MECHANISMS OF ADAPTATION IN CORAL SNAKE MIMICRY

David William Kikuchi

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Approved by:

David W. Pfennig

Allen H. Hurlbert

Karin S. Pfennig

Maria R. Servedio

Kyle Summers

ABSTRACT

DAVID WILLIAM KIKUCHI: MECHANISMS OF ADAPTATION IN CORAL

SNAKE MIMICRY

(Under the direction of David Pfennig)

In Batesian mimicry, an undefended prey species (the mimic) evolves to resemble a

defended one (the model) because of the selective advantage of this resemblance in

deterring predation. Although Batesian mimicry is one of the oldest known examples of

natural selection's power to produce adaptation, many unanswered questions remain

about its evolution, including how mimetic signals coevolve with the perceptual abilities

of predators, how mimetic signals are produced, how important shared evolutionary

history with a model species is for mimics, and if mimicry can evolve over rough

adaptive landscapes. My thesis attempts to address these knowledge gaps by examining

the venomous coral snake *Micrurus fulvius* and its nonvenomous mimic, the scarlet

kingsnake *Lampropeltis elapsoides*. In addition to my empirical studies, I have produced

two reviews: one is a general review of mimicry in the form of an annotated

bibliography, and the other a review of the hypotheses for imperfect mimicry.

In a field experiment, I asked whether or not predators were sensitive to

differences between models and mimics in phenotype, that is to say, imperfect mimicry.

My results revealed that imperfect mimicry was tolerated in some dimensions but not others, and that predators' cognitive biases play a role in perpetuating imperfect mimicry.

Two analytical studies of snake pigmentation revealed that coral snakes, their mimics, and several nonmimetic snakes use the same structures and pigments to produce their coloration. The spectral properties of colors produced by those pigments produce similar perceptual experiences for likely agents of selection in coral snake mimicry. This suggests that sharing developmental systems may facilitate the evolution of mimicry.

In another field experiment I tested the assumption that the adaptive landscape between mimicry and crypsis (from which mimicry is thought to evolve) is always rough, featuring an "adaptive valley" of selection against intermediate phenotypes. Under ecological conditions that produce strong selection for precise mimicry, intermediate phenotypes were selected against; however, this was not the case when selection for mimicry was less intense. Therefore, the assumption that the evolution of mimicry always involves a transition through maladaptive intermediate phenotypes may be unwarranted.

ACKNOWLEDGMENTS

Without the contributions of many individuals besides myself, this thesis would never have been finished. I would like to thank my advisor for his objective yet unstintingly enthusiastic involvement with my projects, and my thesis committee for their feedback on the ideas we produced. The many people who have been associated with the Pfennig labs gave me critical advice on everything from statistics to the practicalities of being a graduate student, and indispensable help with experiments. The much larger, less easily defined community of the UNC Biology Department made no less valuable contributions by creating an atmosphere of intellectual curiosity that perpetually fostered new insight. Thanks to my friends for their support, tolerance, and laughter during these five years of reconciling a bunch of abstract notions with the natural world. And most of all, thank you to my family for your unconditional love, without which none of this would mean a thing.

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CHAPTER I

GENERAL INTRODUCTION

We need to know more about how animal signals are produced and perceived, and the evolutionary causes and consequences of these processes. The chapters of this thesis represent several lines of inquiry into the weird phenomenon of Batesian mimicry (Bates 1862; reviewed in Ruxton et al. 2004), which provides a convenient way of addressing these questions. This convenience stems from the nature of a Batesian mimicry complex, which involves the evolution of one signal to match another.

In its most idealized form, Batesian mimicry consists of a dangerous model, a harmless mimic, and a receiver that attempts to discriminate between the two, selecting for evolutionary convergence. Therefore, mimicry is ideal for asking about the evolutionary dynamics of signaling. For example, mimicry can be used to explore the process of adaptation as the mimicry evolves from nonmimetic phenotypes (e.g. Charlesworth and Charlesworth 1975). The complex nature of mimetic signals also makes them more compelling models for adaptation than the simple phenotypes that are often the focus of contemporary research. Furthermore, although the phenotype of the model gives a coarse depiction of the signal that receivers avoid, the model's signal does not always elicit maximum aversion from receivers (Lynn et al. 2005), nor are all parts of

its signal required to trigger avoidance (Valkonen et al. 2011). Therefore, mimicry also furnishes an opportunity to study the cognitive aspects of how signals are processed. Finally, the similarity in signal form between model and mimic also allows one to ask questions about how essential shared proximate mechanisms are for producing convergent phenotypes (Ford 1953, Joron et al. 2011). Thus, Batesian mimicry is indeed fertile ground for studying many interesting questions in evolution, and this thesis has taken advantage of that fortuitous fact. Below I explain the projects that I have undertaken in a coral snake mimicry complex in the southeastern United States.

The introduction proper to this thesis might be considered Chapter II; it is an annotated bibliography that I prepared for Oxford Bibliographies Online (Kikuchi and Pfennig 2012a), and provides brief overviews and definitive references for the definition, history, subfields, and current areas of research in mimicry. Readers curious to learn a bit about particular topics within the field or find appropriate citations may use it as a quick reference; the online version may be updated in the future.

Chapter III describes an experiment that I originally designed to test the hypothesis that imperfect mimics (scarlet kingsnakes *Lampropeltis elaposoides*) of the venomous coral snake *Micrurus fulvius* occupied a local adaptive optimum rather than a globally adaptive optimum of perfect mimicry, being either developmentally or selectively constrained from altering their phenotype (Kikuchi and Pfennig 2010a). Surprisingly, however, I found that natural predators could not distinguish between perfect and imperfect mimics. This result led me to conclude that imperfect mimicry could be facilitated by imperfect predator cognition that failed to discriminate models from mimics.

Chapters IV addresses the evolution of coral snake mimicry from a proximate perspective. I was interested to see whether or not the remarkable convergence in coloration between coral snakes and kingsnakes was based on different solutions to creating the red, yellow, and black coloration that comprises their signals, or if their similar phenotypes were caused by the same underlying mechanisms. Using a combination of electron microscopy, thin-layer chromatography, and absorbance spectroscopy, I concluded that the pigments in both species of snakes were identical and that they were sequestered in their skin tissue in very similar manners (Kikuchi and Pfennig 2012b).

In Chapter V, I widened my sampling of snake skins to include a variety of snakes found in sympatry in the southwestern United States, including the Arizona coral snake *Micruroides euryxanthus* and some of its putative mimics. I found that all phenotypically similar snakes used essentially the same proximate mechanisms to manufacture their phenotypes. I furthermore modeled how avian predators would perceive the coloration of those snakes to show that indeed, using the same proximate mechanisms to produce phenotype yields a similar perceptual response through the eyes of the relevant predators.

Chapter VI examines the coral snake mimicry complex in an ecological context, examining how variation in ecological conditions can change the adaptive landscape over which Batesian mimicry evolves (Kikuchi and Pfennig 2010b). Specifically, I wanted to know if changing the abundance of venomous models altered selection for mimicry by changing the fitness of phenotypes intermediate between crypsis and mimicry, as it has long been thought that intermediate phenotypes have low fitness relative to either pure strategy. I found that when models are abundant, no adaptive valley exists between

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crypsis and mimicry, but one does when they are rare. Therefore, depending on the ecological circumstances under which mimicry evolves, it may or may not require evolution over rough fitness landscapes.

Chapter VII is a review of the various hypotheses for imperfect mimicry and the evidence for them (Kikuchi and Pfennig *in press*). It also highlights areas which need future research to adequately separate different hypotheses from one another. Over the course of writing the review, I found that a hypothesis which invokes a relaxation of selection to explain imperfect mimicry has currently received the most support. However, because very few systems have comprehensively evaluated multiple hypotheses and hypotheses have been unevenly tested across systems, it is premature to make definitive conclusions about why, in general, imperfect mimics exist. Furthermore, some empirically documented cases of imperfect mimicry cannot be adequately explained by current theory.

CHAPTER II

MIMICRY, AN ANNOTATED BIBLIOGRAPHY[1]

Introduction

Among nature's most exquisite adaptations are examples in which natural selection has favored a species (the mimic) to resemble a second, often unrelated species (the model) because it confuses a third species (the receiver). For example, the individual members of a nontoxic species that happen to resemble a toxic species may dupe any predators by behaving as if they are also dangerous and should therefore be avoided. In this way, adaptive resemblances can evolve via natural selection. When this phenomenon—dubbed "mimicry"—was first outlined by Henry Walter Bates in the middle of the 19th century, its intuitive appeal was so great that Charles Darwin immediately seized upon it as one of the finest examples of evolution by means of natural selection. Even today, mimicry is often used as a prime example in textbooks and in the popular press as a superlative example of natural selection's efficacy. Moreover, mimicry remains an active area of research, and studies of mimicry have helped illuminate such diverse topics as how novel, complex traits arise; how new species form; and how animals make complex decisions.

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[1] This chapter is based on Kikuchi, D. W., and D. W. Pfennig. 2012. Mimicry *in* D. Gibson, ed. Oxford bibliographies online: ecology. New York, Oxford University Press.

General Overviews

Since Bates first published his theories of mimicry in 1862 (see Bates (1862), under Historical Background), there have been periodic reviews of our knowledge in the subject area. Cott (1940) was mainly concerned with animal coloration. Subsequent reviews, such as Edmunds (1974) and Ruxton et al. (2004), have focused on types of mimicry associated with defense from predators. Turner (2005) provides a brief, accessible overview.

Cott, Hugh B. 1940. *Adaptive coloration in animals*. London: Methuen.

Cott's book is a frequent reference source among researchers studying mimicry, camouflage, and other types of coloration. This book is best for advanced graduate students and professionals looking for detailed information on historical hypotheses and for those seeking a broad survey of animal coloration.

Edmunds, Malcolm. 1974. *Defence in animals: A survey of anti-predator defenses*. Burnt Mill, UK: Longman. [ISBN: 9780582441323]

Edmunds' book represents a different way of viewing mimicry: as an anti-predator defense strategy, rather than simply one of many uses for animal coloration. This book will serve advanced graduate students and professionals who seek the perspective of an influential scholar in the area.

Ruxton, Graeme D., Thomas N. Sherratt, and Michael P. Speed. 2004. *Avoiding attack: The evolutionary ecology of crypsis, warning signals and mimicry*. New York: Oxford Univ. Press. [ISBN: 9780198528593]

This book is the definitive reference for researchers interested in all types of protective resemblance, and it includes a chapter on aggressive mimicry. It should serve as the starting place for anyone interested in mimicry.

Turner, J. R. G. 2005. Mimicry. In *Encyclopedia of life sciences*. Vol. 12, pp. 1–9. London and New York: John Wiley.

A brief account of mimicry accessible to a general scholarly audience.

