

REPORT

Alternative prey can change model–mimic dynamics between parasitism and mutualism

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Abstract

Classical (conventional) Müllerian mimicry theory predicts that two (or more) defended prey sharing the same signal always benefit each other despite the fact that one species can be more toxic than the other. The quasi-Batesian (unconventional) mimicry theory, instead, predicts that the less defended partner of the mimetic relationship may act as a parasite of the signal, causing a fitness loss to the model. Here we clarify the conditions for parasitic or mutualistic relationships between aposematic prey, and build a model to examine the hypothesis that the availability of alternative prey is crucial to Müllerian and quasi-Batesian mimicry. Our model is based on optimal behaviour of the predator. We ask if and when it is in the interest of the predator to learn to avoid certain species as prey when there is alternative (cryptic) prey available. Our model clearly shows that the role of alternative prey must be taken into consideration when studying model–mimic dynamics. When food is scarce it pays for the predator to test the models and mimics, whereas if food is abundant predators should leave the mimics and models untouched even if the mimics are quite edible. Dynamics of the mimicry tend to be classically Müllerian if mimics are well defended, while quasi-Batesian dynamics are more likely when they are relatively edible. However, there is significant overlap: in extreme cases mimics can be harmful to models (a quasi-Batesian case) even if the species are equally toxic. A crucial parameter explaining this overlap is the search efficiency with which indiscriminating vs. discriminating predators find cryptic prey. Quasi-Batesian mimicry becomes much more likely if discrimination increases the efficiency with which the specialized predator finds cryptic prey, while the opposite case tends to predict Müllerian mimicry. Our model shows that both mutualistic and parasitic relationship between model and mimic are possible and the availability of alternative prey can easily alter this relationship.

Keywords

Aposematism, avoidance learning, Müllerian mimicry, mutualism, quasi-Batesian mimicry, warning colours.

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INTRODUCTION

The phenomenon where two or more unprofitable prey species resemble each other is called Müllerian mimicry and it was first introduced by Müller (1879). He suggested that as predators are able to learn to avoid defended (aposematic) species, butterfly species that share a single warning pattern (co-mimics) benefit as costs for educating an inexperienced predator to avoid certain colour patterns would be shared between the similarly signalling species.

Müller introduced his theory of close resemblance between species as an alternative explanation to Bates's

(1862) theory. The difference between these theories was that Bates suggested that mimics imitating defended species are deceptive and actually perfectly edible to the predators. Thus, the main difference is that Müllerian mimicry should operate during the avoidance learning period of the predator, and Batesian mimicry while predators generalize their learned avoidance, i.e. use memory. These two mimicries – Batesian (parasitic) and Müllerian (collaboration) – are considered to be two ends of the palatability spectrum (Nur 1970; Turner 1987).

Recently, the theory of Müllerian mimicry has attained critique, because the theory does not consider the effects of

predator behaviour towards differently defended prey in the model : mimic system (e.g. Speed 1993a, 1999; Speed & Turner 1999, but see Joron & Mallet 1998; Mallet 1999; Mallet & Joron 1999). The differences in prey defence are crucial because predator avoidance learning is dependent on the defence of the prey (Lindström *et al.* 1997). This by return brings into question Müller's basic assumption, that predators learn from a fixed number of defended prey eaten (Müller 1879). If one species of the co-mimics is more toxic than the other, the less defended partner of the mimetic relationship can actually dilute the protection of a better defended species (Huheey 1976, 1984; Owen & Owen 1984; Speed 1993a; Speed *et al.* 2000). This has recently been termed quasi-Batesian mimicry (Speed 1993a, 1999).

Thus, instead of strict border between parasitism (Batesian) and mutualism (Müllerian) there would be a parasitism continuum (Speed 1993a; Speed & Turner 1999). This argument arises from the fact that the edibility of prey animals forms a continuous spectrum (between species or even within species variation like in monarch butterfly: Brower *et al.* 1968, 1972). Hence among many warningly coloured mimics we cannot rigidly distinguish the Batesian, edible mimics as a separate and distinct class from the defended, Müllerian mimics. If predators cannot make a distinction between the mimic and model, the less defended could turn the dynamics to resemble Batesian mimicry (i.e. quasi-Batesian dynamics).

