

## High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test

David W. Kikuchi and David W. Pfennig

*Proc. R. Soc. B* 2010 **277**, 1041-1048 first published online 2 December 2009

doi: 10.1098/rspb.2009.2000

---

### Supplementary data

["Data Supplement"](#)

<http://rsob.royalsocietypublishing.org/content/suppl/2009/11/27/rspb.2009.2000.DC1.html>

### References

[This article cites 40 articles, 7 of which can be accessed free](#)

<http://rsob.royalsocietypublishing.org/content/277/1684/1041.full.html#ref-list-1>

### Subject collections

Articles on similar topics can be found in the following collections

[taxonomy and systematics](#) (212 articles)

[ecology](#) (1221 articles)

[evolution](#) (1447 articles)

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

---

To subscribe to *Proc. R. Soc. B* go to: <http://rsob.royalsocietypublishing.org/subscriptions>

---

# High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test

David W. Kikuchi\* and David W. Pfennig

*Department of Biology, University of North Carolina, Chapel Hill, NC, USA*

In Batesian mimicry, a harmless species (the ‘mimic’) resembles a dangerous species (the ‘model’) and is thus protected from predators. It is often assumed that the mimetic phenotype evolves from a cryptic phenotype, but it is unclear how a population can transition through intermediate phenotypes; such intermediates may receive neither the benefits of crypsis nor mimicry. Here, we ask if selection against intermediates weakens with increasing model abundance. We also ask if mimicry has evolved from cryptic phenotypes in a mimetic clade. We first present an ancestral character-state reconstruction showing that mimicry of a coral snake (*Micrurus fulvius*) by the scarlet kingsnake (*Lampropeltis elapsoides*) evolved from a cryptic phenotype. We then evaluate predation rates on intermediate phenotypes relative to cryptic and mimetic phenotypes under conditions of both high- and low-model abundances. Our results indicate that where coral snakes are rare, intermediate phenotypes are attacked more often than cryptic and mimetic phenotypes, indicating the presence of an adaptive valley. However, where coral snakes are abundant, intermediate phenotypes are not attacked more frequently, resulting in an adaptive landscape without a valley. Thus, high-model abundance may facilitate the evolution of Batesian mimicry.

**Keywords:** adaptive landscape; Batesian mimicry; coral snake mimicry; predation; colour pattern

## 1. INTRODUCTION

Batesian mimicry occurs when a harmless species (the ‘mimic’) resembles a dangerous one (the ‘model’) and thereby co-opts the protection from predation that is often afforded to conspicuous, toxic species (Bates 1862; reviewed in Ruxton *et al.* 2004). Although Batesian mimicry has been called ‘the greatest post-Darwinian application of natural selection’ (Fisher 1958), the route evolution takes in producing mimicry is unknown in many systems.

Much of the debate surrounding the evolution of Batesian mimicry centres on explaining whether it can evolve through a gradual process of incremental evolution. In particular, if the starting point for the evolution of mimicry is a cryptic phenotype (as is often assumed; e.g. Nicholson 1927; Charlesworth & Charlesworth 1975; Charlesworth 1994), then it is unclear how a population can transition from an ancestral cryptic phenotype to a derived mimetic one if the population must pass through a phase in which it expresses a phenotype that is intermediate between these two extremes. Such intermediate phenotypes should generally be disfavoured because they should fail to receive the fitness benefits of either crypsis or mimicry (Nicholson 1927; Charlesworth & Charlesworth 1975; Mappes & Alatalo 1997; but see Fisher 1958; Schmidt 1958, 1960). The low fitness of intermediate forms would seem to preclude the gradual evolution from an ancestral cryptic phenotype to a derived mimetic form.

In order to bypass the problem of evolution through intermediate forms of presumably low fitness, some have suggested a two-step evolutionary model in lieu of the gradual process of incremental evolution (Nicholson 1927; Charlesworth & Charlesworth 1975). According to this model, Batesian mimicry evolves when a major mutation of large effect takes the evolving population over the adaptive valley associated with intermediate phenotypes. This initial mutational leap is followed by smaller mutations that perfect resemblance to the model. Indeed, this two-step mechanism is the reigning paradigm for explaining the evolution of Batesian mimicry (Ruxton *et al.* 2004; Turner 2005). Nevertheless, documentation of a system in which there is no adaptive valley between crypsis and mimicry would imply that Batesian mimicry might also be able to evolve gradually. However, few have specifically questioned if ecological circumstances exist in which intermediate phenotypes would not reside in an adaptive valley.

