Notes and Comments

Predator Cognition Permits Imperfect Coral Snake Mimicry

David W. Kikuchi[*] and David W. Pfennig

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599

ABSTRACT: Batesian mimicry is often imprecise. An underexplored explanation for imperfect mimicry is that predators might not be able to use all dimensions of prey phenotype to distinguish mimics from models and thus permit imperfect mimicry to persist. We conducted a field experiment to test whether or not predators can distinguish deadly coral snakes (*Micrurus fulvius*) from nonvenomous scarlet kingsnakes (*Lampropeltis elapsoides*). Although the two species closely resemble one another, the order of colored rings that encircle their bodies differs. Despite this imprecise mimicry, we found that *L. elapsoides* that match coral snakes in other respects are not under selection to match the ring order of their model. We suggest that *L. elapsoides* have evolved only those signals necessary to deceive predators. Generally, imperfect mimicry might suffice if it exploits limitations in predator cognitive abilities.

Keywords: adaptation, Batesian mimicry, coral snake, predation, color pattern.

Introduction

Batesian mimicry, in which harmless prey evolve phenotypic resemblances to dangerous species that predators avoid, provides some of nature's most exquisite adaptations (Bates 1862; Forbes 2009). Nonetheless, Batesian mimics often do not appear to match their model precisely (Ruxton et al. 2004). Why are such imperfect mimics not further improved by natural selection?

One possibility is that selection might not favor improved mimicry, for at least two reasons. First, improvement in mimicry might not be favored when the model is common or especially noxious (Schmidt 1958; Duncan and Sheppard 1965; Sherratt 2002). Specifically, with an abundant and highly deadly model, imperfect mimics might persist because predators generalize traits on mimics that resemble those on models (Lindström et al. 1997; Holloway et al. 2002; Caley and Schluter 2003). A second, less well-explored hypothesis is that selection for improved

* Corresponding author; e-mail: dkikuchi@email.unc.edu.

mimicry might not arise if imperfect mimics exploit limitations in predator cognition (Chittka and Osorio 2007). Specifically, if predators pay attention to only certain phenotypic attributes to identify noxious prey, then mimics might not need to achieve a perfect match with their model (Bain et al. 2007; Chittka and Osorio 2007). This hypothesis predicts that predators will attack mimics if they differ from models in some dimensions of their phenotype but not others. By contrast, the first hypothesis predicts that some variation in any dimension might be tolerated if the model is sufficiently deadly or abundant.

We designed a field experiment to determine whether limitations in predator cognitive abilities can explain imperfect coral snake mimicry. Nonvenomous scarlet kingsnakes (*Lampropeltis elapsoides*; family Colubridae) exhibit imprecise mimicry of deadly coral snakes (*Micrurus fulvius*; family Elapidae). Although both species possess brightly colored rings of red, yellow, and black encircling their bodies, their rings differ in order: *M. fulvius* have a black-yellow-red-yellow ring order, whereas *L. elapsoides* have a black-yellow-black-red ring order (hence the rhyme for distinguishing coral snakes from kingsnakes, "red on yellow, kill a fellow; red on black, venom lack").

