) formalized mathematically this exploration-exploitation trade-off, coupling learning and adaptive foraging decisions, and showed that it could readily explain the observed rise in the number of unprofitable prey attacked with prey density, as well as the generation of spatial mosaics of mimetic phenotypes (Aubier and Sherratt 2015).

To define the nature of mimicry between prey with unequal defenses, we begin from the ground up, by identifying from first principles how predators should behave when they encounter relatively unfamiliar prey items that could potentially belong to one of a range of profitability categories—lifting the restriction of bimodal profitability assumed in the original model (Sherratt 2011). By elucidating the optimal strategy based on the most judicious use of available information, we gain insight as to how predators subject to natural selection would be expected to forage. Once characterized, we elucidate the conditions under which the optimal sampling strategy would lead to parasitic or mutualistic mimetic relationships between prey with unequal defenses. In particular, we provide a formal comparison of the selection imposed by optimally sampling predators with that imposed by Pavlovian predators (Speed 1993). To our knowledge, this is the first model to evaluate the prevalence of quasi-Batesian mimicry based on adaptive predator sampling behavior. Our results suggest that, in contrast to the selection imposed by Pavlovian predators, parasitic quasi-Batesian mimicry should be rare when predators sample optimally, which may explain the scarcity of evidence for it in nature.

Methods

We evaluate the prevalence of parasitic quasi-Batesian mimicry among unequal defended prey under two different models of predation. Pavlovian predators (Speed 1993) adopt probabilistic decision rules for attacking prey based on classical conditioning. Optimal predators identify the payoff-maximizing response to encountering prey of a given appearance (attack or reject) based on the predators’ current information and an understanding of how their knowledge may change if they continue to attack.

Pavlovian Predator

To model the psychology of predation, Speed (1993) assumed that predators would respond to prey in a Pavlovian fashion in which a stimulus (prey of a given appearance) evokes a behavior (probability of attack) that is subsequently modified by experience (depending on how palatable it found the prey). Specifically, the probability $P_i$ of a predator attacking
a prey with an unfamiliar appearance on encounter is assumed to start at 0.5 but is subsequently modified by

\[ \Delta P_i = (0.5 + |\lambda_i - 0.5|)(\lambda_i - P_i), \]  

(1)

where \( \lambda_i \) is the stable attack probability brought about by learning alone on prey belonging to the palatability class \( i \) of the prey item attacked. To represent forgetting, the probability of attack is also modified at each trial (after encountering the prey, irrespective of attack) by

\[ \Delta P_i = a_i(0.5 - P_i), \]  

(2)

with \( a_i \) the rate of forgetting; its value is fixed at 0.02, as in the original model.

Thus, the crucial set of parameters in this model are the \( \lambda_i \) values associated with palatability classes. They simultaneously represent the limiting values of \( P_i \) on prey belonging to a given palatability class \( i \) in the absence of forgetting and dictate the rate at which \( P_i \) converges on this asymptote. In essence, the \( \lambda_i \) values are intended to reflect some function of prey palatability, such that prey types with higher \( \lambda_i \) have higher asymptotic attack rates on encounter. Consumption of a species with \( \lambda_i = 0.5 \) will not alter subsequent attack rates, and such species are therefore regarded as neutrally palatable, while species with \( \lambda_i < 0.5 \) are regarded as unpalatable. In typical simulations with models and identical-looking mimics that differ in palatability, Pavlovian predators are effectively on an emotional roller coaster, repeatedly increasing and decreasing their probability of future attack after attacking prey.

**Optimal Predator**

Contrary to Pavlovian predators, optimal predators sample prey as part of a strategy to maximize their expected future payoff. Thus, the costs or benefits of attacking prey are considered explicitly rather than indirectly through a notion of palatability. An optimal predator that lacks complete information will necessarily revise its beliefs based on its experience. In turn, these beliefs help shape the decision as to whether to attack a given prey item that it has just encountered. Following Sherratt (2011), our exploration-exploitation model combines a representation of learning (Bayesian inference; Bolker 2008) with a multistage optimization algorithm for identifying the long-term payoff-maximizing decision, based on its current information (dynamic programming; Clark and Mangel 2000). The optimal decision is identified simply by comparing the known future payoff to a predator if the prey item is rejected (i.e., a payoff of 0) with the estimated future payoff from attacking it, based on its current estimate of the average (un)profitability of the prey type with a given appearance and assuming the continuous use of its optimal decision rules as it learns more about the properties of the prey type.

**Learning.** We assume that optimal predators are able to classify prey into \( k \) different categorical classes \((k \geq 2)\), with \( p_i \) representing the predator’s estimated probability that a given prey item is of class \( i \), drawn from a probability distribution constrained such that \( \sum_{i=1}^{k} p_i = 1 \). We can define the true probability that any given prey item is of class \( i \) as \( P_i \) (again, \( \sum_{i=1}^{k} P_i = 1 \)). Given that the predator is estimating the likelihood of a prey item belonging to two or more discrete classes under the constraint that the probabilities sum to 1, we assume that \( p_i \) is Dirichlet distributed, which is the conjugate prior for a multinomial (Bolker 2008). Thus, the revised (posterior) hypothesis distribution following classical Bayesian inference after sampling will also follow a Dirichlet distribution, albeit with different parameters based on its experience. The Dirichlet is a continuous probability distribution for the likelihood \( p_i \) that a prey item is a member of each of the \( i \)th class (hence multivariate) with concentration parameters \( \alpha_1, \ldots, \alpha_k \) and expectation \( \pi_i = \alpha_i / \sum_{i=1}^{k} \alpha_i \), so that \( \sum_{i=1}^{k} \pi_i = 1 \) (see fig. S1 for details about the Dirichlet distribution; figs. S1–S11 available online).

