FEATURE SALTATION AND THE EVOLUTION OF MIMICRY

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In Batesian mimicry, a harmless prey species imitates the warning coloration of an unpalatable model species. A traditional suggestion is that mimicry evolves in a two-step process, in which a large mutation first achieves approximate similarity to the model, after which smaller changes improve the likeness. However, it is not known which aspects of predator psychology cause the initial mutant to be perceived by predators as being similar to the model, leaving open the question of how the crucial first step of mimicry evolution occurs. Using theoretical evolutionary simulations and reconstruction of examples of mimicry evolution, we show that the evolution of Batesian mimicry can be initiated by a mutation that causes prey to acquire a trait that is used by predators as a feature to categorize potential prey as unsuitable. The theory that species gain entry to mimicry through feature saltation allows us to formulate scenarios of the sequence of events during mimicry evolution and to reconstruct an initial mimetic appearance for important examples of Batesian mimicry. Because feature-based categorization by predators entails a qualitative distinction between nonmimics and passable mimics, the theory can explain the occurrence of imperfect mimicry.

KEY WORDS: Animal cognition, Batesian mimicry, categorization, defensive coloration, signaling.

The debate on Batesian mimicry evolution (Bates 1862), over whether the process is gradual or saltational (Punnet 1915; Fisher 1927; Goldschmidt 1945), started nearly a century ago. In this debate, the importance of predator perception was acknowledged, but no comprehensive theory of how predators recognize and differentiate prey was developed. The currently prevailing idea of how predators perceive model-mimic similarity is that all aspects of appearance have the same kind of impact on prey recognition and generalization (Turner 1981; Dittrich et al. 1993; Ruxton et al. 2004; Bain et al. 2007). Where strikingly imperfect mimicry has been observed, it is generally explained as wide generalization of a highly distasteful model (Ruxton et al. 2004). A contrasting approach is to apply the claim by Tinbergen (1951) “that an animal does not react to all the changes in the environment that its sense organs can receive, but only to a small part of them” to predators’ learning about prey (Schmidt 1958). This can have important implications for the so-called two-step process of mimicry evolution (Nicholson 1927; Turner 1984; Ruxton et al. 2004). In the two-step process, a large mutation first achieves approximate similarity to the model, after which smaller changes can improve the likeness. Our aim here is to employ ideas from animal psychology about categorization of complex stimuli to explain how predators can perceive the initial mimetic mutant as being similar to the model. The explanation thus sheds light on the crucial first step of Batesian mimicry evolution.

We suggest that predators form categories to decide on prey suitability. If the categorization is based primarily on a single prey trait, a relatively small genetic change in prey may produce a large change in appearance as perceived by predators. Such feature saltation could cause a qualitative shift in categorization.
from suitable to unsuitable prey, thereby initiating mimicry evolution. In contrast, if simultaneous mutational changes in several different traits would be required, the initial phase of the two-step process becomes implausible. For this reason, and based on our evolutionary simulations, we further hypothesize that if the feature used for categorization is made up of more than one trait, selection for mimicry becomes constrained by the appearance of the ancestral state of the mimic-to-be. Thus, one or more components of the feature may need to evolve for nonmimetic reasons (e.g., thermoregulation) before a saltation to mimicry becomes likely. In our simulations, we explore the importance of a feature saltation, the effect of feature dimensionality, and the effect of the appearance of the ancestral state on the probability of Batesian mimicry evolution.

Psychological theories of categorization and concept formation propose that objects are represented as collections of features. By comparing common and distinctive features, individuals categorize objects as similar or dissimilar (Tversky 1977; Treisman and Gelade 1980). Experiments show that animals often use one or a few features when discriminating among stimuli (Troje et al. 1999). There are also studies indicating that such categorization occurs in predators discriminating suitable from unsuitable prey (Schmidt 1958; Aronsson and Gamberale-Stille 2008). A related strategy of similarity judgment is to encode stimuli hierarchically at two levels of detail: category-level information is used first to sort stimuli into crude categories, whereupon fine-grain information completes the judgment (Huttenlocher et al. 2000). We propose a hierarchical or sequential stimulus processing by predators, in which first a feature is used for crude categorization, followed by a comparison of additional prey traits. The significance for mimicry evolution is that, if predators have the tendency to generalize broadly between prey types that share a feature, there may be sufficient advantage for new, imperfect mimics to become established. Fine-grained judgments can then favor subsequent improvement of the mimicry.