Given that predators could distinguish mimics from the model by ring order, why have mimetic kingsnakes not converged on the same ring order as their coral snake models? Although adaptive evolution might be limited by a lack of genetic variation in ring order (such variation is not known to occur in ringed kingsnakes), other colubrid snake species in different coral snake mimicry complexes have evolved the same ring order as the local coral snake model (Greene and McDiarmid 1981; Savage and Slowinski 1992). Thus, the genetic and developmental mechanisms needed to produce coral snake color patterns can evolve in nonelapid taxa. However, if there were variation in ring order in *L. elapsoides*, selection still might not favor reorganization of rings to match *M. fulvius* if predators cannot tell the difference. Furthermore, even if predators could distinguish ring order under ideal conditions, they might not have sufficient time or attention to devote to the task in a natural setting (Chittka and Osorio 2007).
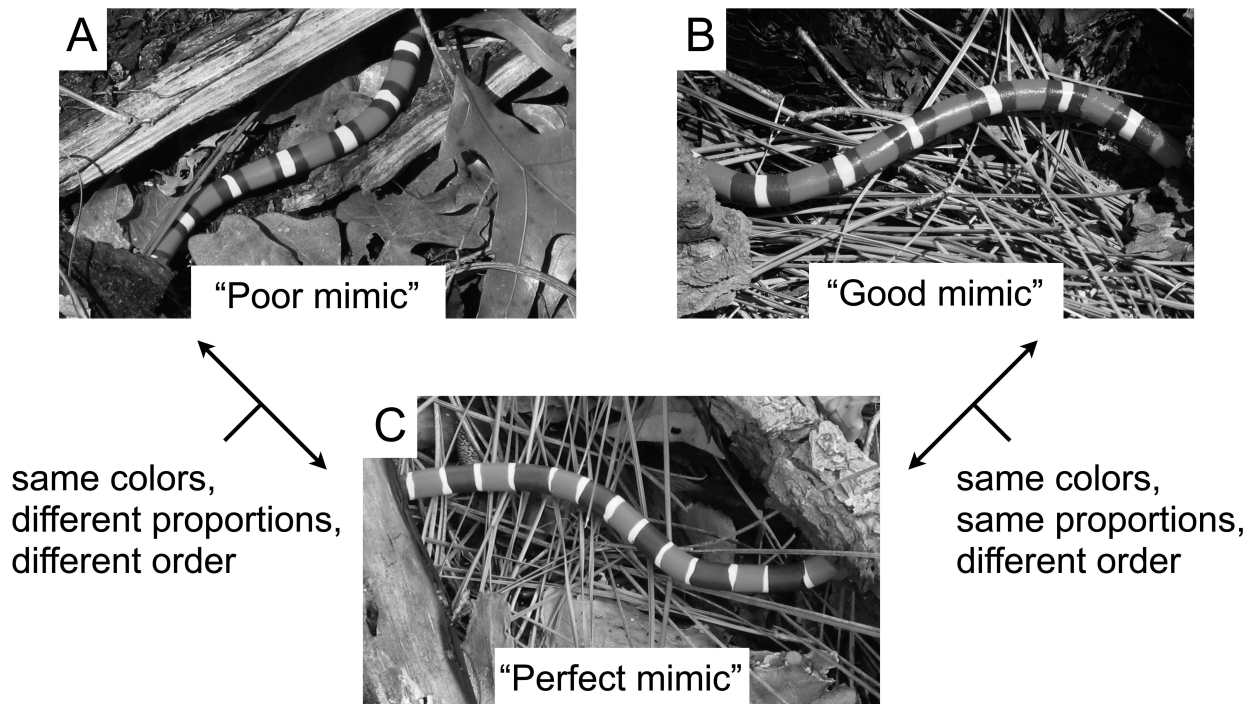
Figure 1: Replicas of snake phenotypes used to measure predation in the field. *A*, Replica of *Lampropeltis elapsoides* from allopatry, representing a "poor mimic" (with more red and less black than the model); *B*, replica of *L. elapsoides* from edge sympatry, representing a "good" mimic (with the same proportions of red and black as the model); and *C*, replica of *Micrurus fulvius*, the model, representing a "perfect" mimic. A color version of this figure is available in the online edition of the *American Naturalist*.

We evaluated predation rates in the wild on replicas of *L. elaposoides* and *M. fulvius* to determine what aspects of phenotype predators might use to identify models and mimics. We found that although selection acts strongly on the proportion of red and black on the dorsum of mimics, it does not appear to operate on ring order. Our results therefore suggest that imperfect mimics exploit predator cognitive abilities and that they mimic only those dimensions of the model's phenotype that are important for avoiding attack.

Methods

The coral snake mimic, *Lampropeltis elapsoides*, has a wider geographical range than its model, *Micrurus fulvius*, such that some populations occur in sympatry with the model, whereas other populations occur in allopatry (Pfennig and Mullen 2010). Selection for mimicry is strongest on the sympatry-allopatry boundary (i.e., edge sympatry), where *M. fulvius* is rare. In such areas, predators discriminate among mimics of varying quality, avoiding only those mimics that match the local *M. fulvius* in proportions of red and black on the dorsum. By contrast, in deep sym-

patry, where *M. fulvius* is abundant, predators avoid even poor mimics (i.e., those with more red and less black on their dorsum than exhibited by the local *M. fulvius*; Harper and Pfennig 2007; Kikuchi and Pfennig 2010). For our study, we therefore chose an area on edge sympatry in southeastern North Carolina where predators should be most likely to distinguish between good mimics and perfect mimics.