Relatively little attention has been given to the effects of alternative prey on model-mimic dynamics, and studies have mainly considered Batesian mimicry (Dill 1975; Luedeman *et al.* 1981; Getty 1985; Nonacs 1985; Hetz & Slobodchikoff 1988), or the effect of alternative prey on the initial evolution of aposematism (Merilaita & Kaitala 2002). As Mallet (1999) argues, mimics never constitute a large portion of the predators' diet and therefore we need to consider the effects of alternative prey to model-mimic dynamics. It is well known that the crucial resemblance between model and mimic in Batesian mimicry can be affected by the availability of alternative prey (Hetz & Slobodchikoff 1988). When food is scarce it pays for the predator to discriminate between, or to test, the models and mimics, whereas if food is abundant predators tend to leave the mimics and models untouched even if the mimics are relatively poor (unpublished data). The availability of alternative prey should be crucial to Müllerian mimicry, if quasi-Batesian dynamics operate. There is little experimental evidence available on the subject but, according to our results, alternative prey seemed to affect the predators' avoidance learning when there is one aposematic prey present (Lindström *et al.* 2001).

Alternative prey can affect model-mimic dynamics in several ways. For example, if the density of alternative prey is high compared with that of aposematic prey, it may be

that signals of the model are not learned unless the predator suffers sufficiently many negative experiences. Under such conditions, a slightly defended mimic could help to push the predator across the threshold where learning begins, making the model-mimic relationship mutualistic. If the density of alternative prey is lower, such learning could take place without the mimic and the mimic brings no benefit. The central question of our paper is to derive the exact conditions when a mimic is harmful or beneficial to the host, depending on the mimic's own edibility, its density (or more generally, capture rate which depends on its visibility too) and the availability of alternative prey.

We base our model on the optimal behaviour in the predator. Previous authors have emphasized the role of predator learning and forgetting (Speed 1993a; MacDougall & Dawkins 1998; Speed & Turner 1999; but see Turner & Speed 1999), as this is what after all determines how many aposematics (models and mimics) and cryptic prey are eaten. Here, we step back one step, to ask if and when it is adaptive for the predator to learn to avoid certain species in the first place (see also Speed 1993b). For example, if edible mimics are commonplace coexisting with models, it may be beneficial to accept aposematic species as prey simply because the risk of encountering toxic prey is sufficiently small. An optimally behaving predator should in this case never learn to avoid aposematic prey, even if it encounters aposematic toxic prey items. However, even rare toxic prey may render an avoidance response adaptive, if the cost of refraining from eating them is small. This is the case if alternative cryptic prey individuals are in abundant supply. Clearly, we need to consider all three species (the model, the mimic and alternative cryptic prey) when assessing whether the mimic's presence is harmful or beneficial to the host.

THE MODEL

We consider a system where a predator has three potential prey species: the model, the mimic and a cryptic non-toxic prey (which can also represent a group of species). Predators should naturally always accept eating cryptic non-toxic prey, but they may be relatively hard to find and/or rare. Therefore, it can be adaptive to eat models and/or mimics too. Mimicry, however, makes it hard for a predator to distinguish between models and mimics. For simplicity, we assume that differentiating between them is impossible: the purpose of our model is not to study the evolution of mimicry per se, but to discuss the consequences of existing mimicry for the relationship between the mimic and the model. All species are of energetic value, but consuming the model is harmful in some other way (e.g. toxin intake). The mimic can also induce this harmful effect, but to a lesser degree or possibly not at all, which allows us to examine the full 'edibility spectrum' *sensu* Brower *et al.* (1968) and Turner (1984).

A predator who refrains from eating mimics and/or models will never suffer from toxins. However, eating them means that a predator finds prey more easily. Comparing these two advantages is possible if we consider the predator’s fitness to depend both on its state of nourishment and on the level of toxins it is exposed to. Here, we outline a simple, schematic model that incorporates these factors and hence describes the trade-off between rates of energy gain and rates of toxin accumulation.

We consider the following discrete time scenario. A foraging predator encounters maximally one potential prey item during one time step. The prey can be one of three species: a model, a mimic or cryptic prey (each of these categories can also be thought of as a group of species). Upon encounter, the predator has to decide whether to take this prey or to continue foraging.