Defining Mimicry

Perhaps because different kinds of resemblances are so widespread and the word "mimicry" is so powerful, it has been employed to describe many phenomena in evolutionary biology and ecology. Pasteur (1982) and Vane-Wright (1976) attempted to classify nearly every possible type of resemblance to avoid ambiguity. However, these schemes make concise treatment of mimicry impossible. Further, categorizing a particular mimicry complex is often unnecessary, unless the specific question requires it (e.g., Rainey and Grether 2007). Given this state of affairs, Endler (1981) suggested that the term "mimicry" by itself is not necessarily a useful descriptor. For the purposes of this article, mimicry is considered to occur when one distinct organism resembles another distinct organism (i.e., both produce similar signals) so that a signal receiver may classify them as being the same. Furthermore, both the mimicking organism (the mimic) and the organism being mimicked (the model) can each influence the evolutionary trajectory of the other. Under this definition, organisms are not mimetic if they cryptically blend into the background, as does a flounder on the sea floor, nor are they mimetic if they resemble an object that is distinct but whose evolution cannot be affected by mimicry, like the bird

droppings that many insect larva resemble. This corresponds to a definition provided in

Vane-Wright (1980), as interpreted in Endler (1981), and which Malcolm (1990)

considers perhaps the most generally useful. However, like other complex natural

phenomena that do not easily lend themselves to a single definition, mimicry may be

most usefully defined according to the question of interest.

Endler, John A. 1981. An overview of the relationships between mimicry and crypsis.

Biological Journal of the Linnean Society 16.1: 25–31.

An excellent, lucid summary of the different ways that mimicry has been defined. The

paper includes a helpful graphic for categorizing various definitions of mimicry.

Malcolm, S. B. 1990. Mimicry: Status of a classical evolutionary paradigm. *Trends in

Ecology & Evolution* 5.2: 57–62.

This review broadly endorses the definition of mimicry in Vane-Wright (1980), and it

discusses other interesting aspects of mimicry as well.

Pasteur, G. 1982. A classificatory review of mimicry systems. *Annual Review of Ecology

and Systematics* 13:169–199.

This review attempts to classify every possible type of resemblance between a single

species and anything. Although the classification scheme that the author proposes is of

dubious utility, this paper does have natural history examples for nearly all proposed

types of mimicry.

Rainey, Meredith M., and Gregory F. Grether. 2007. Competitive mimicry: Synthesis of a

neglected class of mimetic relationships. *Ecology* 88.10: 2440–2448.

Rather than focusing on the use of mimicry in avoiding or facilitating predation, Rainey

and Grether instead place an emphasis on mimicry in competition. They include several

categories of mimicry from Vane-Wright's classification in their term "competitive mimicry " (see Vane-Wright 1976.)

Vane-Wright, R. I. 1976. Unified classification of mimetic resemblances. *Biological Journal of the Linnean Society* 8.1: 25–56.

This schematic for classification of mimicry systems takes into account effects of mimic, model, and receiver on each other, and also the species membership of each party. It provides a useful way of describing almost every relationship based on resemblances.

Vane-Wright, R. I. 1980. On the definition of mimicry. *Biological Journal of the Linnean Society* 13.1: 1–6.

Vane-Wright attempted here to determine what categories of resemblance should be included under the general term "mimicry."

Taxonomic Distribution

Classical and aggressive Batesian mimicry have been documented in a wide array of taxa, and both often evolve between fairly distantly related species. By far the most studied systems are Lepidopteran (see citations listed under General Overviews), although deceptive pollination by orchids has also received much attention (summarized in Jersekova et al. 2006), and flies that mimic bees, ants, and wasps are also well explored (e.g., Dittrich et al. 1993). Emerging systems include coral snake/colubrid snake mimicry (reviewed in Brodie and Brodie 2004), ant/jumping spider mimicry (see Nelson and Jackson 2006), and newt/salamander mimicry (Kuchta et al. 2008). More toxic species may serve as models for more distantly related mimics, such as a coral snake that Brown

(2006) discovered is mimicked by a lepidopteran larvae. Many taxa have members exhibiting reproductive mimicry (see Reproductive Batesian Mimicry). Members of Müllerian mimicry complexes tend to be more closely related than Batesian mimics, but Müllerian mimicry can be found within many groups, including *Heliconus* butterflies, coral snakes, millipedes (Marek and Bond 2009), and even birds (Dumbacher and Fleisher 2001).

Brodie, E. D., III, and E. D. Brodie Jr. 2004. Venomous snake mimicry. In *The venomous reptiles of the Western Hemisphere.* Edited by Jonathan A. Campbell and William W. Lamar, 617- 633. Ithaca, NY: Comstock. [ISBN: 9780801441417]

This is an excellent review of protective mimicry in snakes, a group that has been relatively tractable to field studies.

Brown, R. M. 2006. A case of suspected coral snake (*Hemibungarus calligaster*) mimicry by lepidopteran larvae (*Bracca* sp.) from Luzon Island, Philippines. *Raffles Bulletin of Zoology* 54.2: 225–227.

The tremendous taxonomic breadth that a mimicry complex can span may be best exemplified by this example of a caterpillar that mimics a coral snake.

Dittrich, Winand, Francis Gilbert, Patrick Green, Peter McGregor, and David Grewcock. 1993. Imperfect mimicry: A pigeon's perspective. *Proceedings of the Royal Society B: Biological Sciences* 251.1332: 195–200.

The hymenopteran-dipteran mimicry complexes have been important in the development of mimicry theory, and this paper has served as the impetus for several other projects.

Dumbacher, John P., and Robert C. Fleischer. 2001. Phylogenetic evidence for colour

    pattern convergence in toxic pitohuis: Müllerian mimicry in birds? *Proceedings of the*

    Royal Society B: Biological Sciences 268.1480: 1971–1976.

    Very few higher vertebrates engage in mimicry, but this is one putative example of how

    it might evolve.

Jersakova, J., S. D. Johnson, and P. Kindlmann. 2006. Mechanisms and evolution of

    deceptive pollination in orchids. *Biological Reviews of the Cambridge Philosophical*

    Society 81.2: 219–235.

    Deceptive orchids make up one of the largest mimetic taxonomic groups, and this

    review is a very good introduction to the topic.

Kuchta, Shawn R., Alan H. Krakauer, and Barry Sinervo. 2008. Why does the yellow-

    eyed Ensatina have yellow eyes? Batesian mimicry of Pacific newts (genus *Taricha*) by

    the salamander *Ensatina eschscholtzii xanthoptica*. *Evolution* 62.4: 984–990.

    Amphibian mimicry has been noted throughout the years, but rarely investigated. This

    study provides welcome insight into an interesting system.

Marek, Paul E., and Jason E. Bond. 2009. A Müllerian mimicry ring in Appalachian

    millipedes. *Proceedings of the National Academy of Sciences* 106.24: 9755–9760.

    The phylogeographic approach used to infer mimicry in this system is particularly

    elegant, and the study system itself may lend itself to future experimentation, as it does

    not involve vertebrate mimics and takes place in a relatively simple ecosystem

    compared with tropical mimicry complexes.

Nelson, Ximena J., and Robert R. Jackson. 2006. Vision-based innate aversion to ants

    and ant mimics. *Behavioral Ecology* 17.4: 676–681.

Mimicry of ants by salticid spiders is one of the emerging study systems for investigating receiver psychology, facultative mimicry, behavioral mimicry, and multiple functions of mimicry.

Historical Background

Henry Walter Bates (1862) noted the fascinating resemblance between pairs of *Heliconius* butterfly species and other butterflies in many different localities throughout the Amazon basin. Bates made two observations, which suggested how these resemblances might have evolved. First, he noted that lookalikes always occurred together in the same geographical location; that is, they were sympatric. Second, he observed that while *Heliconius* were toxic (and avoided by predators, such as birds), the non-Heliconid butterflies that resembled them were palatable to predators. From these observations, Bates hypothesized that resemblances between a toxic species and a nontoxic species could evolve by means of natural selection when individuals of the palatable species experienced reduced predation because of their resemblance to the toxic species that predators avoid. This form of mimicry is now known as Batesian mimicry. A second major form of mimicry, dubbed Müllerian mimicry, was discovered in 1878 by Fritz Müller. Müller (1879), showed in a mathematical model that two toxic species of butterfly would each have higher fitness if they resembled each other, because predators would have to sample fewer individuals of both species to learn to avoid their common color pattern. Poulton (1890) produced a comprehensive summary of different types of protective coloration in animals. The work also contained many of his thoughts on how mimicry should be defined and how it evolved. Fisher (1958) summarized much of

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Fisher's contemporaries' thought on both Batesian and Müllerian mimicry. Brower (1958) reported on a series of experiments verifying the efficacy of Batesian mimicry. Duncan and Sheppard (1963) applied signal detection theory to mimicry. Signal detection remains one of the reigning paradigms in mimicry theory. Clarke and Sheppard (1960) is a pioneering work on the genetics of mimicry, taken from a series of papers on *Papilio* butterflies. Forbes (2009) provides a thorough account of the history of mimicry.

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

After reading Bates's paper, Darwin wrote Bates, "You have most clearly stated and solved a most wonderful problem. Your paper is too good to be largely appreciated by the mob of naturalists without souls; but rely on it that it will have lasting value." Bates's understanding of pre-Mendelian evolution was clearly advanced, and for this reason alone his monograph is worth the read.

Brower, Jane Van Zandt. 1958. Experimental studies of mimicry in some North American butterflies. Part 1, The monarch, *Danaus plexippus*, and viceroy, *Limenitis archippus archippus*. *Evolution* 12.1: 32–47.

Brower performed numerous experiments on the function of mimicry in North American butterflies. These experiements ranged from quantifying the ratio of models to mimics to determining the palatability of different species. This paper describes the first in a classic series of studies conducted by Brower that were among the first to examine natural mimicry systems.

Clarke, C. A., and P. M. Sheppard. 1960. The evolution of mimicry in the butterfly *Papilio dardanus*. *Heredity* 14:163–173.

The group of papers on the genetics of the *Papilio* has served as one of the principal sources of our understanding of the genetics of Batesian mimicry, as well as how it can be both polymorphic and sex-limited.

Duncan, C. J., and P. M. Sheppard. 1963. Continuous and quantal theories of sensory discrimination. *Proceedings of the Royal Society B: Biological Sciences* 158.972: 343–363.

One of the most successful modeling paradigms that have been applied to mimicry is signal detection theory, which makes predictions about optimal receiver behavior given uncertainty in the identity of prey. This paper is one of its first applications to mimicry.

Fisher, Ronald Aylmer. 1958. *The genetical theory of natural selection: A complete variorum edition*. New York: Dover.

First published in 1930, this famous book has a nonmathematical section in which Fisher discusses a variety of issues in mimicry that have gone on to attract much attention.

Forbes, Peter. 2009. *Dazzled and deceived: Mimicry and camouflage*. New Haven, CT: Yale Univ. Press. [ISBN: 9780300125399]

This well-researched book considers the development of mimicry and camouflage in science, and the impact that such research has made on military camouflage, art, and other related disciplines.

Müller, Fritz. 1879. *Ituna* and *Thyridia*: A remarkable case of mimicry in butterflies. *Proceedings of the Entomological Society of London* 1879: xx–xxiv.

First published in German in 1878, Müller outlined in this paper his theory, using what may have been the first mathematical model in biology.

Poulton, Edward Bagnell. 1890. *The colours of animals: Their meaning and use, especially considered in the case of insects*. London: Kegan Paul.