To measure selection on different snake phenotypes, we designed polymer clay replicas of snakes (e.g., see Brodie 1993) bearing three different color patterns (fig. 1). Of interest to our question about predator cognition were predation rates on replicas of *M. fulvius* ("perfect mimic") and of *L. elapsoides* from edge sympatry ("good mimic"), which closely match *M. fulvius* in all aspects of phenotype except for ring order. We also included a "poor mimic" based on *L. elapsoides* from allopatry, which differ from *M. fulvius* in both ring order and the relative proportions of red and black on the dorsum. The contrast between predation on the poor mimic and on the good and perfect mimics served as a control, for a previous study demonstrated that the poor mimic is attacked significantly more often than the good mimic in edge sympatry (Harper

Table 1: Where and when transects of replicas were placed in the field

Transect	Latitude (°N)	Longitude (°W)	Start date	End date	Duration (d)
1	34.98538	79.5023	March 13, 2010	April 17, 2010	35
2	34.9925	79.50.727	March 13, 2010	April 17, 2010	35
3	35.01753	79.62209	March 13, 2010	April 17, 2010	35
4	34.52964	80.217	March 14, 2010	April 18, 2010	35
5	34.57256	80.22328	March 14, 2010	April 18, 2010	35
6	34.56645	80.25216	March 14, 2010	April 18, 2010	35
7	34.01567	78.07084	March 20, 2010	April 24, 2010	35
8	34.06461	78.2914	March 20, 2010	April 24, 2010	35
9	34.0985	78.3017	March 20, 2010	April 24, 2010	35
10	34.81287	78.66769	March 20, 2010	April 24, 2010	35
11	35.16744	78.90908	March 28, 2010	May 1, 2010	34
12	35.14969	79.36958	March 28, 2010	May 1, 2010	34
13	35.01344	79.30998	March 28, 2010	May 1, 2010	34
14	35.07172	79.60456	March 28, 2010	May 1, 2010	34
15	34.56422	77.70661	April 2, 2010	May 8, 2010	36
16	34.5643	77.72981	April 2, 2010	May 8, 2010	36
17	34.25962	78.47859	April 3, 2010	May 8, 2010	35
18	34.5797	78.4502	April 3, 2010	May 8, 2010	35

and Pfennig 2007). For details concerning the construction of replicas, see Kikuchi and Pfennig (2010).

In the field, replicas were arranged in triads (consisting of one of each phenotype) and placed in transects of 10 triads (triads were separated from adjacent triads by about 75 m). Eighteen such transects were placed in natural areas where mimics and snake predators are abundant (see table 1; fig. 2). Replicas were collected after 5 weeks. Each replica was scored as having been attacked if it bore a mark consistent with a vigorous attack (e.g., if it had beak, claw, or carnivore bite marks, was bent or torn in a way that would kill a snake, or was carried off completely). Markings consistent with rodent or insect activity were ignored, as these would not constitute threats to real snakes.

We used a linear contrast to test for differences in attack rates on the good versus the perfect mimic. An additional contrast was used to test the prediction that more poor mimics were attacked than both the good mimic and perfect mimic. We tested contrasts using the lmer function of the lme4 package (Bates 2005) in R 2.10.1 (R Development Core Team 2010) to build a generalized linear mixed model using maximum likelihood with binomial errors, where predation served as our response variable, phenotype as a factor, and triad nested within transect as random effects. Random effects were included in the model to account for possible nonindependence of predation on replicas within the same transect (the spatial arrangement of the replicas might have situated entire transects within the home range of a single predator).

Results and Discussion

We tested whether selection favors imprecise mimicry of deadly *Micrurus fulvius* by nonvenomous *Lampropeltis*

elapsoides, both of which have brightly colored rings encircling their bodies, but in different order (fig. 1). Of 537 replicas available for analysis (one triad was discarded as a result of human interference), 66 (12.3%) were attacked. Of these, 10 were attacked by birds and 21 by carnivore mammals, and 35 could not be assigned to a specific predator group. We found that good mimics that differed from the model in ring order but were very similar in other respects were not under selection to resemble their model more closely. Indeed, replicas of those good mimics (based on *L. elapsoides* from edge sympatry with coral snakes) were no more likely to be attacked by naturally occurring predators than were replicas of the model (i.e., perfect mimics; $Z = 0.387$, $P = .7$; fig. 3).

At least two hypotheses might explain why selection does not favor improvement in mimicry. First, predators might generalize aposematic signals of models due to an increasingly high probability of incorrectly identifying prey as mimics grow more similar to models in phenotype (Sherratt 2002). There is widespread support for this hypothesis (e.g., Schmidt 1958; Ford 1971; Dittrich et al. 1993; Mappes and Alatalo 1997; Holloway et al. 2002; Caley and Schluter 2003). With a highly toxic model (such as coral snakes; Roze 1996), risk taking by predators is disfavored. Consequently, predators should avoid a wide range of trait values, thereby maintaining imprecise mimics (reviewed in Edmunds 2000; Sherratt 2002; Gilbert 2005). Evidence for this hypothesis has been found in our system (see "Methods"). Although our results might appear to merely reinforce this already well-established theory, imperfect mimicry in our system is more complex and might depend more on predator cognitive abilities.