Simple foraging models maximize the energy intake rate of a predator (e.g. Charnov 1976; Weissburg 1993; Fortin *et al.* 2002). In our case, such an approach is inappropriate: accepting all food items may give high energy reserves yet yield low fitness because of toxin accumulation. Instead, we make use of a dynamic approach (Houston & McNamara 1999; Clark & Mangel 2000), where foraging or not foraging as well as the type of prey consumed influences the probabilities with which the forager enters different physiological states. The predator’s fitness accumulates depending on its state, until the process is terminated by death (as e.g. in Kokko & Johnstone 1999; Dall & Boyd 2002). For simplicity, we assume that the predator may be in one of three states: S – starving (undernourished and unpoisoned), F – ‘fit’ (nourished and unpoisoned), and P – poisoned (nourished but with poison in body) (Fig. 1).

Due to the diversity of possible reproductive strategies in predatory species, we do not model reproduction explicitly, but simply assume that the predator is the fitter the more time it spends in the ‘F’ state before its death. The Appendix describes the fitness equations in detail. Death can occur either through starvation (in state S) or through being poisoned (in state P).

We assume that the predator can tolerate starvation and toxins to a certain extent. Thus, missing out a prey during one time unit cannot result in death unless the predator is already in an undernourished state. Likewise, eating toxins increases the probability of death only if the predator has already been exposed to toxins. The probability of death is denoted d_s if a predator is already in state S (starving) and does not find or eat a prey item, and d_p if a predator is already in state P (poisoned) and eats another poisonous item. In any other case the predator survives. We call d_s and d_p the sensitivities of the predator to starvation and to poisoning, respectively.

Figure 1 summarizes the transitions that the predator undergoes, arrows indicating probabilities of each transition,

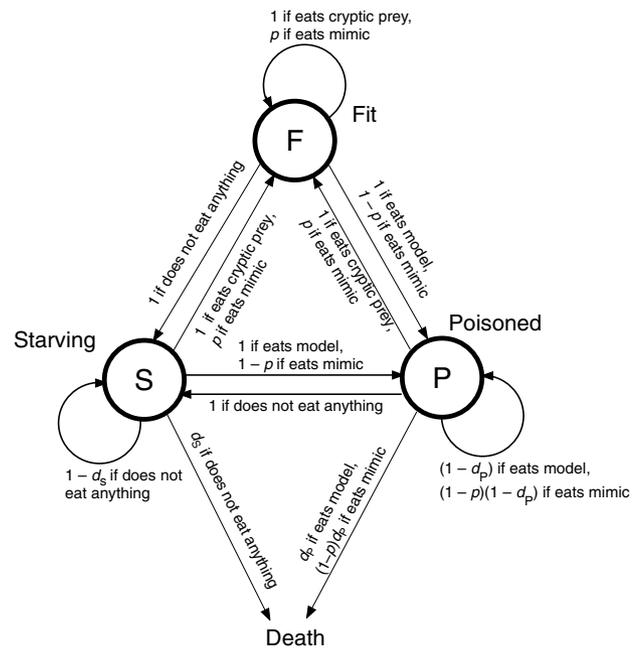


Figure 1 A schematic representation of the model. The predator moves from one state to the other with probabilities indicated with arrows. See text for a more detailed description.

conditional on eating a certain type of prey. Toxins are assumed to be metabolized by the predator, so that a poisoned predator who does not eat anything will become unpoisoned again (and undernourished, state S). Eating the model always leads to poisoning, and eating the cryptic prey always leads to being nourished. The mimic has an intermediate edibility, denoted p . With probability p eating it leads to the same outcome as eating cryptic prey, while with probability $1 - p$ its effect is equivalent to eating the toxic model. Thus, when $p = 0$ the mimic and the model are equally toxic, with $p = 1$ the mimic is completely edible, and intermediate values describe the edibility spectrum. Despite the discrete probabilistic nature of edibility in our model, it is in fact able to describe gradual effects of toxin build-up, because death requires repeated instances of toxin intake, and these are unlikely to follow from eating several items of only mildly toxic prey that has $1 - p$ close to 0.

We assume that predators cannot distinguish between models and mimics. They thus either eat all prey items indiscriminately (strategy 0) or avoid all aposematic prey (strategy 1). For simplicity, we consider here a case where the predator cannot change its behaviour according to its own state.