Poulton's classic book contains ideas that have changed little since its publication, as it touches on little-explored functions of coloration. It also provides an excellent view of early thought on many types of mimicry. However, Poulton does not discuss animal coloration that is not used during predator-prey interactions.

Batesian Mimicry

In Batesian mimicry, the signal of the mimic is dishonest, in that it dupes the signal receiver into misclassifying the mimic. Batesian mimicry of a defended prey species by another, undefended prey species is referred to as classical Batesian mimicry. However, there are also instances of aggressive Batesian mimicry, in which mimics resemble either their prey or a stimulus to which prey are attracted. Because mimicry is used for an exploitative purpose in aggressive Batesian mimicry, brood parasitism, pollinator deception, and simple predatory mimicry are placed in that category (see Aggressive Batesian Mimicry). Intraspecific reproductive mimicry can also be considered Batesian, such as when a male acts like a female in order to avoid aggression from other males or to gain access to females.

Classical Batesian Mimicry

Research Batesian mimicry has had a long history of theoretical predictions supported by empirical experiments. Brower (1960) verified the prediction that Batesian mimicry

could be selected for even when mimics outnumbered models. Oaten et al. (1975) made

one of the more detailed signal detection models of Batesian mimicry. McGuire et al.

(2006) used a human subject to illustrate this phenomenon in an elegant experiment.

Experiments with wild predators in which frequencies of artificial models and mimics

varied (e.g., Lindström et al. 1997) have also confirmed many of the predictions of signal

detection theory as applied to mimicry. Ries and Mullen (2008) shows that mimicry

breaks down in a butterfly system once mimics leave the range of their models, although

Pfennig et al. (2001) found that in a coral snake mimicry system, selection favoring

mimicry decreases in allopatry from models, though mimetic forms nonetheless persist.

Harper and Pfennig (2007) shows that mimicry is most precise where models are rare

(but not absent). One major prediction made by theoretical models, as well as by

experimental studies using artificial prey, is that models should evolve away from mimics

in appearance. However, this prediction has not been satisfied in any natural system.

Brower, J. V. 1960. Experimental studies of mimicry: IV. The reactions of starlings to

different proportions of models and mimics. *American Naturalist* 94.877: 271–282.

The fourth in a series of classic papers, Brower demonstrates that mimics can be

protected even if they are more abundant than models.

Harper, George R., Jr., and David 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* 274.1621: 1955–1961.

This paper verifies one of the predictions of signal detection theory models of mimicry:

when the probable consequence of attacking a model is lower, there is less

disincentinve to prevent predators from attacking mimics. Therefore, the best mimics

should be found where models are rare, relative to where they are common, which is what Harper and Pfennig found in a natural mimicry system.

Lindström, Leena, Rauno V. Alatalo, and Johanna Mappes. 1997. Imperfect Batesian mimicry: The effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society of London B: Biological Sciences* 264.1379: 149–153.

In a laboratory setting in which birds were trained to navigate a "novel world" of unfamiliar stimuli, imperfect mimics benefitted more from more toxic and more numerous models. Novel world experiments have played an important role in mimicry research.

McGuire, Liam, Hans <u>Van Gossum</u>, Kirsten Beirinckx, and Thomas N. Sherratt. 2006. An empirical test of signal detection theory as it applies to Batesian mimicry. *Behavioural Processes* 73.3: 299–307.

This paper details a novel use of computer-simulated prey items that human "predators" were asked to choose from in a game-style scenario. Humans were rewarded for attacking mimics and lost points for attacking models. In a short time, mimetic prey had chased the model through phenotypic space.

Oaten, A., C. E. M. Pearce, and M. E. B. Smyth. 1975. Batesian mimicry and signal-detection theory. *Bulletin of Mathematical Biology* 37.4: 367–387.

This is one of the most comprehensive analytical treatments that has been used to describe the selective pressures expected on Batesian mimics and models. The model is not as accessible as simulation-based models or simpler analytical models, but it is nonetheless very valuable.

Pfennig, David W., William R. Harcombe, and Karin S. Pfennig. 2001. Frequency-

dependent Batesian mimicry. *Nature* 410.6826: 323–323.

To conclusively demonstrate that Batesian mimicry took place in a natural system, the

authors measured predation on mimics over gradients of model abundance, yielding the

predicted result that Batesian mimics experienced higher predation where models were

absent. This is one of the best ways of demonstrating that species are mimetic in the

wild.

Ries, L., and S. P. Mullen. 2008. A rare model limits the distribution of its more common

mimic: A twist on frequency-dependent Batesian mimicry. *Evolution* 62.7: 1798–1803.

This paper shows that sharp hybrid zones between mimetic and nonmimetic groups can

form across sympatry/allopatry boundaries due to frequency-dependent selection.

Aggressive Batesian Mimicry

Historically, aggressive Batesian mimicry (in which the mimic has an active negative

impact on the fitness of the receiver) has been neglected. However, the number of

systems in which aggressive mimicry has been documented—and the sophistication with

which it has been studied—has recently increased. Vereecken and Schiestl (2008) reports

on the used of gas chromatography to test hypotheses about floral mimicry of bees'

pheromones. Haynes et al. (2002) uses a similar method to explore olfactory mimicry by

the bolas spider of moths it hunts. Generally, aggressive mimicry systems have been

more likely to show evolution by the model in response to the mimic than have classical

Batesian mimicry systems (see Classical Batesian Mimicry). Anderson and Johnson

(2006) demonstrates the frequency-dependence of aggressive mimicry in a floral mimicry

system. Takasu et al. (1993) describes a model built to show that brood parasitism (where

one animal dupes another into rearing its offspring) has a strong negative impact on hosts, and that host populations often counter-adapt. Indeed, Stoddard and Stevens (2011) describes the use of objective measures of cuckoo egg mimicry to document coevolution between model and mimic, and Kilner and Langmore (2011) employed a variety of natural history examples to illustrate the possible outcomes of an evolutionary arms race between brood parasites and hosts. Aggressive mimicry often forces prey to compromise on their signal design and receptivity (as Lewis and Cratsley 2008 describes in fireflies), in that system predation pressure by aggressive mimics of receptive females exerts selection on information content of sexual signals. Additionally, Cheney and Cote (2007) shows that signal receivers may have no choice but to run the risk of encountering aggressive mimics when they must interact with models.

Anderson, Bruce, and Steven D. Johnson. 2006. The effects of floral mimics and models on each others' fitness. *Proceedings of the Royal Society B: Biological Sciences* 273.1589: 969–974.

This paper elegantly demonstrates that the presence of high frequencies of unrewarding deceptive flowers can have a negative impact on their pollination rates.

Cheney, Karen L., and Isabelle M. Cote. 2007. Aggressive mimics profit from a model-signal receiver mutualism. *Proceedings of the Royal Society B: Biological Sciences* 274.1622: 2087–2091.

In this paper, Cheney and Cote show that aggressive mimics of cleanerfish have more success attacking potential cleanerfish clients when the clients carry parasites than when they do not. Thus, the success of aggressive mimicry can depend on the condition of the signal receiver, just as in classical Batesian mimicry.

Haynes, K. F., C. Gemeno, K. V. Yeargan, J. G. Millar, and K. M. Johnson. 2002.

Aggressive chemical mimicry of moth pheromones by a bolas spider: How does this

specialist predator attract more than one species of prey? *Chemoecology* 12.2: 99–105.

The bolas spider case illustrates how easily olfactory mimicry can cross a taxonomic

divide, and how such aggressive mimics can switch the species they mimic to

accommodate different prey species. Bolas spiders lure different species of moths by

using different chemical signals, then trap them by swinging strands of adhesive silk at

them.

Kilner, Rebecca M., and Naomi E. Langmore. 2011. Cuckoos *versus* hosts in insects and

birds: Adaptations, counter-adaptations and outcomes. *Biological Reviews* 86.4: 836–

852. [doi: 10.1111/j.1469-185X.2010.00173.x]

This review gives a broad outline of the evolutionary pressures that brood parasites

place on their hosts, and the possible endpoints of their coevolution.

Lewis, Saraa M., and Christopher. K. Cratsley. 2008. Flash signal evolution, mate choice,

and predation in fireflies. *Annual Review of Entomology* 53:293–321.

Although the majority of this review is devoted to firefly biology, there is a useful

section on aggressive mimicry by predatory fireflies.

Stoddard, Mary Caswell, and Martin Stevens. 2011. Avian vision and the evolution of

egg color mimicry in the common cuckoo. *Evolution* 65.7: 2004–2013.

Many of the methods used to quantify color and pattern in this study are cutting-edge,

and studies of other mimicry systems would benefit from their rigor. In addition, this

paper nicely describes how host species that are likely to reject cuckoo eggs select for

better mimicry.

Takasu, Fugo, Kohkichi Kawasaki, Hiroshi Nakamura, Joel E. Cohen, and Nanako

Shigesada. 1993. Modeling the population dynamics of a cuckoo-host association and

the evolution of host defenses. *American Naturalist* 142.5: 819–839.

This model predicts that while models and mimics may coevolve under some

conditions, there may be others that forestall coevolution. Such a problem may afflict

many populations of avian brood parasite hosts.

Vereecken, Nicholas J., and Florian P. Schiestl. 2008. The evolution of imperfect floral

mimicry. *Proceedings of the National Academy of Sciences* 105.21: 7484–7488.

Deceptive orchids that mimic bee pheromones steal pollinator services from plants that

provide rewards to bees for visiting inflorescences, but this study shows that imperfect

floral mimicry actually functions better than perfect mimicry would.

Reproductive Batesian Mimicry

Reproductive Batesian mimicry is an intraspecific phenomenon in which members of one

sex mimic the other, usually as an alternate mating strategy. This topic is reviewed in

Gross (1996), but it is still a subject of ongoing research, especially its implications for

sexual selection. There are numerous empirical studies that document either genetic or

facultative mimicry of females by males, which frees males from male-male competition

and allows access to females. Examples include an obligate polymorphism for dominant

males/female mimics in bluegill sunfish (Dominey 1981), facultative behavioral female

mimicry in rove beetles (Forsyth and Alcock 1990), physiological mimicry of females by

birds in poor condition (Slavsgold and Saetre 1991), and facultative physical mimicry of

female cuttlefish by males (Hanlon et al. 2005). Sometimes, however, natural selection

rather than sexual selection drives intraspecific mimicry; Shine et al. (2001) reports that

male garter snakes emerging from winter hibernacula mimic females in order to attract other males, deceiving those amorous males into helping them warm up. Iserbyt et al. (2011) details how female damselflies that have a genetic polymorphism for andromorphs (females that resemble males) are able to escape unwanted sexual harassment by males. The frequency of andromorphs rises with the operational sex ratio, as predicted by signal detection theory (Sherratt 2001).

Dominey, W. J. 1981. Maintenance of female mimicry as a reproductive strategy in bluegill sunfish (*Lepomis macrochirus*). *Environmental Biology of Fishes* 6.1: 59–64.

The bluegill sunfish exhibits an obligate reproductive polymorphism: some males are destined to become dominant males; others will become female mimics that steal copulations from the dominants. This study system is one of the most elegant examples of such a reproductive mimetic polymorphism.