As the Dirichlet distribution is the conjugate prior of the multinomial, then following sampling of \( r_i \) individuals belonging to class \( i \), the posterior will again follow a Dirichlet, this time with expectation

\[ \pi_i = \frac{\alpha_i + r_i}{\sum_{i=1}^{k} (\alpha_i + r_i)}. \]  

(3)

Note that as more information is collected, it has an increasingly strong effect on the posterior distribution, such that as \( r_i \) increases, the expected probability \( \pi_i \) approaches the limit of \( r_i / (\sum_{i=1}^{k} r_i) \) (fig. 1a). Conversely, the concentration parameters \( \alpha_i \) are in the same dimension as the number of prey types sampled. If their values are high, the information gained by sampling (through \( r_i \) values) has less effect on the posterior distribution.

**Dynamic Programming.** Let \( N \) be the total number of an unfamiliar prey type with a given appearance that the optimal predator can potentially sample in its lifetime. Let \( r_i \) be the number of prey class \( i \) it has so far attacked \((\sum_{i=1}^{k} r_i = n \leq N, \text{ with } n \text{ the total number of prey attacked})\). Attacking an individual from class \( i \) provides a payoff \( f_i \), which may be positive or negative depending on whether it is profitable or unprofitable and may vary in size according to how (un)-profitable it is. With any given predator knowledge state \((r_1, \ldots, r_k)\), let the maximum payoff from the remaining \((N - n)\) trials be represented \( S(r_1, \ldots, r_k) \).

Not attacking prey (defer [D]) of the unfamiliar type in the remaining \((N - n)\) trials gives a long-term known future reward of \( S_\infty(r_1, \ldots, r_k) \) \((= 0)\) for the behavior. By contrast, at the risk of sampling unprofitable prey, attacking (attack [A]) unfamiliar prey of this type will increase the
goodExpectations: expected probabilities increased through Bayesian updating. Therefore, by sampling prey, the long-term rewards from attacking the prey are increased. Prey belong to three palatability classes associated with the appearance and updates the expected probabilities $(\pi_i)$. At each trial, the predator can attack the prey it has encountered or not. If the predator samples the prey it has encountered or runs out of prey. A predator with uniform attack rate $\lambda \in [0, 1]$, while its corresponding palatability class $i$ is defined by its net payoff $f_i \in \mathbb{R}$. An unpalatable/unprofitable class is therefore characterized by $\lambda_i < 0.5$ and $f_i < 0$ and a palatable/profitable class by $\lambda_i > 0.5$ and $f_i > 0$.

Comparison of Pavlovian and Optimal Predators

Palatability/Profitability Classes. Models of Pavlovian predation emphasize the response of a predator to prey with given profitability through $\lambda$ values (hereafter referred to as palatability) and do not consider prey profitability explicitly. By contrast, in order to identify the strategy adopted by the optimal predators, we consider prey profitability explicitly and deduce the payoff-maximizing response. A palatability class $i$ is defined by its asymptotic attack rate $\lambda_i \in [0, 1]$, while its corresponding palatability class $i$ is defined by its net payoff $f_i \in \mathbb{R}$. An unpalatable/unprofitable class is therefore characterized by $\lambda_i < 0.5$ and $f_i < 0$ and a palatable/profitable class by $\lambda_i > 0.5$ and $f_i > 0$.

judged to be less than deferring ($S_a < S_b$), the predator ceases attacking prey with this appearance and does not update its expectations anymore (b). The R code for simulations used for the graphs in this article is available from the Dryad Digital Repository (Aubier et al. 2017).
Normalized Palatability/Profitability. To conduct sensitivity analyses along the palatability/profitability spectrum, we transform the palatability $\lambda$ and profitability $f_i$ values into normalized $\lambda_i$ and $f_i$ values as follows:

$$\dot{\lambda}_i = -\frac{\lambda_i - 0.5}{\lambda_{bad} - 0.5},$$  

(7)  

$$\dot{f}_i = \frac{f_i}{f_{bad}},$$  

(8)  

with $\lambda_{bad}$ and $f_{bad}$ the asymptotic attack rate and the payoff of the most unpalatable/unprofitable class, respectively; $\lambda_i > 0$ and $f_i > 0$ characterize palatable/profitable classes, whereas $\lambda_i < 0$ and $f_i < 0$ characterize unpalatable/unprofitable classes. If $\lambda_i = -1$ and $f_i = -1$, the palatability/profitability class $i$ is defined by $\lambda_i = \lambda_{bad}$ or $f_i = f_{bad}$.

Heterogeneity in Predator Experience

Hungry predators may find certain prey species profitable to attack, while less hungry individuals may find the same species unprofitable. Likewise, optimal predators may vary in their ability to deal with certain species, for example, by tolerating their toxins or employing an attack technique that reduces their chances of injury. To account for this heterogeneity of experience among predators, we vary the profitability to predators from attacking prey from each class. We choose not to evaluate analogous variations of $\lambda$ in the Pavlovian predator because this is not the focus of our interest. Here the payoff associated with each class for each predator is drawn from a normal distribution with mean $f_i$ and standard deviation $\sigma_i$ (same standard deviation for all (un)profitability classes $i$). To investigate genuine cases of quasi-Batesian mimicry, we constrain $f_i$ values, such that unprofitable and profitable classes always incur a cost and a benefit to predators, respectively—yet this assumption is relaxed in supplementary analyses (fig. S11).

Explorations

We explored the implications of predation on mimicry under four different scenarios (summarized in table 1), with both Pavlovian and optimal predators.