In this study we develop the theory of Batesian mimicry evolution in two ways. First, we use individual-based simulations to investigate the evolution of Batesian mimicry when predators process prey stimuli in a sequential or hierarchical manner, involving feature-based categorization followed by generalization over all prey traits. For illustration purposes we use one specific example of mimicry evolution in our simulations, but the qualitative simulation results are general and can be applied to different cases. Second, we explore well-known examples of Batesian mimicry and construct scenarios of mimicry evolution for these, in accordance with the results of our simulations. The scenarios illustrate the two-step process, in which the first step assumes feature categorization by predators and gives rise to an imperfect but passable incipient mimic, which can be seen as a kind of “missing link” in the evolution of mimicry.

**Materials and Methods**

We examined Batesian mimicry evolution through computer simulations of predator–prey communities. The approach is inspired by our previous theoretical work on the evolution of Müllerian mimicry (Balogh et al. 2010). Prey appearance is represented as an array of trait values, \( x = (x_1, \ldots, x_n) \), in an \( n \)-dimensional trait space.

**Nonmimetic Prey Niche**

In Batesian mimicry evolution, a mimic-to-be starts out as a species of “ordinary” palatable prey, which might be part of a larger community that the predator frequently encounters and knows is edible. For the modeling, we need to specify the interaction between these kinds of prey and predators. We have taken into account two types of effects. First, considering the situation in which a hunting predator is in the vicinity, an ordinary prey individual has a reduced probability of being attacked because it might avoid discovery (crypsis), but also because there may be other ordinary prey in the vicinity that attract the predator’s attention, or because body proportions and other aspects of the phenotype of ordinary prey improve their ability to escape an attack, compared to members or mimics of an aposematic species (Ruxton et al. 2004). In general, we can describe a nonmimetic prey niche as a region of trait space and, for simplicity, we use a spherical region. We also use a function to describe fitness effects for this niche:

\[
    f_0(x) = \frac{1}{1 + \exp \left[ \rho_0(|x - x_0| - R_0) \right]}. 
\]

The point \( x_0 \) is the center of the region, \( |x - x_0| \) is the distance of \( x \) from the center, \( R_0 = 0.15 \) is the radius of the region, and \( \rho_0 = 50 \) measures the steepness of the function at the boundary. The proportional reduction in the probability that a nearby predator will successfully attack a focal nonmimetic prey individual is then taken to be

\[
    1 - f_0(x) \kappa, 
\]

where \( \kappa = 0.8 \) is a parameter (between 0 and 1) that measures the strength of effects such as crypsis and escape capability, which serve to protect nonmimetic prey from predation.

Second, we allowed for the possibility that predators learn more slowly about the palatability of individual ordinary prey, in the sense of a lower rate of forming an association between palatability and a particular ordinary prey appearance \( x \). We used a parameter \( L_0 = 0.2 \) (between 0 and 1) to scale the learning rate for prey that a predator classifies as ordinary. For simplicity, we assumed that the probability of this classification is given by \( f_0(x) \), so if a prey item’s traits are in the nonmimetic prey niche, it is likely to be classified as ordinary prey (in principle, other prey
FEATURE-BASED CATEGORIZATION OF UNPALATABLE PREY

One or more of the prey traits can be used by predators for the categorization of unpalatable prey. The reaction of predators to prey appearances may partly be innate (Ruxton et al. 2004), but to a large extent categorization would be the result of a predator’s experience of unpalatable prey. The overall idea is that categorization of prey is an efficient way for predators to deal with a complex world (Kikuchi and Pfennig 2010a). We will not go into details in our modeling about how experiences give rise to categorization. We simply assume that a region of the trait space corresponds to high salience and therefore can play the role of a feature. For one-dimensional features, we used \( x_1 \) as the feature dimension, and the part of the trait space that corresponds to an interval of this dimension as a feature region. The probability that a predator classifies a prey item as possessing the feature is a sigmoid function of the distance of the prey item’s feature trait from the center of the feature interval. Thus, the probability of feature classification is

\[
f(x) = \frac{1}{1 + \exp\left[\rho(|x_1 - x_{1f}| - R_F)\right]}, \tag{3}
\]

where \( R_F \) is half the length of the interval with center at \( x_{1f} \) and \( \rho = 100 \) measures the steepness of the function at the boundary of the region. We also examine features based on two traits, which may reduce the likelihood of a mutational feature saltation and thus constrain mimicry evolution. For these we used \( x_1 \) and \( x_2 \) as feature dimensions, and as feature region the part of the trait space in which these two traits are within a circle of radius \( R_F \) and center at \((x_{1f}, x_{2f})\), with the probability of feature classification given by a relation as the one in equation (3).