Forsyth, Adrian, and John Alcock. 1990. Female mimicry and resource defense polygyny by males of a tropical rove beetle, *Leistotrophus versicolor* (Coleoptera, Staphylinidae). *Behavioral Ecology and Sociobiology* 26.5: 325–330.

In contrast to obligate reproductive polymorphism, the rove beetle can change its sex mimicry from moment to moment depending on the context in which it finds itself. This is an excellent example of behavioral mimicry, which can be more plastic than other forms of mimicry.

Gross, Mart. R. 1996. Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology & Evolution* 11.2: 92–98.

Gross provides an accessible review of the different types of reproductive polymorphisms found in animals. Mimicry is not the focus of the review *per se*, but it does feature prominently due to its pervasive role in reproduction.

Hanlon, Roger T., Marié-Jose Naud, Paul W. Shaw, and Jon N. Havenhand. 2005. Behavioural ecology: Transient sexual mimicry leads to fertilization. *Nature* 433.7023: 212–212.

One of the most vivid examples of facultative sexual mimicry can be found in cuttlefish, where it has been shown that sexual mimicry does indeed lead directly to fertilization, which confirms a major benefit to sexual mimicry that had previously only been assumed

Iserbyt, Arne, Jessica Bots, Stefan <u>Van Dongen</u>, Janice J. Ting, Hans <u>Van Gossum</u>, and Thomas N. Sherratt. 2011. Frequency-dependent variation in mimetic fidelity in an intraspecific mimicry system. *Proceedings of the Royal Society B-Biological Sciences* 278: 3116–3122.

Reproductive Batesian mimicry can sometimes follow the same rules that classical Batesian mimicry does. Iserbyt and colleagues found that reproductive mimics (in the case of the damselflies in this study, females mimic males to avoid sexual harassment) are more precise when the ratio of models to mimics is lower.

Sherratt, T. N. 2001. The evolution of female-limited polymorphisms in damselflies: A signal detection model. *Ecology Letters* 4.1: 22–29.

The signal detection model developed in this manuscript by Sherratt illustrates how theory from classical Batesian mimicry can be adapted to explain other forms of mimicry.

Shine, R., B. Phillips, H. Waye, M. LeMaster, and R. T. Mason. 2001. Benefits of female

mimicry in snakes. *Nature* 414.6861: 267–267.

While reproductive mimicry is often thought of as being a strategy to gain access to

mates, and thus subject to sexual selection, this study gives evidence for a role of

natural selection in driving reproductive mimicry: male garter snakes emerging from

hibernacula mimic females in order to attract the attentions of other males, who transfer

valuable body heat to them.

Slagsvold, Tore, and Glenn-Peter Saetre. 1991. Evolution of plumage color in male pied

flycatchers (*Ficedula hypoleuca*): Evidence for female mimicry. *Evolution* 45.4: 910–

917.

Juvenile flycatchers that are low on resources may delay the development of adult

plumage, thus appearing female, which reduces aggression from other males. However,

there may be a cost to this strategy, because they also cannot attract females. Thus, this

study indicates that there may be trade-offs in reproductive mimicry.

Evolution of Batesian Mimicry

Many theorists have debated how Batesian mimicry could arise. Much of this debate

centers on explaining whether Batesian mimicry can evolve through a gradual process of

incremental evolution, as suggested by Fisher in 1930 (see Fisher 1958), and by Fisher's

followers. Specifically, if the starting point for the evolution of such mimicry is crypsis

(as is generally assumed), 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 be disfavored because they should fail to

receive the fitness benefits of either crypsis or mimicry. Thus, the low fitness of intermediate forms would seem to preclude the gradual evolution from an ancestral cryptic phenotype to a derived mimetic form. As a way around this problem, Punnett (1915) and Goldschmidt (1945) contended that a major mutation was necessary for the evolution of Batesian mimicry. Others supported a two-step process of major mutation followed by gradual refinement. This theory is often attributed to Nicholson (1927) (but see Ruxton et al. 2004 in General Overviews). Evidence for such a two-step hypothesis is found in Clarke and Sheppard (1960), a work on *Papilio* butterflies, which had a few mutations of large effect and many mutations of small effect. Charlesworth (1975) concludes that a two-step process is theoretically likely. More recently, Kikuchi and Pfennig (2010b) shows that, under some conditions, even gradual evolution of mimicry from crypsis is possible. A simulation model put forth in Franks et al. (2009) shows that Batesian mimicry drives the evolution of bright warning coloration in defended prey as an honest signal, making it more difficult for new Batesian mimics to evolve. This topic is reviewed by Leimar et al. (2011).

Charlesworth, D., and B. Charlesworth. 1975. Theoretical genetics of Batesian mimicry: I. Single-locus models. *Journal of Theoretical Biology* 55.2: 283–303.

This elegant model supports a two-step hypothesis for the evolution of mimicry, and has been influential in shaping the way we think about the evolution of mimicry.

Clarke, C. A., and P. M. Sheppard. 1960. The evolution of mimicry in the butterfly *Papilio dardanus*. *Heredity* 14:163–173.

The work on *Papilio* by these authors has given us a very good picture of how a few loci of large effect can control much of the variation between mimetic patterns.

Franks, Daniel W., Graeme D. Ruxton, and Thomas N. Sherratt. 2009. Warning signals

    evolve to disengage Batesian mimics. *Evolution* 63.1: 256–267.

    This is one of the most comprehensive simulation models of Batesian mimicry

    produced to date. In the results produced by this model, one can find suggestions about

    how aposematism first evolves, how mutation sizes are distributed as Batesian mimicry

    evolves, and how mimics chase models through phenotypic space.

Goldschmidt, Richard B. 1945. Mimetic polymorphism, a controversial chapter of

    Darwinism *The Quarterly Review of Biology* 20.2: 147–164.

    Goldschmidt argues that mimicry must evolve by a single macromutation that arises

    from a shared developmental system between model and mimic, rather than multiple

    mutations. This idea was much lampooned at the time, although current evidence

    suggests such mutations may have arisen between *Heliconius* species (which are

    Müllerian mimics).

Kikuchi, David W., and David 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* 277.1684: 1041–1048.

    While a two-step hypothesis may be the most likely explanation for how Batesian

    mimicry evolves, this paper shows that variation in model abundance can modify the

    shape of the adaptive landscape to permit the gradual evolution of mimicry.

Leimar, Olof, Birgitta S. Tullberg, and James Mallet. 2012. Mimicry, saltational

    evolution and the crossing of fitness valleys. In *The adaptive landscape in evolutionary

    biology.* Edited by Erik Svensson and Ryan Calsbeek. Oxford: Oxford Univ. Press.

    [ISBN: 9780199595372]

This book chapter provides a capable review of the topic, with a good overview of history, contemporary theory, and empirical studies.

Nicholson, A. J. 1927. A new theory of mimicry in insects. *Australian Zoologist* 5:10–104.

A long and rambling monograph, this paper nonetheless contains the nucleus of the two-step hypothesis. Most of the substance can be found in contemporary reviews. However, for scholars who need primary sources, this paper is an indispensible citation.

Punnett, Reginald Crundall. 1915. *Mimicry in butterflies*. Cambridge, UK: Cambridge Univ. Press.

Work by Punnett on the genetics of butterflies led his followers (such as Goldschmidt) to hypothesize that mimicry could only arise as a "sport" of macromutation.

Müllerian Mimicry

In Müllerian mimicry, two defended organisms resemble one another so that predators do not have to learn multiple warning signals. Many of the past and current debates about Müllerian mimicry and its relationship to Batesian mimicry are described in Sherratt (2008), including the Batesian-Müllerian spectrum, which recognizes that if two noxious species differ in their level of defense, one may in fact function like a Batesian mimic of the other. Kapan (2001) provides an elegant field experiment demonstrating the function of Müllerian mimicry. Sanders et al. (2006) exemplifies the use of phylogenetics to identify Müllerian mimicry, which separates convergent evolution driven by selection for mimicry from homoplasy. Franks and Noble (2004) shows that Müllerian mimicry rings can be influenced by Batesian mimics, but empirical evidence for this has been difficult

to procure. Rowland et al. (2010a) and Rowland et al. (2010b) show that Müller's original model, in which predators attack a fixed number of prey before learning to avoid a phenotype, is not realistic. In complex, real-world communities, Müllerian mimicry rings often involve many species, and the strong selective forces exerted by predators for mutualistic interactions between them can sometimes even overcome the effects of competition, as shown in Elias et al. (2008) and Alexandrou et al. (2011).

Alexandrou, Markos A., Claudio Oliveira, Marjorie Maillard et al. 2011. Competition and phylogeny determine community structure in Müllerian co-mimics. *Nature* 469.7328: 84-88.

Local assemblages of toxic-barbed catfish have converged in coloration, supporting Müllerian mimicry. However, the species also show phylogenetic niche conservatism in foraging ecology, which appears to be more important than mimicry in determining community structure. The importance of mimicry in community-level interactions is only beginning to become appreciated.

Elias, Marianane, Zachariah Gompert, Chris Jiggins, and Keith Willmott. 2008. Mutualistic interactions drive ecological niche convergence in a diverse butterfly community[http://www.plosbiology.org/article/info:doi/10.1371/journal.pbio.0060300]. *PLoS Biology* 6.12: e300. [doi:10.1371/journal.pbio.0060300]

In *Heliconius* butterflies, selection for mimics to use the same ecological niche as other members of their mimicry rings has driven convergence, even though it may result in greater competition. This is one of the most powerful examples of mimicry in determining evolutionary processes on the community scale.

Franks, Daniel W., and Jason Noble. 2004. Batesian mimics influence mimicry ring

evolution. *Proceedings of the Royal Society B-Biological Sciences* 271.1535: 191–196.

This simulation model includes Batesian and Müllerian mimics. It shows how selection

on an initially divergent array of phenotypes may coalesce into the sorts of mimicry

rings commonly observed in nature.

Kapan, Durrell D. 2001. Three-butterfly system provides a field test of Müllerian

mimicry. *Nature* 409.6818: 338–340.

This classic study employs capture-and-resight methods to demonstrate higher

survivorship in mimetic butterflies that are released at higher densities than lower ones,

illustrating the effect of selection against rare morphs predicted by Müllerian mimicry

theory.

Rowland, Hannah M., Tom Hoogesteger, Graeme D. Ruxton, Michael P. Speed, and

Johanna Mappes. 2010a. A tale of 2 signals: Signal mimicry between aposematic

species enhances predator avoidance learning. *Behavioral Ecology* 21.4: 851–860.

An explicit laboratory test of Müller's prediction that when two unpalatable prey share

a common phenotype, they will each experience the loss of n/2 individuals as predators

learn to avoid them, as opposed to each species losing n individuals if they had different

phenotypes. Results show that predator behavior varies with age.

Rowland, Hannah M., Johanna Mappes, Greame D. Ruxton, and Michael P. Speed.

2010b. Mimicry between unequally defended prey can be parasitic: Evidence for quasi-

Batesian mimicry. *Ecology Letters* 13.12: 1494–1502.