General Conditions. We explore situations where predators are confronted with prey with unfamiliar appearances. Predators encounter all prey available and are assumed to treat prey with distinct appearances separately. Prey of each appearance can potentially belong to more than one palatability/profitability class.

For ease of representation, in most numerical explorations, we explore situations where unfamiliar prey can potentially belong to just three possible profitability classes (this assumption is relaxed in exploration 4), with variation in palatability/profitability among individuals of the same appearance a reflection of potential mutualistic and parasitic mimicry among species. The optimal predator sampling strategy requires that the predators’ classification of prey includes at least one profitable prey class ($f_{good} > 0$) with prior expectation $e_{good} > 0$; otherwise, optimal predators will have no reason to sample. Nevertheless, for all explorations, prey belonging to this profitable class are not present in the communities we implement, yet the predator does not know it before sampling. To explore the implications of the Pavlovian predator under the same conditions, we also allow a prey class with arbitrary palatability $\lambda_{good} = 1$, although since there are no prey from this class in our analyses, then its exact value is of little relevance. We also consider one highly unpalatable/unprofitable class ($\lambda_{bad} \ll 0.5$, $f_{bad} \ll 0$) and one intermediate palatability/profitability class characterized by parameters $\lambda_{int}$ and $f_{int}$ such that $\lambda_{bad} < \lambda_{int} < \lambda_{good}$ and $f_{bad} < f_{int} < f_{good}$. This intermediate palatability/profitability class can be set either palatable/profitable ($\lambda_{int} > 0.5$, $f_{int} > 0$) or moderately unpalatable/unprofitable ($\lambda_{int} < 0.5$, $f_{int} < 0$). The implications of different extents of palatability/profitability are explored under each scenario through the implementation of different values of $\lambda_{int}$ and $f_{int}$.

To assess the selective consequences of predator behavior for prey, we evaluate the mean per capita predation rate on each appearance present in the prey community (see Müller 1879). For each set of conditions, we perform 2,000 forward iterations to determine the mean number of prey sampled by a predator. The per capita predation rate on a given appearance due to the predator sampling behavior is calculated as the number of prey sampled carrying such appearance (until all prey are encountered), divided by the number of such prey originally available. Individuals sharing the same appearance suffer from the same mean per capita predation rate.

Exploration 1. Here we characterize how predators respond to prey with different levels of unpalatability/unprofitability, and we compare the payoffs accruing to Pavlovian and optimal predators directly. We consider a system in which a predator encounters $N$ unfamiliar prey with a single appearance. Prey items belong either to the highly unpalatable/unprofitable class or to the intermediate unpalatability/unprofitability classes (such that $\lambda_{int} < 0.5$, $f_{int} < 0$). We vary the initial density of prey $N$ and the proportion of prey belonging to the intermediate palatability/profitability class.

Exploration 2. Here we ask whether mimicry would evolve as a consequence of the above predatory behaviors, and we evaluate whether this mimicry is mutualistic or parasitic in nature. To do this, we have assumed a community of unfamiliar prey that is composed of prey items with two distinct
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<td>Same as exploration 1</td>
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Note: Explorations conducted with Pavlovian predators were similar, except that profitability classes related to profitability are defined by their asymptotic attack rates $a_{bad} < a_{int}$ and not by their payoffs.

Table 1: Summary of the explorations conducted (from the optimal predator perspective)
appearances. Prey belong either to the highly unpalatable/unprofitable class or to the intermediate palatability/profitability class. There are $N_{\text{model}}$, highly unpalatable/unprofitable prey with a given appearance and $N_{\text{mimic}}$, individuals of the same appearance. These mimics derive from a population of prey that belong to the intermediate palatability/profitability class, leaving $N_{\text{nonmimic}}$ with a distinct appearance. We set densities of the model $N_{\text{model}} = 10$ or $N_{\text{model}} = 50$, and we consider a fixed density of the population of mimics/nonmimics: $N_{\text{mimic}} + N_{\text{nonmimic}} = 50$. Therefore, a proportion $P_{\text{mimic}} = N_{\text{mimic}}/(N_{\text{mimic}} + N_{\text{nonmimic}})$ mimics the model and a proportion $1 - P_{\text{mimic}}$ nonmimics. To elucidate the strength of parasitism/mutualism, we conduct analyses with different $P_{\text{mimic}}$ values.

**Exploration 3.** To confirm that the parasitic and mutualistic mimicry observed in exploration 2 drive selection for mimetic polymorphisms and monomorphisms, respectively, we conduct further simulations. These simulations again considered a community of unfamiliar prey with two distinct appearances and a mimic of the intermediate palatability/profitability but differed in having two rather than one highly unpalatable/unprofitable models (models A and B and no nonmimics). We set densities of the models $N_{\text{modelA}} = N_{\text{modelB}} = 50$, and we consider a fixed density of the mimics: $N_{\text{mimicA}} + N_{\text{mimicB}} = 50$. Among those mimics, a proportion $P_{\text{mimicB}} = N_{\text{mimicB}}/(N_{\text{mimicA}} + N_{\text{mimicB}})$ mimics model B, and a proportion $1 - P_{\text{mimicB}}$ mimics model A. We conduct analyses with different $P_{\text{mimicB}}$ values.

Starting from a condition under which the entire population of the mimic resembles model A ($P_{\text{mimicB}} = 0$), we can determine whether there is a positive selection pressure (which minimizes the per capita predation rate) for the mimic to resemble model B. We can then isolate the $P_{\text{mimicB}}$ value at equilibrium—that is, the smallest $P_{\text{mimicB}}$ values for which mimics resembling model B should not increase in frequency. It allows us to assess the evolutionary dynamics of the mimic appearance, following selection mediated by predation, leading either to monomorphism ($P_{\text{mimicB}} = 0$ or $P_{\text{mimicB}} = 1$ at equilibrium) or to stable balanced polymorphism ($0 < P_{\text{mimicB}} < 1$ at equilibrium).