We next need to specify the capture rates of various prey under the two strategies, denoted 0 and 1. These influence the probabilities of eating specific types (the capture rates) of prey during one time unit in Fig. 1. The rates of capture

additionally depend on the densities of prey species as well as their visibility: for example, for a predator that eats both aposematic and alternative prey, the alternative cryptic prey may be harder to find but nevertheless have a higher capture rate if it is more abundant than aposematic prey. Note that mathematically, 'rates' are used in continuous-time models where they can take any non-negative value, and in our discrete time scenario they translate to probabilities (that must range between 0 and 1) of capturing a specific type prey item. Because the rate of capturing prey over time is simply proportional to the probability of capturing it during one time unit, we use 'capture rate' and 'capture probability' interchangeably, and make sure that the values do not exceed the probability 1.

As we assume that the predator captures at most one prey in a time unit, the events 'capture the model species', 'capture the mimic' and 'capture cryptic prey' are mutually exclusive, and we next specify the probabilities for them. If a predator uses strategy 0 (indiscriminate eating), it captures the model species with probability M , the mimic species with probability m , the cryptic species with probability c_0 and nothing with probability $1 - M - m - c_0$. The higher the density of the prey and the more visible it is, the higher its corresponding capture rate. Thus, if an alternative prey species was abundant but hard to find, it would have a moderate capture rate c_0 . If the predator discriminates, i.e. avoids aposematic prey (strategy 1), we assume it captures a cryptic prey item with probability c_1 . We assume that the total capture rates, $M + m + c_0$ and c_1 both fall below 1, thus a predator is not guaranteed to find any prey in a single time unit.

Note that we assume that the capture rate of the cryptic species can depend on whether the predator avoids aposematism or not, i.e. c_0 does not necessarily equal c_1 . It may be that a predator who specializes in searching for cryptic prey finds them more easily ($c_1 > c_0$). However, avoiding aposematism may also slow down the capture rate of cryptic prey ($c_1 < c_0$), if each prey item needs to be additionally checked for aposematic coloration before it is eaten. We can imagine this to be the case, e.g. when capturing insects flying in the air. For example, Kauppinen & Mappes (2003) describe that hunting dragonflies spot the movement of the prey from a distance, come close and then make their decision according to prey appearance. It should be noted though that the situation can be more complicated, as ignoring some prey items frees some handling time for searching for new prey, and this can clearly reduce the time cost of stopping to checking the appearance of prey. Here we investigate both cases ($c_1 > c_0$ and $c_1 < c_0$) for the sake of completeness.

We can now solve the predator's fitness W_0 or W_1 if it uses strategies 0 (indiscriminate eating) or 1 (avoidance of aposematic prey), respectively. Fitness, as derived in the

Appendix, corresponds to the predator's reproductive value if the number of offspring equals the number of time units spent in the 'fit' state F. If $W_1 > W_0$ the predators are expected to evolve discrimination (avoidance of aposematic prey).

The equations also allow assessing whether the mimic is harmful or beneficial to the model (i.e. whether mimicry is quasi-Batesian or Müllerian). This can be done by first examining whether $W_1 > W_0$, then setting $m = 0$ to simulate the absence of the mimic, and solving the fitness equations again to see if aposematism evolves in the 'mimic absent' case. If the presence of the mimic is required for $W_1 > W_0$ the mimic is beneficial to the model, i.e. the relationship is mutualistic (Müllerian). If the presence of the mimic makes $W_1 > W_0$ turn into $W_1 < W_0$ it is parasitic (Batesian). In any other case the mimic is neutral (see Discussion). Because the fitness equations yield unwieldy expressions for W_0 we present numerical results.

RESULTS

Figure 2a shows how a mimic's presence can be beneficial to the model. As predators can die from starvation as well as from poisoning, and the model assumes that predators can tolerate poisoning to a certain level, it is not always adaptive for the predator to avoid aposematic prey – especially if defended food items are relatively scarce and the probability of lethal poisoning therefore low ($M = 0.2$, Fig. 2). In such a case, it may be that a relatively toxic mimic (i.e. low p) is needed in sufficiently large numbers (i.e. leading to a sufficiently high capture rate m) before the predator begins avoiding aposematic prey. This corresponds to the upper left corner in Fig. 2a. With all other values of p and m in Fig. 2a the presence of the mimic is neutral: the predator does not evolve avoidance behaviour regardless of the presence of the mimic. The mimic's beneficial nature makes this solution an example of classic Müllerian mimicry. Figure 2a shows that edibilities do not need to be equally low (zero) for both species, for Müllerian mimicry to evolve.