FEATURE-BASED GENERALIZATION AND LEARNING

We assume that the processing of similarity judgments occurs hierarchically (Huttenlocher et al. 2000). Consider a predator that has learned to avoid the appearance of the individuals of an aposematic population (the models), who all have a certain feature. When the predator encounters a new prey individual, it first classifies it as either having or lacking the feature. This classification affects the next level of the decision-making hierarchy. If the prey item is classified as having the feature, a broad generalization width \( \omega \) will be used for all trait dimensions. An interpretation is that when the feature is shared, the predator becomes less discriminating with respect to differences in other details of prey appearance. If the feature is present only in the model, we assume that there is no generalization between the model and the new prey. Finally, if the feature would be lacking in both the previously experienced and the new prey, a narrow generalization width \( \sigma \) is used for all traits.

After a successful attack, a predator has information about the prey unpalatability \( y \) (ranging from high palatability, \( y = -1 \) to high unpalatability, \( y = 1 \)), in addition to the multidimensional phenotype \( x \). We describe the predator’s experience as a list of the \( x_i \) and \( y_i \) for the prey it has attacked, together with the feature-based classification. The probability of the predator successfully attacking a discovered prey is written as

\[
g(h, x) = \frac{1 - f_0(x)\kappa}{1 + \exp\left[s(h - h_0)\right]}, \tag{4}
\]

where \( m \) is the number of previously attacked prey, \( F \) is a 0/1 variable that indicates whether the feature was detected for the current prey item, and \( F_i \) is a similar indicator for prey \( i \) in the list of experiences. The probability that \( F = 1 \) is given by equation (3) and the function \( g \) is given by

\[
g(x, x_i, F, F_i) = \begin{cases} 
\exp[-|x - x_i|^2/(2\sigma^2)] & \text{if } F = F_i = 0 \\
\exp[-|x - x_i|^2/(2\omega^2)] & \text{if } F = F_i = 1, \\
0 & \text{if } F \neq F_i
\end{cases} \tag{6}
\]

where

\[
|x - x_i|^2 = \sum_{j=1}^{n} (x_j - x_{ij})^2 \tag{7}
\]

is the squared Euclidean distance between stimuli, and \( \sigma = 0.1 \) and \( \omega = 0.8 \) are the narrow and wide generalization widths.

As in a number of previous modeling studies of the evolution of mimicry (Balogh and Leimar 2005; Franks and Sherratt 2007;
Ruxton et al. 2008; Balogh et al. 2010), the learning process can be viewed as the accumulation of inhibition.

**SIMULATION OF PREDATOR–PREY INTERACTIONS**

At the start of a simulation, the prey populations are monomorphic. The prey individuals reproduce sexually and have a diploid genotype, with one locus for each trait and free recombination between loci. The individuals of the next generation are formed by randomly selecting (with replacement) parents among the survivors from the current generation. Mutations occur with a probability of 0.0005 per allele and mutational increments are drawn from a reflected exponential distribution with standard deviation 0.05.

The community consists of $N_p = 100$ predators and two prey types, $a$ and $b$. Prey type $b$ is the model and has high unpalatability $y_0 = 1$ whereas the potential mimic, prey type $a$, is palatable with $y_a = -0.5$. At the start of every season, the prey types have population sizes $N_a = 100$ and $N_b = 5000$. A predator independently encounters prey at a rate $u = 0.04$ per unit time and prey individual. The population size $N_a(t)$ or $N_b(t)$ changes after every time a predator successfully attacks prey of either type (successful attacks are always fatal). The duration $T = 1$ of a season is divided into small intervals $\Delta t = 0.0004$ of time. The probabilities $P_a$ and $P_b$ of an individual predator encountering prey types $a$ and $b$ in a time interval are

$$P_a = u \cdot \Delta t \cdot N_a(t)$$

and

$$P_b = u \cdot \Delta t \cdot N_b(t).$$

The size of the time interval $\Delta t$ is small enough for both $P_a$ and $P_b$ to be small. In this way, we can ignore the possibility of several encounters during $\Delta t$. Thus, the probability of no prey being encountered at all is

$$P_{\text{none}} = 1 - (P_a + P_b).$$

When encountering a prey individual with appearance $x$, the probability of attack is computed according to equation (4), which depends on the current state of the predator’s inhibition, from equation (5). If there is an attack, the event is added to the predator’s experience. This is repeated for each predator, after which the next time interval is handled in the same way, until the end of the season.