**Exploration 4.** Here we test whether the optimal sampling strategy depends on the number of expected profitability classes. We consider the same prey communities as in exploration 1, but we explore the situation where optimal predators classify prey into five (instead of three) profitability classes. In addition to the profitable ($f_{\text{prof1}}$), unprofitable ($f_{\text{un}}$), and moderately unprofitable ($f_{\text{unp}}$), we implement two supplementary profitability classes ($f_{\text{app1}}$ and $f_{\text{app2}}$) such that $f_{\text{app1}} < f_{\text{un}} < f_{\text{app2}}$, and $|f_{\text{un}} - f_{\text{app1}}| = |f_{\text{un}} - f_{\text{app2}}|$. The priors associated with the intermediate profitability class and the supplementary profitability classes are now set to 1/3, such that the predator has the same expectation of profitability as exploration 1.

**Results**

*What Is the Optimal Sampling Strategy for Unfamiliar Prey with Two Levels of Unprofitability, and Does This Strategy Achieve a Higher Payoff than a Pavlovian Predator?*

With exploration 1, we identify the optimal sampling strategy for unfamiliar prey when prey with this appearance belong to two unprofitability classes. Optimal predators cease attacking prey with an unfamiliar appearance as soon as they identify rejection as the long-term payoff-maximizing decision (fig. 1b). Figure 2 shows that as the number of prey of a given appearance ($N$) increases, so too does the number of individuals sampled by an optimal predator before complete rejection. Moreover, when prey items are particularly costly to attack should they turn out to be unprofitable (low proportion of moderately unprofitable prey in fig. 2) and/or predators are convinced that the prey are highly unprofitable at the outset (Bayesian priors indicating high unprofitability; see fig. S2), then predators should sample fewer prey before rejection.
The optimal predator responds differently to the highly and moderately unprofitable prey when all prey belong to one unprofitability class, sampling fewer highly unprofitable compared to moderately unprofitable prey (when the proportion of moderately unprofitable prey is equal to 0 vs. equal to 1 in fig. 2). This property suggests that mimicry of highly unprofitable prey might be selected for, even in moderately unprofitable prey.

Overall, the optimal predator achieves a higher cumulative payoff than a Pavlovian predator confronted with the same prey community, especially when the number of prey is high (fig. 3). This result is insensitive to the rate of forgetting of the Pavlovian predator (not shown). However, when the number of prey is low (when \( N = 25 \) in fig. 3), Pavlovian predators receive a slightly higher payoff, because they have a neophobic response attack (probability of attack starts at 0.5), which happens to be higher when the predator is dealing with entirely unprofitable prey. It is easy to show that such behavior would have led to an inferior reward if all prey happened to be profitable.

Using exploration 4, we show that the optimal sampling strategy is robust to the number of possible profitability classes implemented. Indeed, if we implement two other possible classes (i.e., if prey can potentially belong to five profitability classes), the optimal sampling strategy is identical (fig. S3), as long as the predator has the same expectation of profitability (\( \sum \alpha_f i \)).

**Would Moderately Unprofitable Prey Gain from Mimicking Highly Unprofitable Ones?**

We assume now a population of \( N_{\text{mod}} \) highly unpalatable/unprofitable prey (\( \lambda_{\text{bad}, f_{\text{bad}}} \)) and \( N_{\text{mimic}} \) moderately unpalatable/unprofitable mimetic individuals (\( \lambda_{\text{int}}, f_{\text{int}} < 0 \)) with a given appearance. We assume that these mimetic individuals are derived from a population with a distinct appearance, leaving \( N_{\text{nonmimic}} \) distinct nonmimics each with unprofitability \( f_{\text{int}} \) (the total number of moderately unprofitable prey is equal to \( N_{\text{mimic}} + N_{\text{nonmimic}} \) and is the same initially for all simulations; exploration 2).

**With Pavlovian Predators.** As Speed (1993) proposed, there is selection for the moderately unpalatable prey to resemble the highly unpalatable model when predators are Pavlovian (fig. 4a; per capita predation rate of combined models-mimics lower than nonmimics). However, intriguingly, we do not observe the opposite selection pressure (with highly unpalatable prey evolving to resemble moderately unpalatable nonmimics) when the warning signal of the nonmimics is more prevalent (when \( N_{\text{mod}} = 10 \)).

![Figure 3: Exploration 1: mean net payoff after predator sampling, measured as the sum of the payoff \( f_i \) of all prey that have been attacked. This prey population is composed of highly unpalatable/unprofitable prey (\( \lambda_{\text{bad}}, f_{\text{bad}} \)) and of moderately unpalatable/unprofitable prey (\( \lambda_{\text{int}} = 0.4, f_{\text{int}} = -0.5 \)) with shared appearance, yielding a negative net payoff. We consider both a Pavlovian predator (a) and an optimal predator (b). In general, the optimal sampling strategy has a higher payoff (see main text for exceptions). Other parameter values are as follows: \( f_{\text{good}} = +5 \), \( (\lambda_{\text{bad}}, \lambda_{\text{int}}, \lambda_{\text{good}}) = (1, 1, 1) \), \( \sigma = 0 \).](image-url)
With Optimal Predators. First, we note that when $N_{model} \geq N_{mimic}$, there is indeed clear selection on the moderately unpalatable prey to resemble the highly unpalatable model, because the predation rate of the non-

mimics is consistently higher than the predation rate of the mimics, whatever the proportion of mimics (when $N_{model} = 50$ in fig. 4b). Only when $N_{model} \ll N_{mimic} = N_{nonmimic}$ is there selection for the highly unpalatable prey to resemble the
less unprofitable nonmimic, and this arises as a consequence of the warning signal of the nonmimics being more prevalent (e.g., when \( N_\text{model} = 10 \) in fig. 4b).