Generally, the factors that can increase the fitness of intermediate phenotypes can also favour the evolution of imperfect mimicry. Two such factors are likely to be particularly beneficial to intermediate phenotypes: (i) high-model toxicity (Duncan & Sheppard 1965; Pilecki & O’Donald 1971; Goodale & Sneddon 1977; Lindström *et al.* 1997) and (ii) high-model abundance (Brower 1960; Lindström *et al.* 1997; Harper & Pfennig 2007). Selection against imperfect mimics decreases under these two conditions for the same reason: the probable payoff to a predator for attacking prey with a given resemblance to the model decreases (Oaten *et al.* 1975; Sherratt 2002). A way of visualizing this is that the ‘cone of protection’ around the model’s phenotype comes to envelop more and more of the phenotypic space around it as

\* Author for correspondence ([dkikuchi@email.unc.edu](mailto:dkikuchi@email.unc.edu)).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.2000> or via <http://rspb.royalsocietypublishing.org>.

models become more numerous and noxious. If models are highly abundant and noxious, the cone of protection may grow so wide that selection acts on intermediate phenotypes to form a smooth slope instead of an adaptive valley.

We studied these issues in a well-documented Batesian mimicry complex (Greene & McDiarmid 1981; Pfennig *et al.* 2001; Brodie & Brodie 2004; Harper & Pfennig 2007, 2008). We begin by presenting a phylogenetic analysis of colour-pattern evolution, which strongly suggests that mimics evolved from cryptic forms in our study system. We then present an empirical test of the hypothesis that predation on intermediate phenotypes relative to cryptic and mimetic phenotypes changes with the abundance of a deadly model. We specifically predicted that in areas of high-model abundance, there would be relaxed selection pressure by predators against intermediate phenotypes and that therefore we would not observe a difference between attack rates on intermediates relative to cryptic and mimetic phenotypes; i.e. in such areas, there would be no adaptive valley associated with intermediate phenotypes. We also predicted that where models are rare, we would find an adaptive valley caused by increased predation on intermediate phenotypes relative to those protected by crypsis and good mimicry. These predictions focus on the presence or absence of an adaptive valley between crypsis and mimicry, not the efficacy of crypsis versus mimicry as alternative strategies for avoiding attack. We are more concerned with the potential existence of an adaptive valley because this dictates the mode of adaptation by which species can transition between these two predator avoidance strategies. To test our predictions, we placed replicas of cryptic, intermediate and mimetic phenotypes in natural areas with high- and low-model abundances to evaluate the selective pressures exerted by predators in each area.

## 2. MATERIAL AND METHODS

### (a) *Study system*

In the southeastern USA, the highly venomous eastern coral snake (Elapidae: *Micrurus fulvius*) is the model for a non-venomous mimic, the scarlet kingsnake (Colubridae: *Lampropeltis elapsoides*). The coral snake's venom is lethal to most predators (Roze 1996). Not surprisingly, many potential predators show an innate aversion to coral snake colour patterns (Gehlbach 1972; Smith 1975, 1977). Such a potent model is an excellent candidate for generating a wide cone of protection.

The geographical distribution of *L. elapsoides* overlaps entirely with that of *M. fulvius*, which ranges from Florida to southern North Carolina. The former's geographical range also extends north into southern Virginia and west to the Mississippi River (see range map in Harper & Pfennig 2007). *Lampropeltis elapsoides* is avoided by predators in sympatry with coral snakes, but not in allopatry (Pfennig *et al.* 2001), confirming that it is indeed a Batesian mimic of *M. fulvius*. Also, *M. fulvius* is relatively more abundant than *L. elapsoides* in Florida than it is in southern North Carolina (Harper & Pfennig 2007). Museum collection data indicate that ratio of the abundance of *M. fulvius* to *L. elapsoides* is approximately six times higher in Florida than in North Carolina (Harper & Pfennig 2007). In Florida, *L. elapsoides* is more variable in colour patterns than in southern North Carolina, where they are more precise mimics, indicating that the cone of protection

in North Carolina may be narrower. Previous field experiments have shown that slightly imperfect mimics are selected against in southern North Carolina (Harper & Pfennig 2007), suggesting that variation in the cone of protection can be measured in this system. However, it is unknown whether predation pressure against intermediate phenotypes is relaxed in areas of high-model abundance (e.g. Florida), such that no adaptive valley exists in these areas.

### (b) *Ancestral character-state reconstruction of colour pattern*

To test whether the mimic, *L. elapsoides*, likely evolved from a cryptic ancestor (as assumed; see §1), we performed an ancestral character-state reconstruction of colour pattern in the snake tribe Lampropeltini. To do so, we used a recently published phylogeny (Pyron & Burbrink 2009) that was built with maximum-likelihood methods and based on three nuclear and six mitochondrial loci. This phylogeny includes all 31 traditionally described species in the Lampropeltini.

We quantified the colour pattern of each species in the phylogeny. We used an ordinal scale developed by Savage & Slowinski (1992) to rank how closely each species' colour pattern matched that of the model, *M. fulvius*. We scored pattern and colour separately. For pattern, a score of 3 was given to species with rings that completely encircle the body (i.e. the same pattern as *M. fulvius*); a score of 2 was given to species with bands that do not completely encircle the body; a score of 1 was given to species with dorsal saddles that encircle the body less than bands (with or without interspersed lateral blotches); and a score of 0 was given to species with any other pattern not matching one of the above three categories. For colour, a score of 1 was given to species with all three of the colours typical of *M. fulvius* (red, yellow/white and black) and a score of 0 was given to species that lacked at least one of these colours.