Figure 2b, in contrast, shows how a mimic's presence can be harmful to the model. In this example, the predator avoids aposematic prey if the mimic is absent. But if a mimic is present in sufficiently large numbers (large m) and it is sufficiently edible (large p), the predator will have higher fitness if it eats all prey indiscriminately than if it avoids aposematic prey. In such a case the predator would further benefit from beginning to discriminate between the model and the mimic, and model individuals would enhance their fitness by evolving to be different from the relatively edible mimics. This example thus shows parasitic, quasi-Batesian mimicry, where the mimic exploits the response of the predator to the model, and the exploitation can lead to the disappearance of avoidance behaviour if the mimic becomes too common.

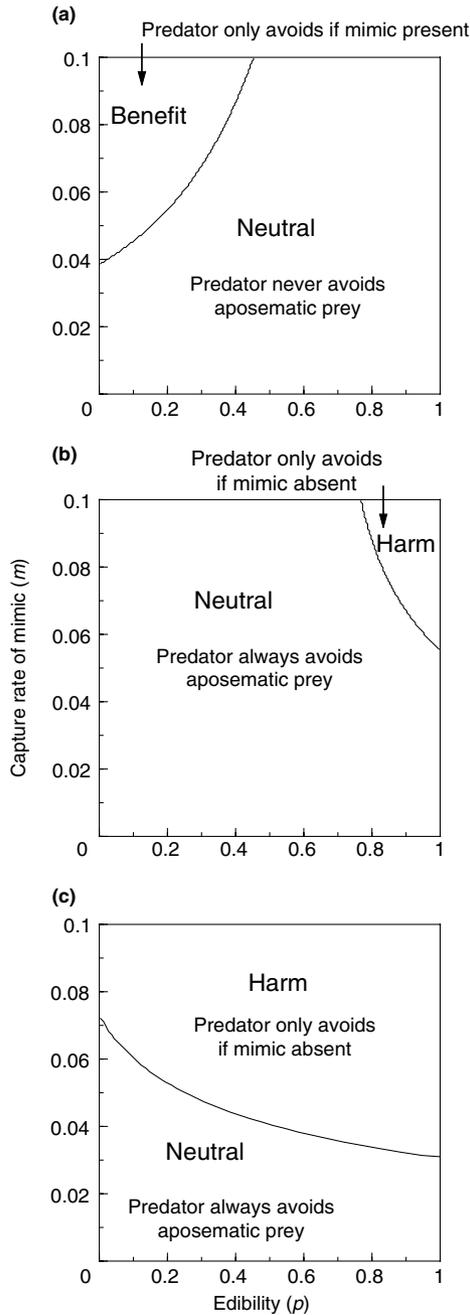


Figure 2 The qualitative effect (neutral, beneficial or harmful) of the mimic on the survival of models, when the predator follows its optimal strategy, and the mimic’s edibility is p as indicated on the x -axis. Each point in the graph is classified as neutral, if the predator follows the same strategy regardless of whether the mimic is absent ($m = 0$) or present (m as indicated on the y -axis). The mimic is considered as beneficial, if the presence of the mimic changes prey behaviour from eating to avoiding aposematic prey, and harmful if it causes the opposite change. In (a), the strategy of the predator does not influence capture rates of cryptic prey ($c_0 = c_1 = 0.7$); other parameters: $M = 0.2$, $d_S = 0.3$, $d_P = 0.5$. The outcome is Müllerian. In (b), predators capture cryptic prey less well if they eat aposematic prey too ($c_0 = 0.6$, $c_1 = 0.7$); other parameters: $M = 0.2$, $d_S = 0.3$, $d_P = 0.5$. The outcome is quasi-Batesian. (c) is as (b), but models are rarer ($M = 0.1$) and starving is a relatively big threat compared with being poisoned ($d_S = 0.3$, $d_P = 0.25$). In this quasi-Batesian case, mimics can be harmful even if they are equally defended as models ($p = 0$). See text for an explanation of how this is possible.

discriminating foragers enjoy increased capture rates of cryptic prey (i.e. if $c_1 > c_0$). If they do, and if starvation is a significant source of mortality, mimics may be harmful to models even if they are equally toxic. An example is found in Fig. 2c, where $c_1 > c_0$, poisoning is not always lethal ($d_P = 0.25$), and predators tolerate starvation relatively poorly ($d_S = 0.3$). The predator should use the discriminating strategy only if the mimic is absent or uncommon (low m). If it is more common, adding the mimic makes predators switch to eating aposematic prey, even if the mimic’s edibility is equally low as that of the model. Thus, Fig. 2c shows a surprising outcome: mimicry can be quasi-Batesian even when models and mimics are equally toxic. Also note that the same abundance and edibility values of the mimic can lead to a mutualistic or parasitic coexistence of models and mimics (Fig. 2a vs. 2c), depending on the availability of alternative prey, and the sensitivity of the predator to starvation vs. poisoning.