**TRAIT SPACE FOR SIMULATION EXAMPLE**

In the simulations, the prey had three traits—green/yellow thorax color $x_1$, gray/black abdomen color $x_2$, and elongated/square abdomen shape $x_3$—each of which was controlled by an unlinked diploid locus. For the coordinates $x_1$ and $x_2$, we used the HSL color space. The saturation ($x_1 = S$) of the yellow thorax color was allowed to vary while keeping the hue (H) and lightness (L) constant, with HSL given by $H = 0.60, 0.10 \leq S \leq 0.91, L = 0.50$. Low values of S correspond to a greenish gray thorax color and high values correspond to bright yellow. The abdomen color was defined as $x_2 = L$, with HSL given by $H = 0.60, S = 0.10, 0.03 \leq L \leq 0.43$, thus varying $L$ and keeping $H$ and $S$ constant. High values of $L$ correspond to a gray abdomen and low values correspond to dark or black shades. We used a genotype–phenotype mapping according to the following sigmoid function:

$$x_1 = a_k + \frac{b_k - a_k}{1 + e^{-(\xi_k + c)z}},$$

where $k = 1, 2, \xi_k$ is a genotypic value in the range $0 \leq \xi_k \leq 1$, $a_k$ is the lower asymptote of $x_1$, $b_k$ is the upper asymptote, $c$ measures the steepness of the sigmoid curve, and $z$ gives the position of the inflexion point (see Fig. S1 in the supporting online material; $a_1 = 0.10, b_1 = 0.91, a_2 = 0.03, b_2 = 0.43, c = 20, z = 0.50$). The mapping is meant to describe the production of pigment, in the case of $x_1$ yellow pigment and in the case of $x_2$ melanin, as a function of the concentration $\xi_k$ of a transcription factor.

For the abdomen shape, we inscribed the abdomen in a rectangle with constant width $= 1$ and defined $x_3$ as the height of the rectangle, with $1 \leq x_3 \leq 2$ (illustrated in Fig. S2). We kept the surface area of the abdomen constant = 1 by assuming an increasingly triangular and elongated shape with increasing values of $x_3$.

The alleles at the diploid loci for each of the three traits additively determine the genotypic values $\xi_1$ and $\xi_2$ in equation (11) and the abdomen length $x_3$.

**CASE SCENARIOS**

To illustrate the results of the evolutionary simulations, we investigated a number of well-known cases of Batesian mimicry. We selected and analyzed the case studies in the following way. First, the unpalatable model whose appearance is mimicked should have a central position in a mimicry ring containing several species. We searched for candidate feature traits among the visually prominent traits that are shared by the members of the ring. Second, it should be possible to reconstruct a likely ancestral appearance of the mimic-to-be, based on phylogenetic information and comparative reasoning. Third, a feature trait was selected based on the possibility of single-locus control. If two or more feature dimensions would be required, and pleiotropic single-locus control of these dimensions seemed unlikely, we examined whether nonmimetic evolution could produce a phenotype that would be a likely starting point for a feature mutation. Proceeding in this way, we obtained scenarios of Batesian mimicry evolution, starting with a reconstructed original appearance of the
MIMICRY EVOLUTION

Results

EVOLUTIONARY SIMULATIONS

Saltational evolution of Batesian mimicry may have occurred in the Yellow-banded sphinx (Rubinoff and Le Roux 2008), which is a moth that mimics bumblebees (see below). We used this example for our evolutionary simulations. Figure 1A illustrates the trait space and the evolution of Batesian mimicry. The green sphere represents the nonmimetic prey niche, which is within the category of “ordinary prey” and is the starting-point of mimics-to-be in a simulation. Predators use thorax color as a feature: for a sufficiently high saturation of yellow, as illustrated by the yellow feature region in Figure 1A, which corresponds to $x_{1f} = 0.85$ and $R_f = 0.15$ in equation (3), they tend to categorize prey as modellike, by generalizing more widely over all prey traits.