Does Mimicry Undermine the Protection Afforded to the More Unprofitable Model?

We continue to assume a prey community with one model species (\( \lambda_{\text{unat}} \), \( f_{\text{unat}} \)) and another species (\( \lambda_{\text{unat}} \), \( f_{\text{unat}} \)) whose individuals are either mimics or nonmimics (exploration 2).

With Pavlovian Predators. If we consider Pavlovian predators, when mimicry of the highly unpalatable prey by moderately unpalatable prey is selected for, under a wide range of conditions the total number of prey sampled of the combined model-mimic before complete rejection increases as the mimetic load (\( N_{\text{mimic}} \)) increases, and so does the per capita predation rate (fig. 4a). This latter result clearly confirms that parasitic quasi-Batesian mimicry can emerge from a Pavlovian model of predator cognition (Speed 1993).

With Optimal Predators. If we consider optimal predators, when mimicry of the highly unprofitable prey by moderately unprofitable prey (\( f_{\text{int}} < 0 \)) is selected for, then under a wide range of conditions, the total number of prey sampled of the combined model-mimic before complete rejection increases as the mimetic load (\( N_{\text{mimic}} \)) increases (fig. 5a). Despite this increase in consumption, however, the highly unprofitable species still benefits from mimicry through a dilution effect. Specifically, when there are more individuals with the appearance of the model and all prey with this appearance are unprofitable, then the per capita predation rate decreases when \( N_{\text{mimic}} \) increases (fig. 4b). By contrast, when we consider profitable mimics (\( f_{\text{int}} > 0 \); i.e., when the mimicry is Batesian), the number of the highly unprofitable prey attacked before cessation of sampling increases (fig. 5b), and so does the per capita predation rate (fig. 4c). When the proportion of profitable prey is high enough, the optimal predator can attack all unfamiliar prey with that appearance without ever deciding to reject the prey (exploration 1; fig. 5a). For this reason, the per capita predation rate can even reach 1 when there are enough profitable prey mimicking the highly unprofitable model (when \( N_\text{model} = 10 \) in fig. 4c).

When the mimic is moderately unprofitable (\( f_{\text{int}} < 0 \)), the increase in the total number of prey attacked comes from both the increase in combined density of the unfamiliar prey type (an inference confirmed by setting both model and mimic to be highly unprofitable and noting that the number sampled before complete rejection increases as the total density increases; see Sherratt 2011), as well as the reduction in the overall average level of unprofitability (an inference confirmed by noting that the total number of the model-mimic attacked before cessation of sampling increases as the profitability \( f_{\text{int}} < 0 \) of the moderately unprofitable mimic increases with total density held constant; exploration 1; fig. S6).

Intriguingly, under some narrowly defined conditions, the per capita survival of the model can be slightly undermined by mimicry by a moderately unprofitable prey type—namely, when the cost associated with unprofitability and the difference in unprofitability between the models and the mimics are high (low \( f_{\text{unat}} \) and high \( f_{\text{int}} < 0 \); fig. S7) or when the predator’s priors are skewed toward an unprofitable experience (fig. S8). Note that the optimal response of an individual predator in our model is not probabilistic but all-or-nothing (reject/attack) and triggered by a discrete threshold (number of each prey type attacked). This discreteness inevitably gives rise to some discontinuities in an individual’s optimal response (zigzag lines in figs. S7, S8), which influence where the specific equilibria will lie. However, all the prey items are unprofitable, and the consequent slight increase in the number of prey sampled rarely counterbalances the dilution effect when moderately unprofitable prey are mimicking a highly unprofitable model.

Is There Selection for Polymorphism in the Moderately Unprofitable Species?

One of the key reasons why quasi-Batesian mimicry has attracted so much interest is that it can in theory generate polymorphisms among moderately unprofitable prey. Thus, as the mimetic load on any given highly unprofitable model increases, then the effectiveness of the signal may be undermined, and the moderately unprofitable mimics would then experience selection to resemble other highly unprofitable models.

To investigate this explicitly, we assumed that there are two highly unpalatable/unprofitable (\( \lambda_{\text{unat}} \), \( f_{\text{unat}} \)) distinct unfamiliar models, model A and model B. These models can be mimicked by another species—the mimic (either mimic A or mimic B)—which belongs to the intermediate palatability/profitability class (\( \lambda_{\text{unat}} \), \( f_{\text{int}} \), see exploration 3 methods for more details). Starting from a condition under which the entire population of the mimic species exclusively mimics model A (\( P_{\text{mimicB}} = 0 \)), we can track the predicted predation rate on the original mimics (mimic A) and that on alternative mimics that resemble the alternative model (mimic B).