How can we explain quasi-Batesian mimicry when models and mimics are equally toxic? From the predator’s perspective, the addition of an equally toxic mimic is equivalent to increasing the abundance of the model (as we assume that predators cannot distinguish between models and mimics). The above solution therefore appears counterintuitive: why should a higher abundance of toxic prey – leading to a higher likelihood of poisoning – make the predator more likely to consume such prey? It is important to realize that in the above example, the assumption $c_1 > c_0$ means that eating aposematic prey has two costs: possibility of death through poisoning and reduced efficiency of foraging for cryptic prey. A predator that handles toxins relatively well but is sensitive to food deprivation ($d_P < d_S$) should therefore pay more attention to total food intake than to toxins. It should

Unsurprisingly, the Müllerian case in Fig. 2a is found at low edibility values of the mimic, and the quasi-Batesian case in Fig. 2b at high edibility values. However, to obtain the two types of mimicry in Fig. 2 it is not sufficient to alter the edibility of the prey. Figure 2b additionally assumes that indiscriminately searching predators do not capture cryptic prey equally well as those that avoid aposematism ($c_1 > c_0$ in Fig. 2b but $c_1 = c_0$ in Fig. 2a). This suggests that a very important predictor of predator behaviour is whether

Table 1 Hundred Müllerian and 100 quasi-Batesian cases were sought, by randomizing parameters as follows until sufficient numbers of solutions were found: p , d_S , d_P and c_1 were independently distributed random numbers between 0 and 1. M , m and e_0 were likewise randomly distributed, but they were additionally scaled so that the sum $M+m+e_0$ was uniformly distributed between 0 and 1

Variable	Müllerian solutions different from quasi-Batesian ones?	Range and median for Müllerian cases	Range and median for quasi-Batesian cases
1. Sensitivity to starvation, d_S	$-(P < 0.001)$	0.00–0.59 (0.08)	0.03–1.00 (0.55)
2. Sensitivity to poisoning, d_P	$+(P < 0.001)$	0.05–0.98 (0.66)	0.00–0.97 (0.36)
3. Capture rate of model, M	n.s.	0.01–0.51 (0.18)	0.00–0.49 (0.14)
4. Capture rate of mimic, m	n.s.	0.04–0.69 (0.29)	0.03–0.74 (0.25)
5. Capture rate ratio mimic/model, m/M	n.s.	0.07–43.3 (1.47)	0.29–2.40 (1.90)
6. General ease of finding cryptic prey, $(e_0 + c_1)/2$	n.s.	0.05–0.69 (0.31)	0.02–0.64 (0.27)
7. Foraging efficiency benefit of discriminating foragers, $c_1 - e_0$	$-(P < 0.001)$	–0.30–0.12 (–0.04)	–0.02–0.54 (0.12)
8. Total capture rate of prey for strategy 0, $M + m + e_0$	$+(P < 0.001)$	0.35–1.00 (0.86)	0.13–0.99 (0.67)
9. Total capture rate of prey for strategy 1, c_1	n.s.	0.01–0.72 (0.26)	0.03–0.73 (0.33)
10. Palatability of mimic, p	$-(P < 0.001)$	0.00–0.65 (0.11)	0.03–1.00 (0.70)

n.s., not significant.

The first column indicates whether we found a significant difference in the distribution of the variable depending on the type of solution (Müllerian or quasi-Batesian; Mann–Whitney U -test, $n_1 = 100$, $n_2 = 100$, all P values Bonferroni-corrected for 10 comparisons; note that non-independence of some explanatory variables makes P values conservative, Rice 1989). The other two columns give the range and (in brackets) median of the measured variable. Note that we did not exclude cases where mimics are more common than models. Subsets of data where mimics were constrained to be rarer than models showed relationships similar to the general pattern (not shown).

thus begin accepting aposematic prey as food only if these are sufficiently abundant to compensate for the reduced time or cognitive capacity that is left to capture cryptic prey.