At the start of the simulation illustrated in Figure 1A and Figure 2, the members of the model population have trait value $x_b = (0.90, 0.05, 1.05)$ and the potential Batesian mimics start at $x_a = (0.15, 0.40, 1.50)$. This means that they initially have traits situated in the center of the nonmimetic prey niche (the green sphere in Fig. 1A), having a greenish gray thorax color, and an elongated, gray abdomen. The model individuals have a saturated yellow thorax, and a black, square abdomen. In Figure 1A, the model traits would be situated in the lower right part of the yellow box. In the simulation, after around 1400 generations, a feature mutant succeeded in entering the mimicry ring (Figs. 1A and 2B), after which the mimic appearance gradually approached the model (Figs. 1A and 2 C, D).

In further simulations, we explored the possibility that predators use the combination of a yellow thorax and a dark abdomen for feature recognition in the Yellow-banded sphinx example. In these simulations, predators used a two-dimensional feature consisting of the combination of a yellow thorax and a dark abdomen. We implemented the corresponding feature region in trait space as the yellow cylinder segment illustrated in Figure 1B (the center of the cylinder is $(x_{1f}, x_{2f}) = (1.0, 0.0)$ and the radius is $R_f = 0.30$). First, we conducted a simulation assuming the same nonmimetic ancestral appearance as in the previous case (Fig. 1A) as the starting point. Over the duration of the simulation (25,000 generations), no successful feature saltation occurred and no similarity to the model was established (Fig. S3). The likely reason is that double mutants, having both a yellow thorax and a dark abdomen, are very rare, and if they occur, recombination fairly rapidly breaks down the trait combination producing the feature, so their descendants inherit the feature only to a limited extent. This implies that simultaneous evolutionary saltations in multiple, mimic-to-be, followed by the application of a feature mutation to this appearance, creating an imperfect first mimic carrying the feature, and finally a number of smaller changes in several traits, leading to the current mimic appearance. Detailed information backing up the scenarios is found in the supporting online material (Supporting Information).

Figure 1. Illustration of the trait space for the Yellow-banded sphinx example. The trait $x_1$ gives the saturation of yellow thorax color, $x_2$ the lightness of the abdomen, and $x_3$ its elongation. (A) Traits within the green sphere correspond to a nonmimetic prey niche, whereas those within the yellow box have a high probability of being classified by predators as possessing the feature, that is, a highly saturated yellow thorax color. The long arrow represents a feature saltation and the train of smaller arrows represents gradual evolution of the mimic towards the model appearance. The sketched phenotypes are drawn in the trait space roughly at positions that correspond to their traits. (B) The feature region is changed to correspond to the combination of a yellow thorax and a dark abdomen. The saltation in (A) no longer results in a passable mimic. However, after an evolutionary change to a darker abdomen (e.g., thermal melanism; dark sphere), a saltation to a yellow thorax produces a passable mimic, which then can evolve towards increased similarity to the model.
Evolutionary simulation of the origin of mimicry through feature saltation (as outlined in Fig. 1A). Prey appearance has three components: thorax color, $x_1$; abdomen color, $x_2$; and abdomen shape, $x_3$. (A) Phenotypes of individuals from mimic and model populations at four points in time: before mimicry evolves, at the first appearance of feature mutants, after further adjustment of mimicry, and when mimicry is nearly perfected. Light blue (orange) points in (B) to (D) indicate traits of randomly sampled individuals of the mimic (model) population. Blue and orange crosses indicate traits of the corresponding phenotypes in (A).

genetically independent feature traits are unlikely to contribute to mimicry evolution.

Second, we assumed a nonmimetic ancestral appearance with a somewhat darker abdomen (Fig. 1B), which for instance could result from selection for thermoregulation in colder conditions (thermal melanism is common in insects; Clusella Trullas et al. 2007). For this ancestral appearance, simulation showed that mimicry can evolve through feature saltation (Figs. 1B and S4), even if the feature is two-dimensional. Effectively, because the starting phenotype already possesses one feature component, the feature saltation is reduced to changing the remaining dimension. In general, the appearance of such preadaptations, enabling a subsequent change to approximate similarity, can be an important ingredient in the evolution of Batesian mimicry.