Because both colour and pattern are important in predator avoidance of coral snakes and their mimics (Smith 1975; Hinman *et al.* 1997), our separate pattern and colour scores were combined. We did so by weighting and summing each so that they contributed equally to a continuous composite colour-pattern variable that ranged from 0 (most cryptic) to 2 (most mimetic). Although our classification scheme assumes that coral snake colour patterns are conspicuous and other colour patterns found in the Lampropeltini are cryptic, these assumptions appear to be valid. Experiments have shown that predator avoidance of coral snake colour patterns is probably due entirely to their aposematic function (Brodie 1993), and that drab, blotched colour patterns of other snakes are probably cryptic (Brodie 1992; King 1992).

The evolutionary history of colour pattern in the Lampropeltini was determined using a parsimony reconstruction for continuous characters in Mesquite 2.6 (Maddison & Maddison 2009). We used a squared-change parsimony model that assigns a cost of  $(x-y)^2$  to a transition from character state  $x$  to character state  $y$ . For taxa whose colours or patterns were difficult to classify, we performed separate analyses with possible alternative values to evaluate the stability of our character-state reconstruction.

### (c) *Experimental evaluation of predation on intermediate phenotypes in high- and low-model abundance areas*

To evaluate attack rates on intermediate phenotypes relative to cryptic and mimetic ones, we measured predation rates



Figure 1. Replicas of different snake phenotypes used to measure predation in the field, along with the species or subspecies of snake that each most closely resembled. (a) Cryptic phenotype, which resembled (b) the eastern milksnake, *L. t. triangulum* (photo by Roger W. Barbour); (c) intermediate phenotype, which resembled (d) the coastal plains milksnake, *L. t. temporalis* (photo by Richard D. Bartlett); (e) mimetic phenotype, which resembled (f) the scarlet kingsnake, *L. elapsoides* (inset: the eastern coral snake, *M. fulvius*, which *L. elapsoides* mimics; photos by Wayne van Devender).

on different snake colour-pattern phenotypes in the wild. Specifically, we placed artificial snake replicas in natural areas where they would be subjected to potential predation by naturally occurring, free-ranging predators. Moreover, as the replicas were made of a soft substance (clay) that takes impressions, predation events were recorded even though the replicas were left unobserved for the long periods of time necessary for predation to occur. This method has been employed successfully to document both avian and mammalian predators on at least three continents (e.g. Madsen 1987; Brodie 1993; Brodie & Janzen 1995; Hinman *et al.* 1997; Pfennig *et al.* 2001, 2007; Wüster *et al.* 2004; Niskanen & Mappes 2005; Buasso *et al.* 2006; Harper & Pfennig 2007), indicating that it is robust to different predator guilds and environments. We constructed our replicas with pre-coloured, non-toxic polymer clay (Polyform Products, Elgin, IL) that were coated with a thin film of clear, low-odour spray latex enamel (Krylon Products Group, Cleveland, OH) to minimize any smell emitted by the clay.

To determine the appropriate colour patterns for our cryptic, intermediate and mimetic phenotypes (figure 1), we used morphometric analyses (D. Kikuchi 2009, unpublished data) of museum specimens of eastern milksnakes (*Lampropeltis triangulum triangulum*;  $n = 16$ ) and published data on *L. elapsoides* (Harper & Pfennig 2007). We included 12 dimensions to describe colour pattern. Phylogenetic analyses show that *L. t. triangulum* is an appropriate representative of a cryptic ancestral phenotype (see §3). To create a 50 per

cent intermediate phenotype, we used the average value of the cryptic and mimetic phenotype for each dimension of colour pattern measured. Our intermediate phenotype resembled *Lampropeltis triangulum sypila* and *Lampropeltis triangulum temporalis*, indicating that it was within the natural range of variation in this genus (compare figure 1c with d).

Before placing replicas in the field, we first arranged them into triads (consisting of one replica of each different phenotype) by tying them to 1 m lengths of clear monofilament fishing line and then attaching one of each phenotype to the same large nail. This ensured that within triads, replicas of each phenotype would share similar micro-habitats. Members of each triad were placed in realistic micro-habitats such as the edges of logs and grass clumps (figure 1). Triads were placed in 750 m transects of 10 triads each so that they were separated from one another by about 75 m. Placing replicas in triads and transects allowed us to use a statistical model in analysing predation that accounted for the possibility that predation events might have non-random spatial distributions. Our sites were protected natural areas such as state parks and national forests. Most of the areas contained longleaf pine forest. *Lampropeltis elapsoides* is closely associated with longleaf pine forests (Palmer & Braswell 1995), which range from Florida to North Carolina and provide relatively constant habitat throughout the range of the mimicry complex, thus controlling for the visual environment in which predators perceive the snakes. In other words, a colour pattern that is cryptic where models are abundant

(Florida) is likely to be equally cryptic where models are rare (southern North Carolina), as the habitat in both regions is similar. We chose 13 sites in Florida (high-model abundance) and 13 sites in southern North Carolina (low-model abundance) to conduct our experiment (appendix SA in the electronic supplementary material). We left the replicas in the field for 30–36 days. At the end of this time, we collected each replica and, based on the presence/absence of tooth and beak marks, scored each as having been attacked or not (for details, see Pfennig *et al.* 2007).