With Pavlovian Predators. Increasing the mimetic load of a moderately unpalatable mimic (\( \lambda_{\text{unat}} < 0.5 \)) on a highly unpalatable model (\( \lambda_{\text{unat}} \)) generally increases the predation rate on the joint model-mimic, so such balanced polymorphism is possible (fig. 5a). We therefore confirm that, under a Pav-
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**Figure 5:** Exploration 3: per capita predation rate caused by a predator foraging in a community containing two model species. The prey community is composed of two highly unpalatable/unprofitable models ($\lambda_{bad} = 0.2, f_{bad} = -1$) with distinct appearances, model A and model B. In addition to these models, there are also mimic individuals that are, in different analyses, either moderately unpalatable/unprofitable ($\lambda_{bad} = 0.4, f_{bad} = -0.5; a, b$) or profitable ($f_{bad} = +0.5; c$). Among those mimics, a proportion $P_{mimic B}$ mimics model B, and a proportion $1 - P_{mimic B}$ mimics model A. We set fixed densities $N_{mimic A} + N_{mimic B} = 50$ and $N_{model A} = N_{model B} = 50$. We consider both Pavlovian predators ($a$) and optimal predators ($b, c$). The points drawn on the graphs correspond to the mean per capita predation rate on each appearance (gray = model A and mimic A, black = model B and mimic B; confidence intervals are so small that we cannot represent them on the graphs). Starting from a condition under which the entire population of the mimic resembles model A ($P_{mimic B} = 0$), gray arrows represent positive selection pressure (which minimizes the per capita predation rate) for the mimic to resemble model B. In the bottom subpanels, black arrows represent the evolutionary dynamics of the mimic appearance, following selection mediated by predation, and the black dots corresponds to stable balanced polymorphism. Note that polymorphisms are predicted as a consequence of the Pavlovian foraging behavior but arise under the optimal sampling rules only when the mimic is profitable. Other parameter values are as follows: $f_{pred} = +5, (\alpha_{good}, \alpha_{bad}, \alpha_{good}) = (1, 1, 1), \sigma_j = 0$.

With Optimal Predators. When the mimic is profitable ($f_{int} > 0$), balanced polymorphism of the mimic is selected for (fig. 5c). By contrast, increasing the mimetic load of a moderately unprofitable mimic ($f_{int} < 0$) on a highly unprofitable model generally decreases the predation rate on the joint model-mimic, so no such balanced polymorphism is possible (fig. 5b). As noted above, balanced polymorphism appears possible with a moderately unprofitable species selected to mimic two different highly unprofitable models under some conditions—when the cost associated with unprofitability and the difference in unprofitability between the models and the mimics are high (low $f_{bad}$ and high $f_{int} < 0$; fig. 5b) or when the predator expects an unprofitable experience (fig. 5d). This phenomenon arises because a slight increase in the number of prey sampled can outweigh the dilution effect and thereby increase the predation rate on the highly unprofitable model. However, these cases of quasi-Batesian mimicry derive from only slight differences in per capita predation rates on models with and without mimics. Despite these exceptions, systematic explorations indicate that balanced polymorphism of quasi-Batesian mimics is unlikely for a wide range of parameters (notably, when normalized $f_{int} < 0$ in fig. 6b), contrary to Batesian mimics (when normalized $f_{int} > 0$ in fig. 6b). Implementing heterogeneity in predator behavior (so that the levels of profitability/unprofitability do not incur exactly the same benefits/costs to different predators) reduces even more the combinations of parameters for which we can observe balanced polymorphism of quasi-Batesian mimics ($\sigma_j = 2$ in fig. 6c).
Figure 6: Exploration 3 (sensitivity analysis): equilibrium outcome for the combination of either profitable or unprofitable mimics that may split between two different models. The prey community is composed of two highly unpalatable/unprofitable models ($\lambda_{un} < 0.5$, $f_{un} < 0$) with distinct appearances, model A and model B. In addition to these models, there are also mimic individuals that are, in different analyses, either moderately unpalatable/unprofitable (normalized $\lambda_{un} < 0$, $f_{un} < 0$) or palatable/profitable ($\lambda_{un} > 0$, $f_{un} > 0$). Among those mimics, a proportion $P_{mimic \_B}$ mimics model B, and a proportion $1 - P_{mimic \_B}$ mimics model A. We consider both Pavlovian predators (a) and optimal predators (b, c). When optimal predators are implemented, there is either uniformity ($\sigma_i = 0$; b) or heterogeneity ($\sigma_i = 2$, with constraints on $f_{un}$, $f_{int}$, and $P_{mimic \_B}$) in the costs or benefits experienced by predators when attacking prey items from each of the three profitability classes. We start from a condition under which the entire population of the mimic resembles model A ($P_{mimic \_A} = 0$). By simulating the predation rates on the prey community for various $P_{mimic \_B}$ Values (as in fig. 5), we can isolate the $P_{mimic \_B}$ value at equilibrium. We conduct a sensitivity analysis on the unpalatability/unprofitability of model species ($\lambda_{un}$ or $f_{un}$) and on the normalized palatability/profitability of mimics species ($\lambda_{mimic}$ or $f_{mimic}$). When $0 < P_{mimic \_B} < 1$ at equilibrium, balanced polymorphism is selected for and is maintained—driven by either quasi-Batesian mimicry or classical Batesian mimicry. We see that the Pavlovian predator generates polymorphism under a wide range of conditions, while the optimally sampling predator tends to do so consistently only when the mimic is profitable. Other parameter values are as follows: $f_{good} = +5$, $(\alpha_{un}, \alpha_{int}, \alpha_{good}) = (1, 1, 1), N_{mimic \_A} + N_{mimic \_B} = 50, N_{model \_A} = N_{model \_B} = 50$.

If we assume that moderately unprofitable prey can become profitable to some predators because the benefit of consuming them outweighs the cost of dealing with their defenses (e.g., some predators are sufficiently hungry to warrant consuming distasteful prey for the nutrients they provide), then such prey can naturally face selection to become parasitic Batesian mimics. This is what we observe when there is variation in the costs and benefits experienced by predators ($\sigma_i = 2$) without constraints $f_{un} < 0$, $f_{int} < 0$, and $f_{good} > 0$ in figure S11.