SCENARIOS OF SALTATIONAL BATESIAN MIMICRY EVOLUTION

The Yellow-banded sphinx occurs in the northern parts of North America and is believed to be a mimic of bumblebees. In the scenario, the ancestral appearance (Fig. 3A) is similar to the extant sister species that shares a green–gray, possibly cryptic, color pattern with the majority of the species in the genus (Rubinoff and Le Roux 2008). The feature mutation consists in an increased yellow pigmentation of the thoracic scales (Fig. 3B). The mutation results in a qualitative change in appearance and could shift the perception of the moth so that many predators categorize it as a bumblebee when it is foraging for nectar. The scenario is based on the evolutionary simulation described in Figure 1A and Figure 2. As an alternative to the scenario in Figure 3, one could also consider the possibility indicated in Figure 1B, that the feature that characterizes the bumblebee mimicry ring is a combination of a yellow thorax and an otherwise dark body. In such a case, thermal melanism (Clusella Trullas et al. 2007) could play the role of a preadaptation for mimicry evolution, as outlined in Figure 1B.

A trait functions as a feature by aiding the efficient classification of prey. A feature should thus be salient, that is, easily perceived by potential predators. To play an important role in
mimicry, it should also be shared by the species in a local mimicry ring. An example is the dark brown or black wing color in the much-studied butterfly mimicry ring centered around the Pipevine swallowtail, *Battus philenor*, a toxic species of Central and North America that is a model for several Batesian and Müllerian mimics (Platt et al. 1971; Platt 1975). The Red-spotted purple, *Limenitis arthemis astyanax*, is known to be a Batesian mimic in this ring (Platt et al. 1971; Platt 1975). In the *Limenitis arthemis*-complex, there are three subspecies; the nonmimicking White-banded admiral, *L. a. arthemis*, and the Pipevine swallowtail mimics *L. a. astyanax* and *L. a. arizonensis*. Figure 4 shows a scenario of Batesian mimicry evolution in this group, with a white-banded form as the ancestral state (Fig. 4A), as white banding is the rule among Palearctic *Limenitis* species (Mullen 2006). The feature mutation involves increased melanism, covering most of the white bands (Platt 1975) (Fig. 4B). White banding is mainly controlled by a single locus (Platt 1975), consistent with the idea that a single feature mutation could produce a large change in visual appearance, shifting the mutant (Fig. 4B) into the same category as the model (Fig. 4D). Subsequent gradual changes on the dorsal side of the wings include an increase in the areas with blue structural color, a decrease in the orange-red spots, and a changed wing shape (Fig. 4C), further improving the similarity to the model.

A spectacular case of polymorphic mimicry occurs in the Mocker swallowtail butterfly, *Papilio dardanus* (Ruxton et al. 2004). The species is distributed across sub-Saharan Africa, with around 25 different female color morphs, many of which are mimetic, and with nonmimetic, monomorphic males (Clark and Vogler 2009). Phylogenetic and biogeographical evidence supports a single origin of mimicry in the species (Clark and Vogler 2009), and the widespread female morph hippocoon and the similar-looking allopatric hippocoonides are thought to resemble the original mimetic variant (Clarke and Sheppard 1960; Nijhout 2003). These two morphs mimic populations of the Friar, *Amauris niavius*, and there is observational evidence that the mimicry is Batesian (Carpenter 1942). To characterize the origin of mimicry as a feature saltation (Fig. 5), one needs to specify the appearance of the female Mocker swallowtail before mimicry evolved, as well as the first mimetic form. In the scenario, the ancestral female appearance (Fig. 5A) is a modification of the females of the sister species (Clark and Vogler 2009), the Apple-green swallowtail *Papilio phorcas*, in the direction of the current males of the Mocker swallowtail, representing a correlated response to presumed sexual selection on the males, who have diverged from a typical *Papilio* male appearance (see Fig. S5 in the supporting online material). In this way, the scenario incorporates the principle illustrated in Figure 1B, that nonmimetic evolutionary change
might be needed to set the stage for a mimetic feature saltation. Starting from the ancestral female appearance (Fig. 5A), a mutant having the light yellow forewing area split into separated patches (Clarke and Sheppard 1960; Nijhout 2003) (Fig. 5B) becomes a passable mimic of the Friar model (Fig. 5D). Morphologically, the mutant consists in an increased melanism of interspaces on the forewing (Clarke and Sheppard 1960; Nijhout 2003). The mimicry would be passable if predators use this aspect of the Friar’s color pattern—light patches, two on each side of the body, surrounded by a dark pattern (Fig. 5D)—as a feature for classification of prey. This role as a feature is supported by the sharing of the characteristic color pattern by several mimics of the Friar model, both Batesian and Müllerian, for instance in a local West African mimicry ring (Owen 1974). Further, fine-tuning of the hippocoon mimic includes a loss of the tails, a whitening of the background color, and a modification of the shape of the black pattern (Fig. 5C).