Given our prediction that there would be an adaptive valley in areas of low-model abundance but not in areas of high-model abundance, we analysed our data using an *a priori* contrast to compare the fitness of the intermediate phenotype with the combined fitness of the cryptic and mimetic phenotypes. We used the *lmer* function in the *lme4* package (Bates 2005) for R 2.8.1 (R Development Core Team 2008) to build generalized linear mixed models with binomial error distributions for predation data from high- and low-model abundance areas. We used replica fate (attacked or not attacked) as the binary response variable, replica phenotype as the predictor variable and triad nested within transect as random effects.

### 3. RESULTS

#### (a) *Ancestral character-state reconstruction of colour pattern*

Mapping colour pattern onto a phylogeny of the Lampropeltini showed that all strong mimetic resemblances (colour-pattern value > 1) are within a single clade that contains the mimic, *L. elapsoides* (figure 2). Outside this clade, some snakes have colour-pattern values above 0 (where 0 denotes a cryptic pattern), but these snakes have three drab colours arranged as dark saddled blotches with black edges on a light background, much as they are in *L. t. triangulum* (see figure 1*b*). Such colour patterns are still highly cryptic and do not resemble the model, *M. fulvius*.

The last common ancestor of the clade containing mimetic snakes and the clade formed by *Bogertophis* and *Pseudelaphe* was probably very similar to *L. t. triangulum* in phenotype, most likely having a saddled pattern of three drab colours. This result was robust to altering values of colour pattern for *P. flavirufa* and *Pantherophis guttatus*, both of which were difficult to classify owing to variability in appearance (results not shown). Furthermore, reconstructed values of colour pattern at deeper nodes are all close to zero, indicating that the basal character state for the Lampropeltini was cryptic. We consider this strong evidence that conspicuous mimics evolved from cryptic ancestral phenotypes, and also that *L. t. triangulum* is an appropriate representation of that ancestral phenotype.

#### (b) *Experimental evaluation of predation on intermediate phenotypes in high- and low-model abundance areas*

Of 780 replicas that we placed in the field, we discarded 32 (4.1%) owing to loss, fire or human interference. Of the 748 that remained for analysis, 104 (13.9%) were attacked. Attacks were evenly distributed, with 55 replicas attacked in Florida and 49 attacked in North Carolina ( $p > 0.5$ ). Most attacks were by large mammals such as

black bear, *Ursus americanus*, and small mammals such as opossum, *Didelphis virginiana*. Attacks by birds were rare. Markings consistent with rodent or insect activity were ignored, as these would not constitute threats to real snakes.

In Florida, where coral snakes are relatively common, the intermediate phenotype was not attacked more than the cryptic and mimetic phenotypes (figure 3*a*;  $n = 389$ ,  $Z = -0.01$ ,  $p > 0.9$ ). By contrast, in southern North Carolina, where coral snakes are relatively rare, the intermediate phenotype was attacked more frequently than the other two (figure 3*b*;  $n = 359$ ,  $Z = 1.95$ ,  $p = 0.05$ ).

### 4. DISCUSSION

Our results demonstrate that Batesian mimicry can arise from cryptic ancestral phenotypes, and that predation on intermediate phenotypes relative to cryptic and mimetic phenotypes changes with the abundance of a deadly model. In particular, an ancestral character-state reconstruction revealed that mimetic coloration evolved in a single clade of Lampropeltini from cryptic ancestors. Moreover, our field experiment confirmed our prediction (see §1) that when a strongly aversive model is common, there is no increased predation associated with phenotypes that are intermediate between cryptic and mimetic forms. By contrast (and also consistent with our prediction), when such models are rare, there is an adaptive valley associated with intermediate phenotypes, verifying that model abundance probably influenced the changes in the adaptive landscape. This study therefore indicates that an adaptive valley may not be present in all circumstances under which Batesian mimicry might evolve, widening the number of scenarios that can explain its evolution.

As noted in §1, evolutionary biologists have long debated how Batesian mimicry evolves. Because it is generally assumed that there will be an adaptive valley associated with phenotypes that are intermediate between cryptic and mimetic forms, recent opinion has considered a two-step mechanism as the likely explanation for the evolution of Batesian mimicry (Ruxton *et al.* 2004; Turner 2005). According to this model, the first step occurs when a major mutation of large effect takes an evolving population over the adaptive valley associated with intermediate phenotypes. Later, the second step occurs when mutations of small effect perfect the resemblance of the mimic to the model. It is important to note that the *raison d'être* for a two-step hypothesis is the supposed constant presence of a valley in the adaptive landscape. Yet prior to the present study, research had not evaluated empirically whether conditions might exist under which no such adaptive valley is present.