Mildly defended artificial prey depress the fitness of well-defended prey when the

former are present at high frequencies. This supports the existence of the Batesian-

Müllerian mimicry spectrum, which supposes that unless defended prey are equally defended, sometimes one partner may get more out of mimicry than the other. A large bulk of literature on this subject is reviewed in Sherratt 2008.

Sanders, K. L., A. Malhotra, and R. S. Thorpe. 2006. Evidence for a Müllerian mimetic radiation in Asian pitvipers. *Proceedings of the Royal Society B: Biological Sciences* 273.1590: 1135–1141.

Two important conclusions can be drawn from this study: mimicry need not necessarily involve highly conspicuous color patterns, and phylogenetic evidence can be a valuable way of inferring mimetic relationships where direct tests of selection are difficult to obtain. Other studies have since used similar methods to demonstrate mimetic relationships.

Sherratt, Thomas N. 2008. The evolution of Müllerian mimicry. *Naturwissenschaften* 95.8: 681–695.

This is a review of Müllerian mimicry from a theoretical and empirical perspective that emphasizes current topics of interest in the field. This paper is highly recommended for all who are interested in Müllerian mimicry and the Batesian-Müllerian spectrum.

Functions of Mimetic Signals

Mimetic signals can sometimes serve more than one function. For example, a particular instance of mimicry might simultaneously constitute Batesian and aggressive mimicry if an organism's phenotype both protects the organism from predators and disguises it from prey. Cheney (2010) describes a possible example in bicolored fangblenny, a species of fish that resembles another toxic (but nonaggressive) fish. This resemblance enables the

bicolored fangblenny to simultaneously avoid predators (which mistake the bicolored fangblenny for another, toxic species) and gain access to prey (which mistake the bicolored fangblenny for a nonaggressive species that poses no predation risk). Mimetic signals might also have additional functions that are not related to mimicry. For example, Goodman and Goodman (1976) hypothesizes that the bright rings of Batesian coral snake mimics also have an aggressive function in attracting the attention of nesting birds. In addition to deterring predation, mimetic signals may also play an important role in sexual selection (see Jiggins et al. 2001).

Cheney, K. L. 2010. Multiple selective pressures apply to a coral reef fish mimic: A case of Batesian-aggressive mimicry. *Proceedings of the Royal Society B: Biological Sciences* 277.1689: 1849–1855.

The bicolored fangblenny mimics the forktail blenny, and as a result both receive protection from predators and enjoy increased access to prey. This study raises the question of how exclusive the mimetic functions of a particular phenotype are.

Goodman, John D., and Jeanne M. Goodman. 1976. Contrasting color and pattern as enticement display in snakes. *Herpetologica* 32.2: 145–148.

This paper presents an interesting alternative function for the bright red, yellow/white, and black rings on many snakes that are presumed to be coral snake mimics. Like many proposed alternative functions of mimicry, this hypothesis has gone untested.

Multimodal Mimicry

Mimics can utilize alternative sensory modalities. For example, papers by Stevens and colleagues on brood parasites have explored how vision in the ultraviolet can select for

mimicry in that region of the spectrum, and several other aggressive mimicry systems also utilize alternative sensory modalities, such as olfaction (see Aggressive Batesian Mimicry). Nonvisual sensory modalities are particularly interesting, because they open the door for great disparity between the taxonomic affinities and body plans of model-mimic pairs. For example, Rowe et al. (1986) reports on Batesian mimicry of rattlesnakes by burrowing owls. Nevertheless, acoustic mimicry can take place between closely related taxa (Barber and Conner 2007).

Barber, Jesse R., and William E. Conner. 2007. Acoustic mimicry in a predator-prey interaction. *Proceedings of the National Academy of Sciences* 104.22: 9331–9334.

A system involving palatable and unpalatable tiger moths shows that acoustic Batesian and Müllerian mimicry exist. This manuscript is a useful departure point for acoustic mimicry studies, being one of its first rigorous tests.

Rowe, Matthew P., Richard G. Coss, and Donald H. Owings. 1986. Rattlesnake rattles and burrowing owl hisses: A case of acoustic Batesian mimicry. *Ethology* 72.1: 53–71.

Rodents and burrowing owls may compete for burrows, so by mimicking rattlesnake hisses, burrowing owls may both deter predators and rodents that might wish to occupy their burrows (see also Rainey and Grether 2007, cited under *Defining Mimicry*).

Imperfect mimicry

Intuitively, mimics that most closely resemble their models should have the highest fitness. However, numerous cases of imperfect mimicry abound (reviewed in Gilbert 2005). Edmunds (2000) reviews hypotheses for imperfect mimicry and builds a model showing how a mimic ranging over two types of habitat might benefit from an

intermediate phenotype. Sherratt (2002) reports on the construction an influential alternative model showing how selection for better mimicry diminishes as mimics match their model more closely. Using artificial replicas of varying levels of mimicry, Caley and Schluter (2003) found empirical data that supports Sherratt's model in a marine system (Sherratt 2002), while Harper and Pfennig 2007 (see Classical Batesian Mimicry) shows how variation in the risk of attacking a model affects the precision of mimicry. Johnstone (2002) models a scenario in which kin selection might prevent increased perfection of mimicry. Servedio and Lande (2003) and Holen and Johnstone (2004) model systems where mimicry is costly, resulting in equilibrium that supports imperfect mimicry. Furthermore, limitations in the abilities of receivers to perceive imperfections in mimicry may also permit imprecise mimics to persist (see Influence of Receiver Perception).

Caley, M. Julian, and Dolph Schluter. 2003. Predators favour mimicry in a tropical reef fish. *Proceedings of the Royal Society B: Biological Sciences* 270.1516: 667–672.

This is an elegant demonstration of the decreasing benefits of better mimicry as the mimic approaches the model in phenotype. The study examines a real mimicry system, which is an added benefit considering the profusion of artificial systems often used to study mimicry.

Edmunds, Malcolm. 2000. Why are there good and poor mimics? *Biological Journal of the Linnean Society* 70.3: 459–466.

In addition to reviewing the topic, Edmunds develops a model that shows how, under a certain suite of circumstances, a wide-ranging mimic may have to compromise its

appearance to mimic multiple models over different habitats. This intriguing model has not been adequately tested.

Gilbert, Francis. 2005. The evolution of imperfect mimicry. In *Insect evolutionary ecology.* Proceedings of the Royal Entomological Society 22nd Symposium, University of Reading, 2003. Edited by M. D. E. Fellowes, G. J. Holloway, and J. Rolff, 231–288. Wallingford, UK: CABI. [ISBN: 9780851998121] [class:conference-paper]

This review summarizes work on imperfect mimicry. Although the paper focuses on Hymenoptera, it contains a good overview of theory, along with helpful diagrams explaining signal detection theory.

Holen, Øistein Haughton, and Rufus A. Johnstone. 2004. The evolution of mimicry under constraints. *American Naturalist* 164.5: 598–613.

This general model assumes that mimics pay a cost that increases nonlinearly as their mimicry improves. When receivers discriminate finely between models and mimics, imperfect mimicry can be selectively favored, because it is not worth paying much cost for very good mimicry. The predictions made by this model deserve empirical attention.

Johnstone, Rufus A. 2002. The evolution of inaccurate mimics. *Nature* 418.6897: 524–526.

Perhaps one of the most creative explanations for the perpetuation of imperfect mimicry is presented in this paper; namely, that the evolution of better mimics may be disfavored by kin selection.

Servedio, Maria R., and Russell Lande. 2003. Coevolution of an avian host and its parasitic cuckoo. *Evolution* 57.5: 1164–1175.

The authors hypothesize that imperfect mimicry may be maintained by a physiological cost to resembling the model. To explain imperfections in the mimicry of brood parasites, they assume a cost to mimicry of hosts by cuckoos due to differences in optimal egg size, and show that it can produce stable imperfect mimicry.

Sherratt, Thomas N. 2002. The evolution of imperfect mimicry. *Behavioral Ecology* 13.6: 821–826.

Although this model includes a scenario in which multiple models favor imperfect mimicry, it is most known for formally demonstrating the decreasing selection for better mimicry as mimics approach models in phenotype.

Genetics of Mimicry

Until relatively recently, much of the research on the genetics of mimicry came from work on *Papilio* butterflies by Clarke, Sheppard, and Nijhout (see Clarke and Sheppard 1960; Nijhout 2003). Nijhout (1991) reviews the development of butterfly wing patterns. More recently, research on *Heliconius* has uncovered a supergene locus that appears to be involved in controlling much of the variation between color morphs of some species that mimic each other closely (Joron et al. 2006). In one instance, a mutation at a single locus appears to have caused *H. cydno* to switch mimicry rings and diverge from *H. melpomene*, as sexual selection on color pattern causes prezygotic isolation while selection for mimicry causes postzygotic isolation (Jiggins et al. 2001). A number of candidate genes have been identified at the locus of two *Heliconius* supergenes that control a number of pattern elements across the genus (Baxter et al. 2010). Recently, the *optix* gene has been shown to control much of the diversity of red color pattern elements

in *Heliconius* (Reed et al. 2011). There are also many independently segregating modifier genes that appear to affect coloration in the entire *Heliconius* genus (Baxter et al. 2009). Plants that are Müllerian mimics of each other also feature independently assorting mimicry genes: in the monkeyflower genus *Mimulus*, it appears that at least three loci of major effect are responsible for making two species attractive to hummingbird pollinators (Bleiweiss 2001).

Baxter, S. W., S. E. Johnston, and C. D. Jiggins. 2009. Butterfly speciation and the distribution of gene effect sizes fixed during adaptation. *Heredity* 102.1: 57–65.

This review contains a discussion of the evolution of mimicry (see Evolution of Batesian Mimicry), but focuses more on Müllerian systems. It also summarizes preliminary quantitative trait loci analysis of *Heliconius* wing patterns, and finds broad support for the two-step hypothesis in the evolution of Müllerian mimicry based on the distribution of gene effect sizes.

Bleiweiss, Robert. 2001. Mimicry on the QT(L): Genetics of speciation in *Mimulus*. *Evolution* 55.8: 1706–1709.

This is a very brief paper using quantitative trait loci analysis to describe the effect sizes of genes contributing to color pattern differences between species of *Mimulus* monkeyflowers, some of which are Müllerian mimics that share pollinators. A few loci of large effect do contribute to most of the differences in pattern.

Counterman, Brian A., Felix Araujo-Perez, Heather M Hines et al. et al. 2010. *Genomic hotspots for adaptation: The population genetics of Müllerian mimicry in the *Heliconius melpomene*

clade[http://www.plosgenetics.org/article/info:doi/10.1371/journal.pgen.1000796]*.

PLoS Genetics 6.2: e1000796. [doi:10.1371/journal.pgen.1000796]

The authors describe the genetics of color pattern in *Heliconius* using an evolutionary genetics approach to examine selection on loci of interest.

Jiggins, C. D., R. E. Naisbit, R. L. Coe, and J. Mallet. 2001. Reproductive isolation caused by colour pattern mimicry. *Nature* 411.6835: 302–305.

One of the most interesting stories to come out of the *Heliconius* system is this one of a single mutation that caused a population of a species involved in Müllerian mimicry to switch rings and mate assortatively.