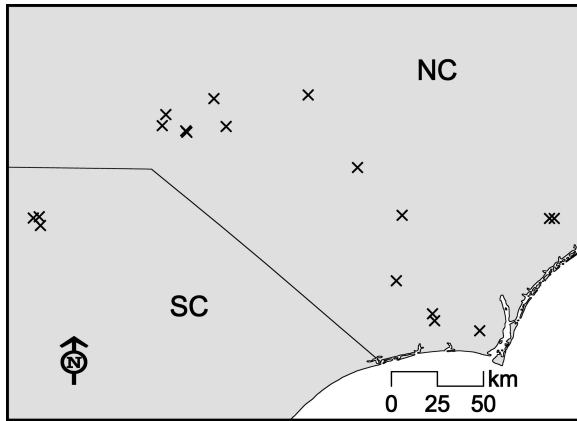Even though the hypotheses of generalized avoidance

Figure 2: Map of field sites where replicas were placed in North Carolina (NC) and South Carolina (SC). Transect locations are represented by x's. Detailed information on field sites is in table 1.

and cognitive limitations in predators are not mutually exclusive, this study provides evidence for the importance of the latter. Our control contrast between the poor mimic and good and perfect mimics revealed strong selection on the proportion of red and black on the dorsum to match that of *M. fulvius* very closely: attack rates on poor mimics were significantly higher than on the other two phenotypes ($Z = 2.523$, $P = .012$). If generalization of a highly toxic model were the only factor promoting imperfect coral snake mimicry, then we would expect to observe loose selection on the proportions of dorsal colors. Instead, low model abundance makes predators willing to take risks by sampling *L. elapsoides* whose dorsal color proportions differ from *M. fulvius*, but those same predators also ignore the information contained in ring order, which could reliably distinguish model from mimic.

The difference in predation rates on good and poor mimics can best be reconciled if mimics exploit a limitation in predator cognition. If only certain traits are required to deceive predators, then mimics need not resemble their model exactly (Carter 1948; Bain et al. 2007; Chittka and Osorio 2007). The fact that good mimics did not suffer any greater predation than perfect mimics (fig. 3) suggests that good mimics achieved complete protection by resembling the model in color proportions alone (or, for deterring attacks by mammalian predators that might lack color vision [Kelber et al. 2003], good mimics achieved complete protection by resembling the model in proportions of different shades of gray). We cannot rule out the possibility that predators might only recognize imperfect mimics that differ from the model in both ring order and color proportion because we did not include a phenotype with coral snake ring order but different pro-

portions of red and black. However, in a tropical system with multiple species of coral snakes with different color patterns, Hinman et al. (1997) reported that predators avoided imperfect mimics with black rings the same width as those of a local coral snake, even if the red rings were increased in size and the yellow rings were combined. This earlier study, combined with our results, suggests that predators are insensitive to ring order.

Generally, predators might have difficulty in distinguishing mimics from models based on ring order alone. Although humans can do so, this task can be difficult to execute rapidly under natural conditions. In encounters with *L. elapsoides* in the wild, we have found that one must hesitate to make certain that a snake is not *M. fulvius*. Such speed-accuracy trade-offs might influence predator foraging decisions (Chittka et al. 2009). Whether a speed-accuracy trade-off or an intrinsic inability to determine ring order is responsible for predator attacks on our replicas, *L. elapsoides* appear to have evolved to exploit limitations in mammalian and avian sensory perceptions (unfortunately, we did not have sufficient power to determine whether mammalian and avian predators differed in discrimination ability). Indeed, deficiencies in predator cognitive abilities might allow imperfect mimicry to persist in many systems.

Why some mimics match their local coral snake model perfectly (Greene and McDiarmid 1981; Savage and Slowinski 1992), whereas others (such as *L. elapsoides*) do

Figure 3: Bar plot depicting the probability of predation for each phenotype with its associated standard error, as estimated from our model. Note that estimates were back-transformed from a logistic scale, and confidence intervals are therefore not symmetrical. Replicas of poor mimics were preyed on significantly more often than replicas of perfect and good mimics, but perfect and good mimics experienced similar attack rates, despite having a different ring order.

not, is unclear. These differences might reflect differing starting points in mimicry evolution or contrasting selective pressures acting on predators or mimics in different mimicry complexes. For example, selection might not favor a change in ring order if mimics use this trait for mate recognition. In sum, although one might expect strong selection on mimics to resemble their model as closely as possible, imperfect mimicry might suffice if it exploits predator cognition.