Our study fills this gap. By demonstrating that conditions do indeed exist under which there is no adaptive valley associated with phenotypes that are intermediate between cryptic and mimetic forms, our data imply that the two-step process need not be considered essential for the evolution of Batesian mimicry. Thus, our study suggests that there are situations under which Batesian mimicry can evolve gradually through a process of incremental evolution. We hasten to add, however, that our results in no way demonstrate that a two-step process could not have unfolded in our (or any other) system.

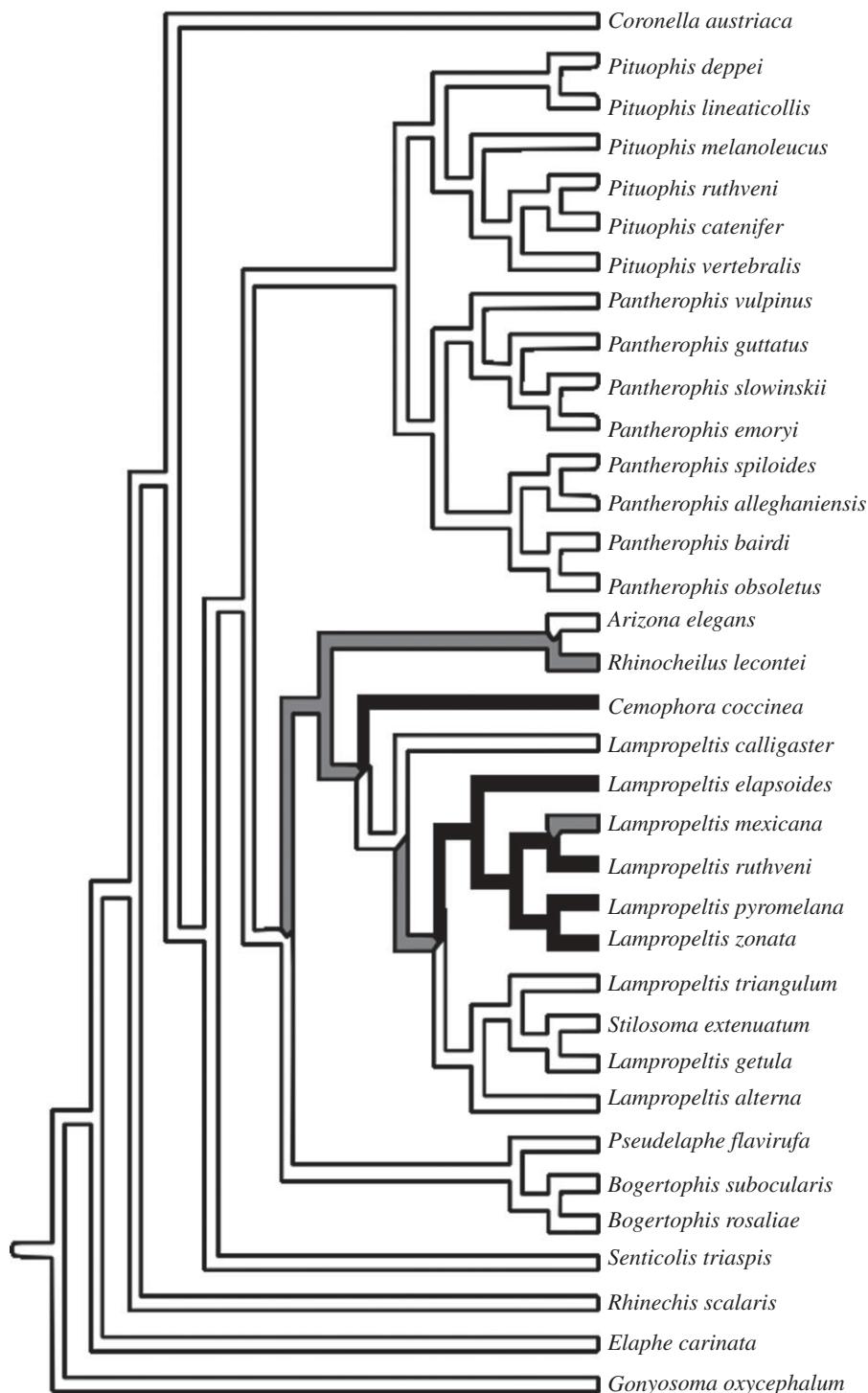


Figure 2. Ancestral character-state reconstruction of colour pattern in the tribe Lampropeltini, the so-called North American ratsnakes. *Coronella austriaca*, *Rhinechis scalaris*, *Elaphe carinata* and *Gonyosoma oxycephalum* are European species used as outgroups. Black, mimetic (colour-pattern score  $> 1.33$ ); grey, intermediate ( $1.33 \geq$  colour-pattern score  $\geq 0.66$ ); and white, cryptic (colour-pattern score  $< 0.66$ ).

Our results merely suggest that such a two-step process need not have occurred because of the constant presence of a valley in the adaptive landscape, as long assumed.

Debate over whether mimicry evolves gradually or begins with a mutation of large effect is essentially about what mechanism is responsible for enabling a population to access the adaptive peak of mimicry. Hypothesizing that mimicry evolves without the first, major mutation implicitly invokes another mechanism to create the requisite smooth adaptive landscape.