Joron, Mathieu, Riccardo Papa, Margarita. Beltrán et al. 2006. A conserved supergene locus controls colour pattern diversity in *Heliconius* butterflies[http://www.plosbiology.org/article/info%3Adoi%2F10.1371%2Fjournal.pbio.0040303]. *PLoS Biology* 4.10: e303. [doi:10.1371/journal.pbio.0040303]

This paper nicely summarizes the genetic architecture of a locus of major effect in the *Heliconius* genome, with visual aids of the genomic region in question.

Nijhout, H. Frederik. 1991. *The development and evolution of butterfly wing patterns*. Washington, DC: Smithsonian Institution Press. [ISBN: 9780874749212]

This authoritative monograph will be of interest to researchers pursuing butterfly-specific studies. It contains a wealth of information on the development of wing patterns, essential for investigation in the development of mimicry.

Reed, Robert D., Riccardo Papa, Arnaud Martin et al. 2011. *optix* drives the repeated convergent evolution of butterfly wing pattern mimicry. *Science* 333:1137–1141.

In a culmination of many studies of *Heliconius* genetics, the authors examine transcripts expressed in color pattern development to isolate the *optix* gene from a region of interest. Further experiments implicate it in controlling divergence between color morphs.

Polymorphic and Sex-Limited Mimicry

One of the most enduring topics of fascination to evolutionary biologists has been the existence of polymorphic mimetic species that resemble multiple models. Often, this polymorphic mimicry is limited to only a single sex. This phenomenon is reviewed in Joron and Mallet (1998), Mallet and Joron (1999), and Kunte (2009). Both the genetic systems controlling such polymorphism (see Nijhout 2003) as well as the ecological factors behind polymorphic mimicry have received consideration (Joron 2005, Darst and Cummings 2006). Mimetic polymorphism can also arise through phenotypic plasticity. In addition to examples from reproductive mimicry (see Reproductive Batesian Mimicry), some octopuses exhibit polymorphic mimicry while foraging by facultatively mimicking many different model species (including different species of toxic fish and deadly sea snakes). Which species are imitated depends on which are most prevalent in the octopus's current environment (Norman et al. 2001).

Darst, Catherine R., and Molly. E. Cummings. 2006. Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature* 440.7081: 208–211.

This is a rare example of polymorphic Batesian mimicry outside the Lepidoptera. It also presents the interesting result that when multiple models are present, a mimic resembles just one model rather than being an imperfect "compromise" mimic of several models.

Joron, Mathieu. 2005. Polymorphic mimicry, microhabitat use, and sex-specific

behaviour. *Journal of Evolutionary Biology* 18.3: 547–556.

In a refreshing departure from typical explanations for polymorphic and sex-limited

mimicry, Joron builds a slight modification to Müller's model that describes a degree of

microhabitat segregation between sexes, which leads to increased benefits from

Müllerian mimicry that might drive the tight maintenance of spatial polymorphisms.

Joron, Mathieu, and James L. B. Mallet. 1998. Diversity in mimicry: Paradox or

paradigm? *Trends in Ecology & Evolution* 13.11: 461–466.

This review is brief and focuses primarily on the issue of polymorphism in classical

Batesian and Müllerian mimicry and warning coloration. This paper was the subject of

a reply and response that should also be read.

Kunte, Krushnamegh. 2009. Female-limited mimetic polymorphism: A review of theories

and a critique of sexual selection as balancing selection. *Animal Behaviour* 78.5: 1029–

1036.

In this review, sexual selection hypotheses for the maintenance of female-only mimicry

in butterflies are criticized as suffering from a lack of support, and frequency-dependent

selection is touted as the probable agent maintaining polymorphism.

Mallet, James, and Mathieu. Joron. 1999. Evolution of diversity in warning color and

mimicry: Polymorphisms, shifting balance, and speciation. *Annual Review of Ecology

and Systematics* 30:201–233.

A longer, more detailed view of mimicry than in the TREE review by these authors

(Joron and Mallet 1998). This paper focuses on the causes and consequences of

diversity in mimetic systems.

Nijhout, H. Frederik. 2003. Polymorphic mimicry in *Papilio dardanus*: Mosaic dominance, big effects, and origins. *Evolution & Development* 5.6: 579–592.

This study presents an analysis of the covariance between different wing pattern elements and the effects of major genes on their patterns. Nijhout suggests that either a supergene or a modifier locus may be responsible for the polymorphism of *Papilio dardanus*.

Norman, Mark D., Julian Finn, and Tom Tregenza. 2001. Dynamic mimicry in an Indo-Malayan octopus. *Proceedings of the Royal Society of London B: Biological Sciences* 268.1478: 1755–1758.

One of the most stunning examples of mimicry concerns this octopus, which not only mimics many dangerous species very well, but can facultatively switch to resembling another model by dynamically changing the color patterns of its skin.

Role in Speciation

There are many connections between the study of speciation and mimicry, especially because the strong selective forces that act on mimetic characters make mimicry ideal for studying ecological speciation (Jiggins 2008, Chamberlain et al. 2009). Mimicry can bring about speciation in several ways. One way that has attracted a tremendous amount of attention is hybridization between mimetic taxa that leads to the formation of a novel warning color. The population with the new signal then differentiates from its parent species because predators exert stabilizing selection on the new pattern (Mallet 2007). Mazarev et al. (2006) and Salazar et al. (2010) provide evidence supporting a hybrid origin of *Heliconius heurippa* from *H. melpomene* and *H. cydno* (but see Brower 2011).

Single-locus mutations can also cause reproductive isolation between populations of butterflies (see Jiggins et al. 2001). In sexually deceptive orchids (*Orphrys*), speciation may occur when a population diverges in the odor bouquet that it offers to its specialist pollinators, although the genetics behind these switches are not yet understood (Stokl et al. 2009). Hybrid speciation in butterflies and the evolution of novel floral odor bouquets in orchids have the potential to occur in sympatry with model species. However, speciation may take place across geographic lines where mimicry ceases to function. The ranges of many mimics that extend into allopatry from their models may provide opportunities for speciation to take place because sympatric and allopatric populations experience different selective regimens (Pfennig and Mullen 2010).

Brower, Andrew V. Z. 2011. Hybrid speciation in *Heliconius* butterflies? A review and critique of the evidence. *Genetica* 139.5: 589–609.

Brower plays devil's advocate to evidence suggesting that *Heliconius heurippa* arose via a hybridization event between *H. cydno* and *H. melpomene*.

Chamberlain, Nicola L., Ryan I. Hill, Durrell D. Kapan, Lawrence E. Gilbert, and Marcus R. Kronforst. 2009. Polymorphic butterfly reveals the missing link in ecological speciation. *Science* 326.5954: 847–850.

Heliconius cydno alithea is a white/yellow polymorphic butterfly whose two morphs participate in different mimicry rings and mate assortatively. However, the two morphs show no background genetic differentiation or postzygotic isolation. Therefore, it may be an intermediate step in the speciation process.

Jiggins, Chris D. 2008. Ecological speciation in mimetic butterflies. *Bioscience* 58.6: 541–548.

This review of reproductive isolating barriers in *Heliconius* places a stronger emphasis on the importance of simple allopatry in maintaining isolation than one might imagine if reading only reports of selection on mimetic coloration. However, assortative mating, selection for mimicry, and postzygotic isolation all play important roles, too.

Mallet, James, Margarita Beltran, Walter Neukirchen, and Mauricio Linares. 2007. Natural hybridization in heliconiine butterflies: The species boundary as a continuum[http://www.biomedcentral.com/1471-2148/7/28]*. *BMC Evolutionary Biology* 7.1.

The extent of hybridization in the species complex of these butterflies ranges from frequent to rare, and is correlated with genetic distance. This paper provides a framework with which to think about useful species concepts when dealing with taxa that are undergoing rapid ecological speciation, in part driven by mimicry.

Mavarez, Jesús, Camilo A. Salazar, Eldredge Bermingham, Christian Salcedo, Chris D. Jiggins, and Mauricio Linares. 2006. Speciation by hybridization in *Heliconius* butterflies. *Nature* 441.7095: 868–871.

This study postulated a hybrid origin for *Heliconius heurippa*, leading to a flurry of interest in hybrid speciation in *Heliconius*.

Pfennig, David W., and Sean P. Mullen. 2010. Mimics without models: Causes and consequences of allopatry in Batesian mimicry complexes. *Proceedings of the Royal Society B: Biological Sciences* 277:2577–2585.

This review focuses on the geographic distributions of models and their Batesian mimics, which (contrary to the predictions of mimicry theory) are often discordant. The widespread existence of allopatric populations of Batesian mimics may set the stage for

speciation, in which these allopatric populations become reproductively isolated from sympatric populations.

Salazar, Camilo, Simon W. Baxter, Carolina Pardo-Diaz et al. 2010. Genetic evidence for hybrid trait speciation in *Heliconius* butterflies[http://www.plosgenetics.org/article/info%3Adoi%2F10.1371%2Fjournal.pgen.1000930]. *PLoS Genetics* 6.4: e1000930. [doi:10.1371/journal.pgen.1000930] The introgression of a genomic region that controls pattern formation into *Heliconius cydno* from *H. melpomene* may have formed *H. heurippa*. The locus in question would control ecological selection and assortative mating, thus representing the transfer of a "magic trait" between populations that would catalyze speciation.

Stökl, Johannes, Philipp M. Schlüter, Tod F. Stuessy et al. 2009. Speciation in sexually deceptive orchids: Pollinator-driven selection maintains discrete odour phenotypes in hybridizing species. *Biological Journal of the Linnean Society* 98.2: 439–451. Although much work remains to be done on this study system, the authors present evidence that divergence to lure different pollinators has maintained some degree of reproductive isolation between species of sexually deceptive orchids.

Influence of Receiver Perception

Researchers have long realized that the perception of signal receivers must play an important role in shaping the evolution of mimetic signals. However, explicit hypotheses of receiver psychology, and the influence of receiver cognition on the evolution of mimicry, have been wanting, primarily because it is difficult to know how nonhuman observers perceive stimuli. In Cheney and Marshall (2009), a model of animal color

vision is used to see how closely mimetic fishes' colors match through the eyes of predators. This is a significant advance, but perhaps even more importantly, Darst (2006) and Chittka and Osorio (2007) provide hypotheses about how the cognitive processes of signal receivers might lead to deviations from the expectations of simple models of mimicry that assume particular forms of predator behavior, such as strict obedience to signal detection theory. Building on the hypotheses of Chittka and Osorio (2007), Balogh et al. (2010) simulated the evolution of Müllerian mimicry in a system with predators that classify prey according to particular aspects of phenotype. Bain et al. (2007) uses a neural network approach on a large dataset to identify features that birds might use to distinguish hoverflies from Hymenopterans, which is a useful step forward in exploring predator cognition. Kikuchi and Pfennig (2010a) and Spottiswolde and Stevens (2010) show that, in field experiments, signal receivers ignore useful information that could allow them to distinguish models from mimics, suggesting that mimics can exploit limits in receiver perception. However, Schaefer and Ruxton (2009) argue that some putative forms of mimicry may exploit receivers' preexisting biases that have nothing to do with a particular model. Generally, this topic is open for inquiry.