Discussion

Genuine Quasi-Batesian Mimicry Should Be Rare

When profitable species are selected to resemble unprofitable species as a consequence of the optimal sampling regime, then the relationship is typically parasitic—the more profitable mimics there are, the higher the per capita attack rates are on both mimics and models. Indeed, as we have seen, Batesian polymorphisms readily arise as a consequence of the gradual erosion of the effectiveness of any given warning signal. By contrast, we have shown that as the number of moderately unprofitable mimics on highly unprofitable prey increases, then the per capita attack rates of predators on mimics and models typically decrease. Thus, the relationship is typically mutualistic. We therefore have little evidence that the optimal sampling strategy of predators has widespread or marked quasi-Batesian properties, with consequent selection for polymorphism among unpalatable prey.

Intuitively, adding a moderately unprofitable mimic to a population of highly unprofitable models will cause a predator to sample more such prey for two important reasons. First, there will be more such prey with the appearance, and so there will be a greater incentive for the predator to dis-
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Our model focused primarily on elucidating the selection gradients generated by a population of identical optimal sampling predators foraging in a multispecies prey community. As such, we have implicitly assumed that the selection gradients are indicative of the evolutionary dynamic and that the results are robust to variation in predator behavior, just as the vast majority of models (including Müller 1879; Speed 1993). Future work should explore the evolutionary implications of optimal sampling behavior under an even wider set of conditions, including a spatial model.

Mimics May Be either Müllerian or Batesian, Depending on Predators’ Energetic State

Our analysis has concentrated on investigating genuine cases of moderately unprofitable mimics acting as parasites on even more unprofitable prey. However, profitability is a moveable feast. In particular, chemically defended prey contain both toxins and nutrients, and such prey may be profitable to attack when alternative prey are in short supply or when predators do not have a high toxin dose. For instance, Barnett et al. (2007) showed that European starlings (Sturnus vulgaris) increase their attack rates on distinctly colored, chemically defended (quinine sulfate–injected) mealworm larvae (Tenebrio molitor) when their body masses and fat stores were experimentally reduced (and subsequently restored in cycles). Likewise, Skelhorn and Rowe (2007) revealed that the dose of quinine sulfate administered to European starlings affected the number of chemically defended prey that they were subsequently prepared to consume, with birds receiving high toxin doses less inclined to eat chemically defended prey. Rowland et al. (2010) also found that the feeding rates of the birds on models and mimics were affected by their individual toxin burdens.

When prey species become profitable to attack because the benefit of consuming them outweighs the cost of dealing with their defenses, then such prey could face selection to become parasitic Batesian mimics. So prey that we might consider Müllerian mimics may in fact be Batesian mimics to at least some predators, in some conditions—a possibility raised by Wallace (1882). Our model does not consider nutritional state explicitly (for complementary approaches see Kokko et al. 2003; Sherratt 2003; Sherratt et al. 2004), but varying the profitability of different classes of prey had the anticipated effect in complementary analyses (fig. S11), generating parasitic mimicry for just the same reasons that Batesian mimicry is parasitic. So moderately defended prey can act as parasites of better-defended models under the optimal sampling strategy, but it typically arises when predators are so hungry that it becomes profitable for them to attack moderately defended prey. Mimicry under these conditions is best considered Batesian mimicry rather than quasi-Batesian mimicry.

cover their properties. Second, on attacking a moderately unprofitable mimic, the predator might form the belief that while the phenotype is largely costly to attack, it is not as costly to attack as it originally believed and therefore worthy of further sampling. This is precisely what we have observed here. Nevertheless, even if more mimics and models are attacked as a consequence of mimicry, then this does not necessarily mean that the presence of the mimics will increase the mortality of the model. If prey with this appearance are eventually avoided, then adding moderately unprofitable mimics to an existing population of models will share the mortality cost over more individuals, a phenomenon we can call a dilution effect. When mimics are profitable, then any attack on a mimic is effectively a vote in favor of continued attack, so the number of prey sampled by predators increases at a higher rate than their combined density increases, and the per capita mortality of models and mimics consequently increases. By contrast, when both model and mimic are unprofitable, then an attack on either prey type is effectively a vote in favor of cessation of attacking, a conclusion that remains the same, whatever the mimetic load. The net effect is that the marginal increase in the total number of prey sampled is outweighed by the dilution effect when the mimics are themselves unprofitable, and the per capita mortality of models and mimics decreases. Lindström et al. (2001) have shown that increasing the number of artificial toxic prey presented to great tits (Parus major) increased the number of individuals sampled but decreased the per capita attack rate on such prey in the manner predicted by our model.

Nevertheless, our model does show that moderately unprofitable mimics can occasionally have a parasitic effect on the more unprofitable models. So zero profitability of the mimic is not an absolute threshold. In particular, when the model is highly unprofitable, the difference in profitability between the unprofitable models and the moderately unprofitable mimics is high, and predators are pessimistic in that their priors lead them to expect unprofitable prey, then the weakly unprofitable mimics can indeed act in a parasitic manner. However, under these conditions, the degree of parasitism is consistently weak. When such parasitism arises, leading to selection for polymorphism, multiple equilibrium states are possible because of the flatness of the mortality curves under different mimetic loads. One can wonder whether balanced polymorphism would really emerge from such weak parasitism.

In contrast to the above results, the Pavlovian predator readily generated quasi-Batesian mimicry, and it is informative to pinpoint precisely why this is so. The Pavlovian models of Speed and their relatives (e.g., Speed and Turner 1999) did not allow for dilution effects because they allowed a nonzero asymptotic attack rate without invoking an additional model that would generate a saturation of predation rate with density (e.g., a type II functional response).
Ambiguous Evidence for Quasi-Batesian Mimicry in Experiments

So far the experimental evidence for quasi-Batesian mimicry has been somewhat mixed. Speed et al. (2000) found that increasing the density of moderately unpalatable mimics at the expense of distinct (non)mimetic controls increased the mortality of the more unpalatable model. However, the (non)mimetic unpalatable controls were attacked at high frequency when rare and increasing frequency over time when common. This leaves one to wonder whether mimics were really unprofitable to predators or whether the experiment was done with an increasing density of predators.