Changes in selective pressures, such as those caused by varying model abundance, appear to lie behind many populations' transitions to new adaptive peaks (Fear & Price 1998). It appears that mimicry, long regarded as an exception among adaptations, has the potential to evolve in the same manner as many other traits.

This study provides further evidence that the coral snake mimicry complex in the southeastern USA conforms to the theoretical expectations of a Batesian mimicry system. Previous research established the

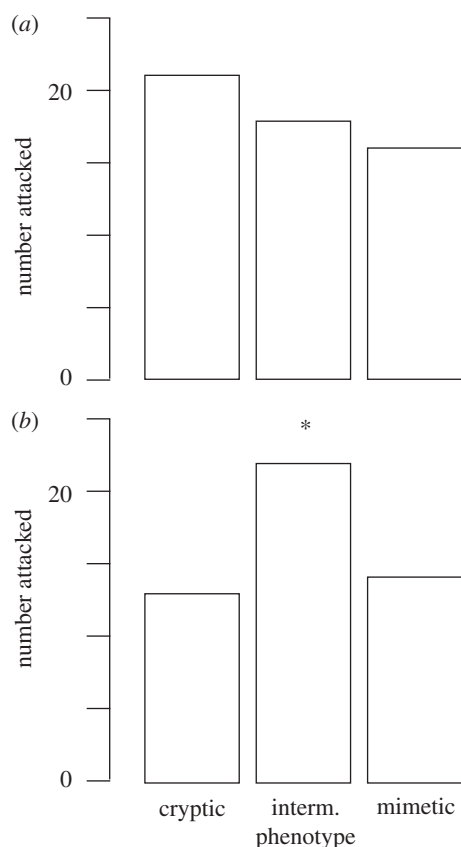


Figure 3. Two alternative adaptive landscapes observed in a coral snake Batesian mimicry complex. (a) No adaptive valley in Florida where coral snakes are highly abundant models. An *a priori* contrast showed no difference between the attack rate on the intermediate phenotype (interm.) versus the attack rate on cryptic and mimetic phenotypes. (b) Selection against intermediate phenotypes around southern North Carolina where coral snakes are rare. The intermediate phenotype is attacked at a higher rate than cryptic and mimetic phenotypes. Asterisk indicates statistical significance.

mimetic function of red, yellow and black patterns on scarlet kingsnakes, showing that protection of good mimics increased with the abundance of models (Pfennig *et al.* 2001). A subsequent study showed that the cone of protection around the coral snake's appearance may change with its abundance because the mimetic scarlet kingsnake is more variable in Florida than in North Carolina (Harper & Pfennig 2007). Replicas of poorly mimetic snakes were also attacked more than good mimics in North Carolina, even though they still had the general appearance of coral snakes (Harper & Pfennig 2007). Here, we have shown that this cone of protection varies to such a degree that in Florida, where coral snakes are relatively common, an intermediate phenotype that barely resembles a coral snake is protected as well as either cryptic or mimetic phenotypes. By contrast, in North Carolina, where coral snakes are relatively rare, the same intermediate phenotype would likely suffer reduced fitness. In these areas, mimicry and crypsis are better strategies for avoiding attack. Such variation in the cone of protection around the model has been predicted by signal detection theoretical models of mimicry (Oaten *et al.* 1975; Getty 1985; Sherratt 2002), which

describe whether or not receivers (in this case, predators) of a certain signal should accept or reject senders (prey) of the signal based on the relative risks of each alternative (Reeve 1989). In essence, in areas where the probability of mistakenly attacking a deadly model is high (such as where models are common), predators are less willing to risk attacking an intermediate mimic than they are in areas where the probability of mistakenly attacking a deadly model is lower (such as where models are rare).

Another prediction of mimicry theory is that when the abundance of *mimics* increases relative to that of models, predators' willingness to attack intermediate and mimetic phenotypes should increase, reducing the cone of protection (Getty 1985; Lindström *et al.* 1997). In our study, we focused on the role that changes in model abundance play in influencing the shape of this cone. However, theory suggests that our results may be confounded by the fact that Batesian mimics were already present in our study areas. Thus, it might be argued that the presence of such mimics might have increased attacks on intermediate and mimetic phenotypes, making our study an inaccurate representation of conditions present when mimicry first originated. We do not believe that this poses a problem with respect to our hypothesis precisely because increased attacks on intermediate phenotypes would render our test conservative. If anything, the adaptive landscape in an area where models are abundant and mimics are absent (as the area where mimicry evolved may have been) should have been less likely to have an adaptive valley than the current one.