Bain, Roderick S., Arash Rashed, Verity J. Cowper, Francis S. Gilbert, and Thomas. N. Sherratt. 2007. The key mimetic features of hoverflies through avian eyes. *Proceedings of the Royal Society B: Biological Sciences* 274.1621: 1949–1954.

Using a large dataset of decisions made by pigeons on whether or not to attack hymenopterans and their mimics, the authors used a machine-learning approach to fit a model to the pigeon's choice criteria, identifying the salient features for prey

categorization. This illustrates a potential approach for deconstructing predator

cognition.

Balogh, Alexandra C. V., Gabriella Gamberale-Stille, Birgitta S. Tullberg, and Olof

Leimar. 2010. Feature theory and the two-step hypothesis of Müllerian mimicry

evolution. *Evolution* 64.3: 810–822.

Most models of mimicry assume either optimal predator behavior with respect to signal

detection theory, or an algorithm that approximates it. This model instead designs the

predator from psychological processes first, including prey categorization. More work

on predator psychology will enhance our understanding of the evolution of mimicry.

Cheney, Karen L., and N. Justin Marshall. 2009. Mimicry in coral reef fish: How

accurate is this deception in terms of color and luminance? *Behavioral Ecology* 20.3:

459–468.

Applying recent advances in modeling the vision of animals, this paper represents a

step away from describing mimicry in human terms and a movement towards

describing it in ecologically relevant terms: the perception of the signal receivers.

Chittka, Lars, and Daniel Osorio. 2007. Cognitive dimensions of predator responses to

imperfect

mimicry?[http://www.plosbiology.org/article/info%3Adoi%2F10.1371%2Fjournal.pbio

.0050339] *PLoS Biology* 5.12: e339. [doi:10.1371/journal.pbio.0050339]

Addresses the potential for certain psychological processes of predators—particularly

speed-accuracy trade-offs and categorization—to cause their behavior to deviate from

the assumptions of models built on signal detection theory. This article helped spark

recent interest in the influence of predator psychology on mimicry.

Darst, Catherine R. 2006. Predator learning, experimental psychology and novel

predictions for mimicry dynamics. *Animal Behaviour* 71.4: 743–748.

Focusing on the way that predators learn and forget, Darst makes a number of useful

suggestions for how predator psychology might influence the evolution of mimicry, but

many have yet to receive attention.

Kikuchi, David W., and David W. Pfennig. 2010a. Predator cognition permits imperfect

coral snake mimicry. *American Naturalist* 176.6: 830–834.

In one of the few field demonstrations of the influence of receiver cognitive processes

on the evolution of mimicry, Kikuchi and Pfennig showed that imperfect mimicry is

maintained by predators' inability to analyze some dimensions of prey phenotype.

Schaefer, H. Martin, and Graeme D. Ruxton. 2009. Deception in plants: Mimicry or

perceptual exploitation? *Trends in Ecology & Evolution* 24.12: 676–685.

The distinction between a mimic that takes advantage of a specific deficiency in

predator cognition should not be conflated with a general exploitation of preexisting

receiver responses to broad classes of stimuli, Schaefer and Ruxton contend in this

review.

Spottiswoode, Claire N., and Martin Stevens. 2010. Visual modeling shows that avian

host parents use multiple visual cues in rejecting parasitic eggs. *Proceedings of the

National Academy of Sciences* 107.19: 8672–8676.

This study provides a good example of how to examine mimicry from a receiver's

perspective. It also shows that although hosts discriminate finely in some dimensions of

egg phenotype, they nonetheless ignore a critical aspect that would allow them to

completely exclude cuckoo eggs.

CHAPTER III

P<small>REDATOR</small> C<small>OGNITION</small> P<small>ERMITS</small> I<small>MPERFECT</small> C<small>ORAL</small> S<small>NAKE</small> M<small>IMICRY</small>[2]

Summary

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.

Introduction

Batesian mimicry, in which harmless prey evolve phenotypic resemblances to dangerous

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[2] This chapter is based on Kikuchi, D. W., and D. W. Pfennig. 2010. Predator cognition permits imperfect coral snake mimicry. American Naturalist 176:830-834.

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 (Lindstrom et al. 1997; Holloway et al. 2002; Caley and Schluter 2003). A second, less well-explored hypothesis is that selection for improved 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 (Chittka and Osorio 2007, Bain et al. 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 McDiamid 1981; Savage and Slowinski 1992). Thus, the genetic and developmental mechanisms needed to produce coral snake color patterns can evolve in non-elapid taxa. However, were there 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 (Chikkta and Osorio 2007).

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, *L. elapsoides*, has a wider geographical range than its model, *M. 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 sympatry, 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 2010b). 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 (Figure 3.1). 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 and Pfennig

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

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 3.1, Figure 3.2). Replicas were collected after five 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 non-independence 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 *M. fulvius* by nonvenomous *L. elapsoides*, both of which have brightly colored rings encircling their bodies, but in different order (Figure 3.1). Of 537 replicas available for analysis (one triad was discarded due to human interference), 66 (12.3 %) were attacked. Of these, 10 were attacked by birds, 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 which 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; $Z = 0.387$, $p = 0.7$; Figure 3.3).

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 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 ($Z = 2.523$, $p = 0.012$). If generalization of a highly toxic model were the only factor promoting imperfect coral snake mimicry, then we would have expected 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 (Figure 3.3) 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 at 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 proportions 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, suggest 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 tradeoffs might influence predator foraging decisions (Chittka et al. 2009). Whether a speed-accuracy tradeoff 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 if 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 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.

Table 3.1. Where and when transects of replicas were placed in the field

Transect	Latitude	Longitude	Start date	End date	Duration (d)
1	34.98538	79.5023	13-Mar-2010	17-Apr-2010	35
2	34.9925	79.50727	13-Mar-2010	17-Apr-2010	35
3	35.01753	79.62209	13-Mar-2010	17-Apr-2010	35
4	34.52964	80.217	14-Mar-2010	18-Apr-2010	35
5	34.57256	80.22328	14-Mar-2010	18-Apr-2010	35
6	34.56645	80.25216	14-Mar-2010	18-Apr-2010	35
7	34.01567	78.07084	20-Mar-2010	24-Apr-2010	35
8	34.06461	78.2914	20-Mar-2010	24-Apr-2010	35
9	34.0985	78.3017	20-Mar-2010	24-Apr-2010	35
10	34.81287	78.66769	20-Mar-2010	24-Apr-2010	35
11	35.16744	78.90908	28-Mar-2010	1-May-2010	34
12	35.14969	79.36958	28-Mar-2010	1-May-2010	34
13	35.01344	79.30998	28-Mar-2010	1-May-2010	34
14	35.07172	79.60456	28-Mar-2010	1-May-2010	34
15	34.56422	77.70661	2-Apr-2010	8-May-2010	36
16	34.5643	77.72981	2-Apr-2010	8-May-2010	36
17	34.25962	78.47859	3-Apr-2010	8-May-2010	35
18	34.5797	78.4502	3-Apr-2010	8-May-2010	35

Figure Legends

Figure 3.1. Replicas of snake phenotypes used to measure predation in the field. (*a*) replica of *L. elapsoides* from allopatry, representing a "poor mimic" (with more red and less black than the model); (*b*) replica of *Lampropeltis 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.

Figure 3.2. 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 3.1.

Figure 3.3. Barplot depicting the modeled 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 upon 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.

Figure 3.1
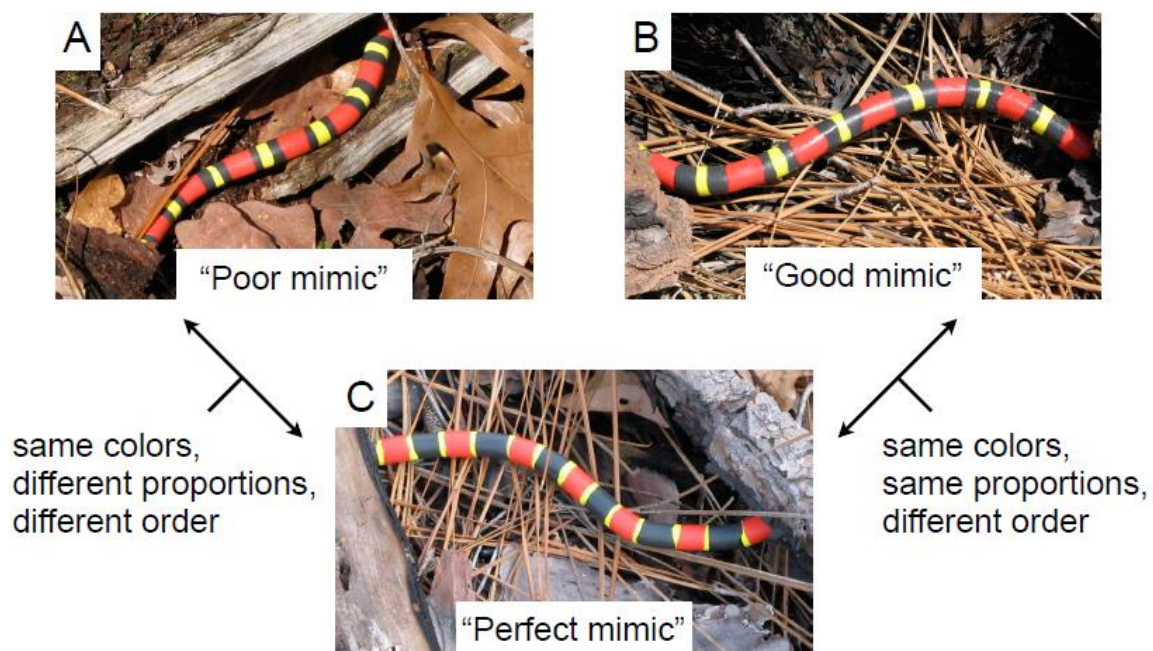
Figure 3.2
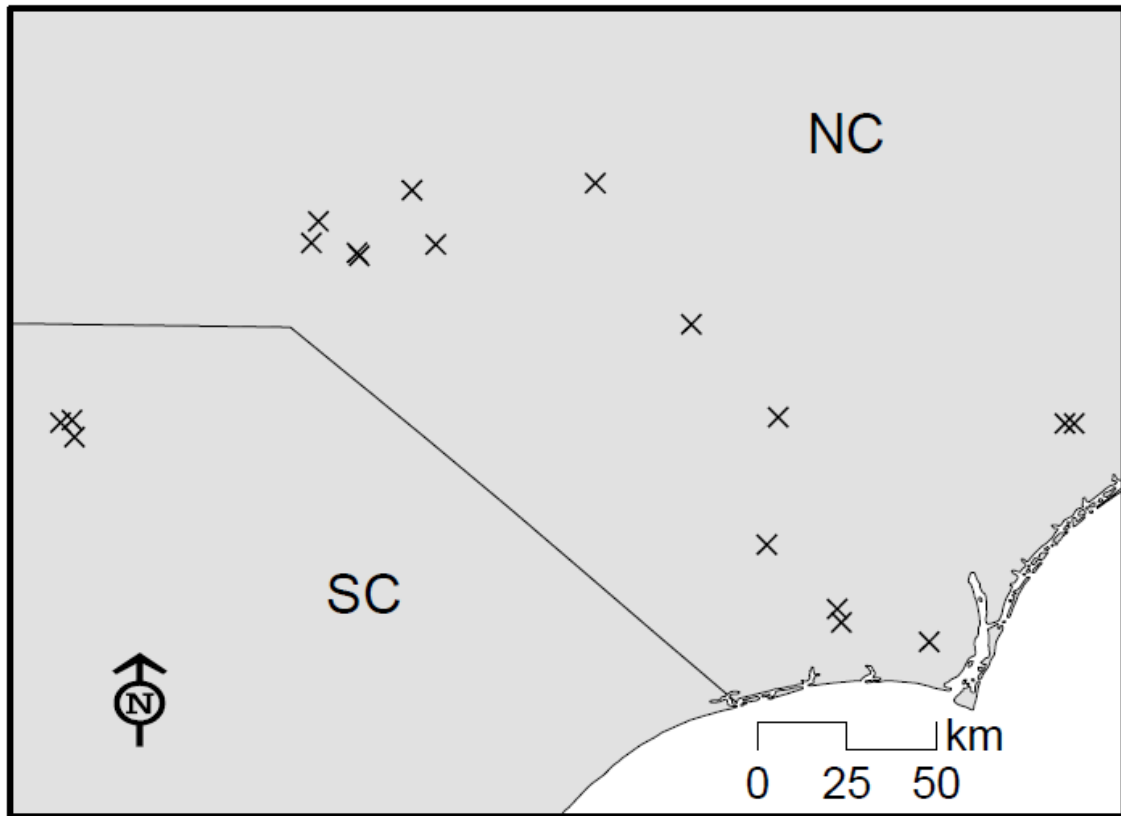
Figure 3.3