These results show that the same edibility value (e.g. zero) can produce Müllerian (Fig. 2a with $p = 0$), quasi-Batesian (above example) or neutral (Fig. 2b with $p = 0$) interspecific relationships between models and mimics. If there is overlap in the values of edibility that lead to quasi-Batesian or to Müllerian mimicry, we need to examine the role of other parameter values as determinants of the nature of the interspecific relationship. Because the equations are relatively complicated (Appendix), it is not straightforward to see whether each parameter pushes the relationship in a more mutualistic or in a more parasitic direction.

To examine this issue, we randomized parameter values (details in Table 1) and solved for optimal predator behaviour until we had found 100 parameter combinations of Müllerian mimicry (mimic beneficial to model), and 100 cases of quasi-Batesian mimicry (mimic harmful to model). We then compared the distribution of parameter values in the Müllerian and quasi-Batesian cases (Table 1). As suspected, Müllerian mimicry was associated with lower edibility values than quasi-Batesian mimicry, but there was substantial overlap in the edibility spectrum: in our sample we found Müllerian mimicry with edibility values ranging

from 0.00 to 0.65, and quasi-Batesian mimicry with edibility values between 0.03 and 1.00 (Table 1).

Müllerian cases were significantly associated with the following factors (all Bonferroni-corrected): low predator sensitivity to starvation, high predator sensitivity to poisoning, little or negative benefit of discrimination when searching for cryptic prey, high foraging efficiency of indiscriminate foragers and low edibility of the mimic (variables 1, 2, 7, 8 and 10; Table 1). Capture rates of models or mimics, the relative capture rate of mimics to models, the general ease of finding cryptic prey, and the foraging efficiency of discriminating predators did not have a significant influence on the nature of the interspecific relationship (variables 3, 4, 5, 6 and 9; Table 1).

DISCUSSION

This model suggests the dynamics of model-mimic interactions can be altered by changing the availability of alternative edible prey. This has been disregarded in most previous studies of Müllerian mimicry, but not in studies of Batesian mimicry (Dill 1975; Luedeman *et al.* 1981; Getty 1985; Nonacs 1985; Hetz & Slobodchikoff 1988), where the availability of alternative prey can affect several aspects of model-mimic dynamics. Our model confirms that mimics do not have to be equally toxic as models in order to

produce mutualism between models and mimics, which is the case in classic Müllerian mimicry (see Mallet 1999). On the contrary, we also show that mimics do not have to be completely edible to harm the model and produce quasi-Batesian mimicry dynamics (Speed 1993a; Speed *et al.* 2000).

Most surprisingly, even completely defended mimics can exhibit quasi-Batesian mimicry, if food deprivation is a more serious threat to predator fitness than is poisoning (Fig. 2). This overlap in the edibility spectrum means that we need to consider other parameter values: specifically, the nature of the trade-off between food intake and toxin intake in the predator (see also Turner & Speed 1999; Speed *et al.* 2000). If predators handle toxins relatively well but are likely to be limited by food intake, quasi-Batesian mimicry becomes more likely. This is quite a realistic scenario, as aposematic prey animals are known to show a palatability spectrum (Brower *et al.* 1968, 1972; Sargent 1995), and predators can consume them in low numbers if densities of favoured prey items are low. For example, pied flycatchers can occasionally eat ladybirds in suboptimal habitats where alternative prey are scarce (Cramp 1985).

A particularly important parameter is whether discriminating predators benefit in terms of their capture rate of cryptic prey. If they do (e.g. by forming a better search image of the cryptic species), quasi-Batesian cases become much more likely. Müllerian cases are mostly found when discrimination is not beneficial but costly when foraging for cryptic prey. Similarly, if the predator generalizes very broadly we can expect the quasi-Batesian mimicry. This could suggest that the classical Müllerian mimicry would be most beneficial in a case where predators have trouble finding alternative prey, and therefore prey heavily on mimics. Whereas if alternative prey is abundant, edibility differences may increase between models and mimics without causing severe costs for either mimics nor models.

Like all models, ours has limitations. For example, it may be seen as a limitation that we do not allow predators to distinguish between models and mimics at all, that edibility is formulated as a discrete probability of poisoning, or that predators never die from eating the first toxic prey item. However, our model has sufficient complexity to produce the essential distinguishing feature between Müllerian and quasi-Batesian mimicry: that the mimic can either harm or benefit the model, depending on its abundance and edibility. Because death does not immediately follow from poisoning, the model allows the build-up of toxins despite the discrete nature of poisoning, and captures the basic trade-off that the predator experiences between foraging efficiency and avoidance of toxins. Considering more advanced topics such as discrimination between models and mimics would potentially cloud this insight and is thus beyond our current scope.