Our scenarios so far have dealt with insects, but the same principles of mimicry evolution can be applied to other groups of organisms. New World coral snakes in the family Elapidae are venomous and often brightly colored, typically with red, black, and yellow rings encircling the body. Many species of harmless snakes, for instance in the family Colubridae (e.g., milk snakes and king snakes) adopt a coloration similar to that of coral snakes, which has been interpreted as Batesian mimicry (Greene and McDiarmid 1981; Pough 1988; Savage and Slowinski 1992). Based on phylogenetic information for Lampropeltini, it has been argued that crypsis is the ancestral state and that coral snake mimicry has evolved from crypsis within this group (Pyron and Burbank 2009). A typical colubrid coloration is that of Lampropeltis triangulum triangulum (Bryson et al. 2007), which has darkish brown blotches lined with black on a lighter background (Fig. 6A) and is considered to be cryptic through background matching and/or disruptivity. Other populations with ringed color patterns in the species, as represented by L. t. elapsoides (Scarlet kingsnake), are considered as good mimics of M. fulvius (Bryson et al. 2007), whereas the form L. t. temporalis, has red blotches instead of rings, and has been regarded as a poor mimic (Pfennig et al. 2007).

Figure 6. Mimicry evolution in the snake tribe Lampropeltini. Batesian mimicry evolves from an ancestral cryptic color pattern (A), initiated by a change of color in the dorsal blotches from brown to red, resulting in an imperfect mimic (B), followed by fine-tuning of the appearance into more perfect mimicry (C) of the highly poisonous Eastern coral snake model (D). The ancestral appearance (A) is a common cryptic pattern in extant Lampropeltini. The change to red blotch color in the mutant (B) is used as a feature by predators to classify dangerous prey. The more perfect mimicry (C) has body-encircling rings, a change from light brown to yellow color, and broader black bands.

It has been suggested that an incipient Batesian mimic would require at least two coral snake colors (Hinman et al. 1997). From the principle illustrated in Figure 1B, emphasizing the difficulty of simultaneous salient evolution in genetically independent traits, this implies that one coral snake color would need to be present before a feature mutation occurs. In our scenario, the feature mutation involves a change of brown areas (Fig 6A) to red in which the resulting poor mimic (Fig. 6B) might still be relatively cryptic at a distance, and therefore the transition may not be very costly in terms of detectability. The appearance of black-bordered red blotches, two coral snake colors, repetitively displayed, could be a feature used by predators to categorize dangerous and therefore unsuitable prey and may thus constitute the first step of mimicry evolution in Lampropeltis and other lampropeltine snakes (cf. Fig. 1 in Kikuchi and Pfennig 2010a). This kind of a feature-based categorization could explain the rough and imperfect mimicry in some milk snakes (Bryson et al. 2007). Following the feature mutation, further improvements in the resemblance to the model (Fig. 6D) are for instance the formation of rings from blotches, the change from light brown to yellow, and an increase in the width of the black bands (Fig. 6C) to a more perfected mimic as occurs in for instance L. elapsoides, L. alterna, L. pyromelana, and L. zonata.

Discussion
The evolution of mimicry has offered a puzzle because it often involves major changes in a suite of characters. The main difficulty for incipient mimicry is that mutants may find themselves in an adaptive valley, because their similarity to the model is insufficient and, in the case of Batesian mimicry, deviation from other prey and perhaps a loss of crypsis reduce fitness. There is experimental evidence for adaptive valleys in Batesian mimicry evolution (Mapes and Alatalo 1997), suggesting that the phenomenon could be common. In some cases, however, there might not be a valley, which has been proposed in the context of coral snake mimicry. In situations of high model toxicity and abundance,
predators might generalize so widely that intermediates between an original appearance and accurate mimics are not attacked more frequently than the original appearance (Kikuchi and Pfennig 2010a). Batesian mimicry evolution would then become a straightforward hill-climbing process.