Acknowledgments

Literature Cited

Bain, R. S., A. Rashed, V. J. Cowper, F. S. Gilbert, and T. N. Sherratt. 2007. The key mimetic features of hoverflies through avian eyes. Proceedings of the Royal Society B: Biological Sciences 274:1949–1954.

Bates, D. 2005. Fitting linear mixed models in R. R News 5:27–30.

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon valley (Lepidoptera: Heliconidae). Transactions of the Linnean Society of London 23:495–556.

Brodie, E. D., III. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution 47:227–235.

Caley, M. J., and D. Schluter. 2003. Predators favour mimicry in a tropical reef fish. Proceedings of the Royal Society B: Biological Sciences 270:667–672.

Carter, G. S. 1948. Colour and colour vision in animals. Nature 162:600–601.

Chittka, L., and D. Osorio. 2007. Cognitive dimensions of predator responses to imperfect mimicry? PLoS Biology 5:2754–2758.

Chittka, L., P. Skorupski, and N. E. Raine. 2009. Speed-accuracy tradeoffs in animal decision making. Trends in Ecology & Evolution 24:400–407.

Dittrich, W., F. Gilbert, P. Green, P. McGregor, and D. Grewcock. 1993. Imperfect mimicry: a pigeon's perspective. Proceedings of the Royal Society B: Biological Sciences 251:195–200.

Duncan, C. J., and P. M. Sheppard. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. Behaviour 24:269–282.

Edmunds, M. 2000. Why are there good and poor mimics? Biological Journal of the Linnean Society 70:459–466.

Forbes, P. 2009. Dazzled and deceived: mimicry and camouflage. Yale University Press, New Haven, CT.

Ford, H. A. 1971. Degree of mimetic protection gained by new partial mimics. Heredity 27:227–236.

Gilbert, F. 2005. The evolution of imperfect mimicry. Pages 231–288 *in* M. D. E. Fellowes, G. J. Holloway, and J. Rolff, eds. Insect evolutionary ecology. CABI, Wallingford.

Greene, H. W., and R. W. McDiarmid. 1981. Coral snake mimicry: does it occur? Science 213:1207–1212.

Harper, G. R., and D. W. Pfennig. 2007. Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? Proceedings of the Royal Society B: Biological Sciences 274:1955–1961.

Hinman, K. E., H. L. Throop, K. L. Adams, A. J. Dake, K. K. McLauchlan, and M. J. McKone. 1997. Predation by free-ranging birds on partial coral snake mimics: the importance of ring width and color. Evolution 51:1011–1014.

Holloway, G., F. Gilbert, and A. Brandt. 2002. The relationship between mimetic imperfection and phenotypic variation in insect colour patterns. Proceedings of the Royal Society B: Biological Sciences 269:411–416.

Kelber, A., M. Vorobyev, and D. Osorio. 2003. Animal colour vision: behavioural tests and physiological concepts. Biological Reviews 78:81–118.

Kikuchi, D. W., and D. W. Pfennig. 2010. High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test. Proceedings of the Royal Society B: Biological Sciences 277:1041–1048.

Lindström, L., R. V. Alatalo, and J. Mappes. 1997. Imperfect Batesian mimicry: the effects of the frequency and the distastefulness of the model. Proceedings of the Royal Society B: Biological Sciences 264:149–153.

Mappes, J., and R. V. Alatalo. 1997. Batesian mimicry and signal accuracy. Evolution 51:2050–2053.

Pfennig, D. W., and S. P. Mullen. 2010. Mimics without models: causes and consequences of allopatry in Batesian mimicry. Proceedings of the Royal Society B: Biological Sciences 277:2577–2585.

R Development Core Team. 2010. R: a language and environment for statistical computing, version 2.10.1. R Foundation for Statistical Computing, Vienna.

Roze, J. A. 1996. Coral snakes of the Americas: biology, identification, and venoms. Krieger, Malabar.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2004. Avoiding attack. Oxford University Press, New York.

Savage, J. M., and J. B. Slowinski. 1992. The coloration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). Biological Journal of the Linnean Society 45:235–254.

Schmidt, R. S. 1958. Behavioural evidence on the evolution of Batesian mimicry. Animal Behaviour 6:129–138.

Sherratt, T. N. 2002. The evolution of imperfect mimicry. Behavioral Ecology 13:821–826.