Another limitation that we do not consider particularly serious is that we do not specify any particular learning behaviour of the predator. Our focus is instead on the question of whether it pays for the predator to (learn to) avoid aposematic prey in the first place; thus we simply assume that if it pays to do so, the predator will have an evolutionary or cognitive mechanism for developing the appropriate behaviour. Inherited avoidance plays a very important role when the predator has to deal with lethally toxic prey species (Smith 1975, 1977). On the contrary, predators owning enough cognitive capacity for avoidance learning are found from variety of taxa from invertebrates (mantids, Berenbaum & Miliczky 1984; Bowdish & Bultman 1993; dragonflies, Baird 1991; Kauppinen & Mappes 2003) to vertebrates (great tit, e.g. Alatalo & Mappes 1996; chicken, e.g. Gittleman & Harvey 1980; toad, Brower *et al.* 1970; lizard, Boyden 1976; fish, Tullroth 1998; snake, Terrick *et al.* 1995). Thus, we assume that it is quite realistic to assume that predators can develop responses to toxic prey, either innately or through learning.

Some limitations of the model are more interesting to discuss. We have assumed that there is only one predator species, and often we predict no change in predator behaviour when the mimic is added to the system (neutral cases). However, the addition of a mimic can still increase or reduce the fitness difference between the two predator strategies. It is easy to conceive that two or more predator species, slightly varying in their parameter values, would have different thresholds for the necessary abundance of the mimic that produces a qualitative change in predator behaviour. Therefore, mimic abundance and edibility could have a more continuous relationship to the Müllerian/quasi-Batesian question than we have been able to show here. More substantial variation among predators could further mean that the same mimic is parasitic in an area where one predator species is common, and mutualistic in an area where another predator dominates.

Furthermore, other ecological interactions can interfere and influence aspects of parasitism/mutualism. For example, if a mimic is quite edible and abundant, then its presence can increase the size of the predator population, which in turn could harm the model (the model and mimic are then said to be in apparent competition, Holt & Kotler 1987; Abrams *et al.* 1998). Along these lines, a further interesting question is the effect of the model–mimic dynamic on the fitness of cryptic prey. In particular, we have assumed that the cryptic prey and the mimic are two (or more) different species. If they were instead interpreted as two morphs of the same species, that vary in their conspicuousness and/or edibility, our modelling approach could also shed light on the initial evolution of aposematism. We can only conclude that the role of alternative prey on model–mimic systems warrants much more study.

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APPENDIX

The fitness of a predator in states S, F and P are solved from a set of equations describing transition probabilities between the three states. For a predator that uses strategy 0, these equations are

$$\begin{aligned}
 W_S &= [1 - M - m - a_0](1 - d_S)W_S + [pm + a_0]W_F \\
 &\quad + [M + (1 - p)m]W_P \\
 W_F &= 1 + [1 - M - m - a_0]W_S + [pm + a_0]W_F \\
 &\quad + [M + (1 - p)m]W_P \\
 W_P &= [1 - M - m - a_0]W_S + [(1 - p)m + a_0]W_F \\
 &\quad + [M + pm](1 - d_P)W_P
 \end{aligned} \tag{1}$$

For a predator that uses strategy 1, the equations are

$$\begin{aligned}
 W_S &= [1 - c_1](1 - d_S)W_S + c_1W_F \\
 W_F &= 1 + (1 - c_1)W_S + c_1W_F \\
 W_P &= 0
 \end{aligned} \tag{2}$$

These equations assume the predator gains one unit of fitness each time it spends in state F. Note that the transition probabilities from one living state to another do not sum up to 1. This is because the remaining probability is the probability of dying, which results in a fitness value of 0.

Assuming that the predator starts its life in state S (not poisoned but undernourished), we need to solve for its fitness $W_0 = W_S$ according to the set of eqns (1), and for $W_1 = W_S$ according to the set of eqns (2). For the latter, the solution is simple: $W_1 = d_S c_1 (1 - c_1)^{-2}$. However, for W_0 the resulting equation is unwieldy and gives little direct insight. For the sake of brevity, we do not show it here; it is available on request from the authors.

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