Rowland et al. (2007) found no evidence for quasi-Batesian mimicry. Thus, they found that when moderately unpalatable mimics were added to a system with highly unprofitable models, then great tits attacked more prey in the model-mimic mixture than one would expect if all the prey were highly unprofitable. However, despite this increase in overall consumption, the presence of moderately unprofitable mimics actually decreased the mortality on the models through a simple dilution effect, suggesting that the net effect of moderately unprofitable mimics was mutualistic rather than parasitic. Although we did not show the effect of increasing the total number of unprofitable prey available directly, their finding is consistent with our model predictions. Thus, we have already shown that the per capita mortality of mimics and models declines as the number of mimics increased and prey with distinct appearances are treated independently by predators in our model.

More recently, Rowland et al. (2010) conducted an analogous experiment, this time keeping the total density of prey constant by reducing the density of distinct (non)mimetic controls as the number of moderately unprofitable mimics increased. In contrast to their earlier work, they found that the per capita mortality of the moderately unpalatable mimics and more unpalatable models went up as the proportion of mimics increased, suggesting evidence for quasi-Batesian mimicry. Rowland et al. (2010) suggested that the differences in results of their two studies arose as a consequence of whether the total density prey was fixed. However, you might expect predators to treat prey with distinct appearances entirely independently from models and mimics, and in both experiments the combined densities of models and mimics were increased in comparable ways. Of course, it is possible that some of the moderately unpalatable prey were profitable to consume by the birds (indeed, Rowland et al. 2010 showed evidence that toxin content influenced foraging decisions). An alternative possibility is that the requirement that birds eat 50 prey before completion of a trial, coupled with the avoidance of the distinct nonmimic control when it was rare, meant that more mimics and models had to be eaten before the trial was terminated.

Lack of Empirical Evidence for Quasi-Batesian Mimicry in Nature

Many cases of polymorphism in unprofitable prey can be reasonably explained by hypotheses other than quasi-Batesian mimicry. The polymorphic Neotropical butterfly Heliconius numata has been proposed to be a quasi-Batesian mimic (Charlesworth and Charlesworth 2011). However, H. numata is actually more unpalatable than some of its major mimics (Arias et al. 2016). Similarly, polymorphic Heliconius doris may be slightly more palatable than some of its comimics (Chai 1990), but it seems to be effectively unpalatable in the field (Mallet 1999). Polymorphisms of H. numata and of H. doris are therefore perhaps more likely to be maintained by a tight equilibrium between migration and local selection (Joron et al. 1999; Mallet 1999; Joron and Iwasa 2005) rather than through quasi-Batesian relationship.

Speed and Turner (1999) also suggested that the polymorphism of the two-spot ladybird Adalia bipunctata (Brakefield 1985) could be explained by quasi-Batesian mimicry. However, experiments have shown that the two-spot ladybird produced no apparent toxic effects in birds (Marple et al. 1989; Marple 1993). Therefore, its polymorphism appears to be better explained by parasitic Batesian mimicry of two toxic models—the seven-spot ladybird Coccinella septempunctata and the four-spot pine ladybird Exochomus quadripustulatus.

The polymorphism of defended African monarch Danaus chrysippus (Gordon 1984) has also been hypothesized to arise as a consequence of quasi-Batesian mimicry (Speed and Turner 1999). However, there is little evidence for difference in unpalatability with its comimics. Its polymorphism might rather result from massive introgression between previously isolated races (Owen et al. 1994; Smith et al. 1998). This species would be kept polymorphic by the fact that it is normally so abundant as to saturate its predators—that is, polymorphism would be neutral (Turner and Speed 1999).

For all these examples, there are alternative plausible hypotheses to explain polymorphism in Müllerian mimics. Therefore, the observation of polymorphism in unpalatable species, while intriguing, does not in itself represent evidence for quasi-Batesian mimicry.

Conclusion

Previous theoretical results, based solely on predators’ associative learning, have come to the conclusion that mimicry between unequally defended species is often, if not always, parasitic, where such quasi-Batesian mimics are expected to degrade the protection of their models. This finding has attracted much interest (and controversy), because such a view radically impacts the way we can envision the formation of large mimicry rings (characterizing tropical insect...
communities in particular), as well as the rules underlying the diversification of mimetic clades. If mutualistic relationships were rare or even impossible, communities of mimetic organisms would be ruled by antagonistic evolutionary dynamics and coevolutionary arms races, promoting the convergence of mimics to models but perhaps also a tendency for models to escape their parasite by evolving new signals.

Nevertheless, if prey of a given appearance are consistently unprofitable to attack, then one might wonder why predators in the above learning models do not eventually cease attacking such prey altogether. Here, we have shown that mimicry between species with unequal defenses should actually nearly always be mutually beneficial when predators employ the optimal sampling strategy. All mathematical models are abstract and simplified representations of the real world. However, if the implications of our model are robust, then it suggests that, despite variation in defense levels, mimetic communities should be structured mainly by positive interactions, promoting a real and effective strength in numbers and explaining the numerous species participating in certain mimicry rings and the intriguing findings of convergent niche evolution shaping prey communities.

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The unpalatable *Heliconius numata* butterfly, here shown sitting on a *Heliconia* flower, once considered a quasi-Batesian mimic because it occurs in several different co-occurring forms. Photo credit: Mathieu Joron.