Do the conclusions from this study apply to other mimicry systems with less noxious models? After all, coral snakes are highly toxic, and they should generate a much wider cone of protection than would less toxic models. Our results should apply to other mimicry systems for the simple reason that even models less deadly than coral snakes can still be strongly aversive. For example, Lepidopteran larvae (which often serve as models and are often considered to be less toxic) have been known to cause death in potential predators (Poulton 1890), and therefore may still incur high costs on their attackers. Moreover, other Batesian mimicry systems feature models dangerous enough to warrant the evolution of innate aversion in potential predators (Schuler & Hesse 1985; Nelson & Jackson 2006). In any event, it is not the noxiousness of the model *per se* that determines the cone of protection around the model; both model noxiousness and abundance impinge on the shape of the probability density function that describes the predator's likelihood of sampling prey as prey approach the model in resemblance. It is the shape of that distribution itself, in conjunction with that associated with cryptic coloration, which ultimately decides the shape of the adaptive landscape. Even weakly aversive models may fill in a valley in the adaptive landscape if they are highly abundant. Therefore, both types of landscapes observed in this study should occur in other Batesian mimicry systems.

We thank K. Pfennig, R. Martin, A. Leichthy, J. Weiss and two anonymous reviewers for helpful comments. We also thank Y. Choi, E. Christenson, S. Clarke, R. Searles and G. Zhang for assistance in the lab and field. The North Carolina State Museum of Natural Sciences furnished

preserved specimens used in this study. This work was funded by the US National Science Foundation and a Theodore Roosevelt Memorial Grant. All procedures complied with applicable state and US federal regulations.

## REFERENCES

- Bates, H. W. 1862 Contributions to an insect fauna of the Amazon valley (Lepidoptera: Heliconidae). *Trans. Linn. Soc. Lond.* **23**, 495–556. (doi:10.1111/j.1096-3642.1860.tb00146.x)
- Bates, D. 2005 Fitting linear mixed models in R. *R News* **5**, 27–30.
- Brodie, E. D. 1992 Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* **46**, 1284–1298. (doi:10.2307/2409937)
- Brodie, E. D. 1993 Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47**, 227–235. (doi:10.2307/2410131)
- Brodie, E. D. & Brodie, E. D. 2004 Venomous snake mimicry. In *The venomous reptiles of the Western Hemisphere*, vol. 2 (eds J. A. Campbell & W. W. Lamar), pp. 617–633. Ithaca, NY: Cornell University Press.
- Brodie, E. D. & Janzen, F. J. 1995 Experimental studies of coral snake mimicry: generalized avoidance of ringed snake patterns by free-ranging avian predators. *Funct. Ecol.* **9**, 186–190. (doi:10.2307/2390563)
- Brower, J. V. 1960 Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *Am. Nat.* **94**, 271–282. (doi:10.1086/282128)
- Buasso, C. M., Leynaud, G. C. & Cruz, F. B. 2006 Predation on snakes of Argentina: effects of coloration and ring pattern on coral and false coral snakes. *Stud. Neotrop. Fauna Environ.* **41**, 183–188. (doi:10.1080/01650520600630725)
- Charlesworth, B. 1994 The genetics of adaptation: lessons from mimicry. *Am. Nat.* **144**, 839–847. (doi:10.1086/285710)
- Charlesworth, D. & Charlesworth, B. 1975 Theoretical genetics of Batesian mimicry. I. Single-locus models. *J. Theor. Biol.* **55**, 283–303. (doi:10.1016/S0022-5193(75)80081-6)
- Duncan, C. J. & Sheppard, P. M. 1965 Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour* **24**, 269–282. (doi:10.1163/156853965X00066)
- Fear, K. K. & Price, T. 1998 The adaptive surface in ecology. *Oikos* **82**, 440–448. (doi:10.2307/3546365)
- Fisher, R. A. 1958 *The genetical theory of natural selection: a complete variorum edition*. Oxford, UK: Oxford University Press.
- Gehlbach, F. R. 1972 Coral snake mimicry reconsidered: the strategy of self-mimicry. *Forma et Functio* **5**, 311–320.
- Getty, T. 1985 Discriminability and the sigmoid functional-response: how optimal foragers could stabilize model-mimic complexes. *Am. Nat.* **125**, 239–256. (doi:10.1086/284339)
- Goodale, M. A. & Sneddon, I. 1977 Effect of distastefulness of model on predation of artificial Batesian mimics. *Anim. Behav.* **25**, 660–665. (doi:10.1016/0003-3472(77)90117-8)
- Greene, H. W. & McDiarmid, R. W. 1981 Coral snake mimicry: does it occur? *Science* **213**, 1207–1212. (doi:10.1126/science.213.4513.1207)
- Harper, G. R. & Pfennig, D. W. 2007 Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proc. R. Soc. B* **274**, 1955–1961. (doi:10.1098/rspb.2007.0558)
- Harper, G. R. & Pfennig, D. W. 2008 Selection overrides gene flow to break down maladaptive mimicry. *Nature* **451**, 1103–1106. (doi:10.1038/nature06532)
- Hinman, K. E., Throop, H. L., Adams, K. L., Dake, A. J., McLaughlan, K. K. & McKone, M. J. 1997 Predation by free-ranging birds on partial coral snake mimics: the importance of ring width and color. *Evolution* **51**, 1011–1014. (doi:10.2307/2411177)
- King, R. B. 1992 Lake erie water snakes revisited: morph-specific and age-specific variation in relative crypsis. *Evol. Ecol.* **6**, 115–124. (doi:10.1007/BF02270706)
- Lindström, L., Alatalo, R. V. & Mappes, J. 1997 Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. *Proc. R. Soc. Lond. B* **264**, 149–153. (doi:10.1098/rspb.1997.0022)
- Maddison, W. P. & Maddison, D. R. 2009 Mesquite: a modular system for evolutionary analysis. Version 2.6. <http://mesquiteproject.org>
- Madsen, T. 1987 Are juvenile grass snakes, *Natrix natrix*, aposematically colored? *Oikos* **48**, 265–267. (doi:10.2307/3565512)
- Mappes, J. & Alatalo, R. V. 1997 Batesian mimicry and signal accuracy. *Evolution* **51**, 2050–2053. (doi:10.2307/2411028)
- Nelson, X. J. & Jackson, R. R. 2006 Vision-based innate aversion to ants and ant mimics. *Behav. Ecol.* **17**, 676–681. (doi:10.1093/beheco/ark017)
- Nicholson, A. J. 1927 A new theory of mimicry in insects. *Aust. Zool.* **5**, 10–104.
- Niskanen, M. & Mappes, J. 2005 Significance of the dorsal zigzag pattern of *Vipera latastei gaditana* against avian predators. *J. Anim. Ecol.* **74**, 1091–1101. (doi:10.1111/j.1365-2656.2005.01008.x)
- Oaten, A., Pearce, C. E. M. & Smyth, M. E. B. 1975 Batesian mimicry and signal-detection theory. *Bull. Math. Biol.* **37**, 367–387.
- Palmer, W. M. & Braswell, A. L. 1995 *Reptiles of North Carolina*. Chapel Hill, NC: University of North Carolina Press.
- Pfennig, D. W., Harcombe, W. R. & Pfennig, K. S. 2001 Frequency-dependent Batesian mimicry. *Nature* **410**, 323. (doi:10.1038/35066628)
- Pfennig, D. W., Harper, G. R., Brumo, A. F., Harcombe, W. R. & Pfennig, K. S. 2007 Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common. *Behav. Ecol. Sociobiol.* **61**, 505–511. (doi:10.1007/s00265-006-0278-x)
- Pilecki, C. & Odonald, P. 1971 Effects of predation on artificial mimetic polymorphisms with perfect and imperfect mimics at varying frequencies. *Evolution* **25**, 365–370. (doi:10.2307/2406928)
- Poulton, E. B. 1890 *The colours of animals: their meaning and use, especially considered in the case of insects*. London, UK: Kegan Paul.
- Pyron, R. A. & Burbrink, F. T. 2009 Neogene diversification and taxonomic stability in the snake tribe Lamprodelphini (Serpentes: Colubridae). *Mol. Phylog. Evol.* **52**, 524–529. (doi:10.1016/j.ympev.2009.02.008)
- R Development Core Team 2008 *R: a language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing.
- Reeve, H. K. 1989 The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407–435. (doi:10.1086/284926)
- Roze, J. A. 1996 *Coral snakes of the Americas: biology, identification, and venoms*. Malabar, FL: Krieger Publishing Company.
- Ruxton, G. D., Sherratt, T. N. & Speed, M. P. 2004 *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. New York, NY: Oxford University Press.