In situations where there is a fitness valley, our evolutionary simulations and scenarios show that the valley can be crossed if predators pay particular attention to some characters and use these as features for categorization of complex prey stimuli. Feature-based categorization can thus be a crucial element in the evolution of Batesian mimicry and the results we obtained give credence to the hypothesized two-step process in a space of realistic, multitrait appearances. The idea of feature-based classification by predators can also help explain the evolution of Müllerian mimicry (Balogh et al. 2010), by minimizing the effect of selection against intermediates between aposematic forms. In addition, feature salutation could also help explain the occurrence of major gene effects in mimicry evolution (Baxter et al. 2009), and thus contribute to the on-going investigation of genetic changes during adaptation (Orr 2005).

The number of characters used for unprofitable prey recognition considerably limits the probability for Batesian mimicry to evolve. Our simulations suggest that if predators use multidimensional features, and changes are needed in several genetically independent dimensions of prey appearance, no salutation occurs and therefore no mimicry evolves. However, it is possible that some of the characters involved may evolve for other reasons, allowing mimicry evolution to follow. Such a case is illustrated for the Yellow-banded sphinx (Fig. 1B), where a presumed melanism precedes mimicry evolution. Also, in the scenario with the Mockers swallowtail butterfly (Fig. 5), we assumed preadaptation of the ancestral female appearance. Our reasons for the assumed ancestral appearance is that it is unlikely for mimicry to evolve from a color pattern similar to that of the sister species P. phorcas, as it is unlikely that a single genetic change could give rise to a passable mimic. Our assumed ancestral appearance in the scenario is instead an intermediate between the female color pattern of the sister species P. phorcas and the male P. dardanus appearance, which could come about through sexual selection and genetic coupling between male and female characters during the evolution of the male P. dardanus appearance.

Because feature-based categorization by predators entails a qualitative distinction between nonmimics and passable mimics, our theory could explain the occurrence of imperfect mimicry (Chittka and Osorio 2007). If the balance between feature-based categorization and narrow generalization over many traits is shifted towards feature-based categorization, there is relaxed selection pressure on mimics towards further increases in similarity, and imperfect mimicry is expected. Experiments have shown that predators ignore certain stimulus properties when generalizing from unsuitable prey, such as patterns on differently colored artificial prey (Aronsson and Gamberale-Stille 2008), the amount of black in the black and yellow pattern in puffer fish mimics (Caley and Schluter 2003), or ring order in coral snake mimicry (Kikuchi and Pfennig 2010b). There are also other explanations for imperfect mimicry, of which perhaps the most frequently suggested is that common and highly distasteful models are compatible with imperfect mimicry (Lindström et al. 1997). Other possibilities are a plentitude of alternative prey (Lindström et al. 2004) or the alternation over a season of different models (Sherratt 2002). There is evidence that mimetic accuracy can correlate negatively with model abundance (Harper and Pfennig 2007), but in general the relative importance of the different possible explanations is not known.

A feature mutant represents a kind of “missing link” in Batesian mimicry evolution. We propose that its appearance can be reconstructed and suggest potential scenarios of character evolution for several well-known cases of mimicry. These scenarios are based on several pieces of information, foremost the likely ancestral and model character states and in most cases the type of genetic inheritance of traits. We suggest a new line of research where the likelihood of specific scenarios are investigated in experiments in which manipulated prey are used to test whether the suggested character saltations function in predator categorization of unpalatable prey. In conclusion, we propose that the incorporation of established psychological theories of categorization into the analysis of mimicry can be fruitful.

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LITERATURE CITED

Bryson, R. W., Jr., J. Pastorini, F. T. Burbrink, and M. R. J. Forstner. 2007. A phylogeny of the Lampropeltis mexicana complex (Serpentes:


Supporting Information

The following supporting information is available for this article:

**Figure S1.** Genotype–phenotype mappings for \( x_1 \) and \( x_2 \).

**Figure S2.** Definition of the abdomen shape parameter \( x_3 \).

**Figure S3.** Evolutionary simulation corresponding to the illustration in Figure 1B, in which the feature region represents a combination of a yellow thorax and a dark abdomen, so that a single-trait saltation to passable mimicry no longer is possible when starting from the nonmimetic prey niche indicated by the green sphere in Figure 1B.

**Figure S4.** Evolutionary simulation corresponding to the illustration in Figure 1B, in which the feature region represents the combination of a yellow thorax and a dark abdomen.

**Figure S5.** Reconstruction of an ancestral nonmimetic *P. dardanus* appearance.

**Appendix S1.** Details of case scenarios.

**Appendix S2.** Code and data files for the simulations.

Supporting Information may be found in the online version of this article.

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