- Savage, J. M. & Slowinski, J. B. 1992 The coloration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). *Biol. J. Linn. Soc.* **45**, 235–254. (doi:10.1111/j.1095-8312.1992.tb00642.x)
- Schmidt, R. S. 1958 Behavioural evidence on the evolution of Batesian mimicry. *Anim. Behav.* **6**, 129–138. (doi:10.1016/0003-3472(58)90042-3)
- Schmidt, R. S. 1960 Behaviour and the perfection of incipient mimetic resemblances. *Behaviour* **16**, 149–158. (doi:10.1163/156853960X00089)
- Schuler, W. & Hesse, E. 1985 On the function of warning coloration—a black and yellow pattern inhibits prey-attack by naive domestic chicks. *Behav. Ecol. Sociobiol.* **16**, 249–255. (doi:10.1007/BF00310988)
- Sherratt, T. N. 2002 The evolution of imperfect mimicry. *Behav. Ecol.* **13**, 821–826. (doi:10.1098/rspb.2001.1944)
- Smith, S. M. 1975 Innate recognition of coral snake pattern by a possible avian predator. *Science* **187**, 759–760. (doi:10.1126/science.187.4178.759)
- Smith, S. M. 1977 Coral-snake pattern recognition and stimulus generalization by naive great kiskadees (Aves: Tyrannidae). *Nature* **265**, 535–536. (doi:10.1038/265535a0)
- Turner, J. R. G. 2005 Mimicry. In *Encyclopedia of life sciences*, pp. 1–9. New York, NY: John Wiley and Sons, Ltd.
- Wüster, W. *et al.* 2004 Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. *Proc. R. Soc. Lond. B* **271**, 2495–2499. (doi:10.1098/rspb.2004.2894)