CHAPTER IV

A BATESIAN MIMIC AND ITS MODEL SHARE COLOR PRODUCTION MECHANISMS[3]

Summary

Batesian mimics are harmless prey species that resemble dangerous ones (models), and thus receive protection from predators. How such adaptive resemblances evolve is a classical problem in evolutionary biology. Mimicry is typically thought to be difficult to evolve, especially if the model and mimic produce the convergent phenotype through different proximate mechanisms. However, mimicry may evolve more readily if mimic and model share similar pathways for producing the convergent phenotype. In such cases, these pathways can be co-opted in ancestral mimic populations to produce high-fidelity mimicry without the need for major evolutionary innovations. Here, we show that a Batesian mimic, the scarlet kingsnake *Lampropeltis elapsoides*, produces its coloration using the same physiological mechanisms as does its model, the eastern coral snake *Micrurus fulvius*. Therefore, precise color mimicry may have been able to evolve easily in this system. Generally, we know relatively little about the proximate mechanisms underlying mimicry.

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[3] This chapter is based on Kikuchi, D. W., and D. W. Pfennig. 2012. A Batesian mimic and its model share color production mechanisms. Current Zoology 58:658-667.

Introduction

Batesian mimicry, where a harmless organism resembles a dangerous one and thus receives protection from predators, has long served as an exemplar of how natural selection can create complex adaptations (Bates 1862; reviewed in Ruxton et al. 2004; Forbes 2009). Mimicry also illustrates how two different taxa can converge on the same phenotype. This process can entail many difficulties, especially if mimics arise from cryptic species and must cross a selective valley between crypsis and mimicry, during which period they receive neither the benefits of crypsis nor mimicry (Leimar et al. in press). Even once mimicry evolves, it may retain imperfections (Sherratt 2002; Ruxton et al. 2004). Both the difficulty of initially evolving mimicry, as well as its degree of fidelity to its model, depend ultimately on the underlying similarity between the proximate mechanisms that models and mimics use to produce their phenotypes. By this, we mean the underlying genetic architecture, developmental processes, and metabolic pathways used to produce the convergent phenotypes of models and mimics (Arendt and Reznick 2007; Manceau et al. 2010).

When models and mimics share mechanisms of phenotype production, new mimics may evolve easily. In such cases, just a few mutations may be needed for the mimic to match the phenotype of its model, and low-fitness intermediate phenotypes may be bypassed (Leimar et al. in press). Moreover, in such a situation, high fidelity mimicry becomes more likely. By contrast, when models and mimics do not share mechanisms of phenotype production, high fidelity mimicry may be more difficult to evolve. The use of

different proximate mechanisms by mimic and model may be especially likely to occur in populations in which intermediate phenotypes are not selected against (e.g. Kikuchi and Pfennig 2010b) or in which perfect mimicry is not favored (e.g. Dittrich et al. 1992; Sherratt 2002).

Little is known about how models and mimics produce their phenotypes. Most of what we do know comes from work on a Müllerian mimicry complex involving butterflies in the genus *Heliconius*. Recently, *cis*-regulatory elements in a single gene were shown to control covariation between the red elements of patterns in *H. erato* and *H. melpomene*, whose variously colored subspecies mimic each other throughout Latin America (Reed et al. 2011). However, these species are very closely related, and it is thus not necessarily surprising that co-mimic pairs use essentially the same mechanisms of producing their patterns.

The coevolution between Batesian mimics and their models may be much more fruitful for understanding adaptation in general, because in Batesian mimicry complexes, models and mimics tend to be more distantly related. Batesian models and mimics also have intrinsic differences defined by their roles as defended models and undefended mimics, so any mechanism common to the production of secondary defenses and warning signals may further decrease the likelihood of closely shared proximate means of signal production. For example, if the larvae of a model butterfly species feeds on a plant that provides it with both a toxin and a pigment, while its mimic feeds on a plant that provides neither, the mimic might have to obtain an alternative dietary pigment or manufacture its own in order to deceive potential predators. The possibility that the environment may play a role in generating the mimetic phenotype further highlights the critical importance

of understanding how models and mimics produce their phenotypes. Some Batesian

mimics of the butterfly clades *Papilio* and Dismorphiinae use different pigments to

produce their red coloration than do their models (Ford 1953), so they use different

mechanisms at least for this aspect of phenotype. Moreover, some of those pigments are

environmentally derived.

Here, we report an analysis of the pigments used to produce warning signals in a

Batesian mimicry complex. The defended model is the venomous eastern coral snake,

Micrurus fulvius, which is mimicked by the harmless scarlet kingsnake, *Lampropeltis*

elapsoides. Both species are characterized by having bright red, yellow, and black rings

encircling their body (Figure 4.1). We therefore sought to determine whether or not the

same pigments were used in each of these color elements. Additionally, we explored the

cellular structures associated with coloration in the skin of models and mimics. Much

future work remains to be done to elucidate genetic and developmental aspects of color

production in this system, but this study represents a first step in understanding the

mechanistic basis of mimicry in a well-studied Batesian mimicry complex, and it is also

the first detailed study of the mechanisms underlying coloration in snakes.

Methods

Reptile coloration

Our study system is attractive for asking whether or not coloration has evolved using the

same mechanisms in models and mimics for at least three reasons. First, scarlet

kingsnakes are attacked by a wide array of both mammalian and avian predators (Pfennig

et al. 2007; Kikuchi and Pfennig 2010b). Therefore, mimics should be under selection to

be good color mimics of their models due to the wide variety of photoreceptors that their guild of predators possess. Second, the scarlet kingsnake and eastern coral snake are separated by a greater genetic distance than the Müllerian mimics in the butterfly genus *Heliconius*, whose coloration is better studied. The Kimura two-parameter genetic distance for cytochrome oxidase unit 1 between the eastern coral snake and *Elaphe carinata* (a colubrine snake in the same clade as the scarlet kingsnake) is 0.2404, whereas this same comparison made between *H. pachinus* and *H. hewitsoni* returns a genetic distance of only 0.1013 (GenBank accession numbers GU045453.1, JF700159.1, AY748076.1, and GQ398195.1). A third advantage to our system is that a variety of different pigments and cellular elements have been found to color the skin of lower vertebrates. It is this last point on which we focus here.

In fish, amphibians, and reptiles, color patterns are composed of dermal cells called xanthophores, iridophores, and melanophores, collectively known as chromatophores (reviewed in Cooper and Greenberg 1992). Iridophores contain guanine crystals that can cause both iridescence and structural coloration in reptiles (Gosner 1989; Morrison et al. 1995; Kuriyama et al. 2006). Melanophores contain the dark, endogenous tyrosine pigment melanin. Xanthophores (also called erythrophores when they hold red pigments) can sequester both pteridine and carotenoid pigments (Macedonia et al. 2000; Steffen and McGraw 2009).

Pteridine and carotenoid pigments represent two different possible mechanisms of color production. Pteridines are metabolically derived from guanine triphosphate (Kim et al. 2006; Kim et al. 2009) and are found in taxa as diverse as insects, fish, amphibians, and reptiles (Watt 1967; Fukushima 1970; Silva and Mensu 1988; Pfleiderer 1992). In

contrast, carotenoid pigments are environmentally derived and their concentration can vary greatly from individual to individual depending on diet (Olson and Owens 1998). Both pteridines and carotenoids may contribute to coloration in the same tissue type (Macedonia et al. 2000; Grether et al. 2001; Steffen and McGraw 2009), and the color achieved sometimes depends on their relative concentrations (Grether et al. 2005). Alternatively, color can be produced by just one type of pigment in isolation (Macedonia et al. 2000). Many different pteridines can be produced in the pteridine biosynthetic pathway, and although not all function in pigmentation, those that do range from red to ultraviolet in their hues. The type of carotenoids present depends on diet, but they typically have a red to yellow color.

Iridophores, which are found in a layer of cells below the xanthophores, can also contribute to coloration. When iridophores contain guanine crystals in parallel layers of uniform thickness, they can give rise to coloration by reflecting only the wavelength of light that corresponds to the thickness of the layers, referred to as thin-layer interference (Morrison et al. 1995). When iridophores contain less organized groups of small crystals, they reflect short wavelength light more than long wavelength light through a process known as Tyndall scattering. Regardless of whether crystals are organized to cause coloration though Tyndall scattering or thin-layer interference, iridophores typically contribute to reflectance in the ultraviolet, blue, and green areas of the spectrum (Gosner 1989; Morrison et al. 1995; Kuriyama et al. 2006). In combination with melanophores and xanthophores that absorb other wavelengths, iridophores can contribute to colors produced by the reflection of narrow bands of light, such as green (Nielson and Dyck 1978; Gosner 1989).

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Melanophores in lower vertebrates have to date only been shown to contain the blackish pigment eumelanin, which is found in animal tissues ranging from squid ink to mouse hair (Ito and Wakamatsu 2003). However, melanin pigments also include the reddish-yellow pheomelanins, which are found in mammals and birds (Ito and Wakamatsu 2003). In lower vertebrates, melanins have been poorly explored, and it is possible that the absence of pheomelanins from all taxa but birds and mammals is simply a product of incomplete sampling. Reptiles use eumelanin to darken skin because it absorbs relatively uniformly across the ultraviolet and visible spectrum (Shawkey et al. 2009), but the use of pheomelanins by some taxa to produce red or yellow hues remains an open possibility, and represents an alternative pathway by which taxa might converge in color production.

Histology of the eastern coral snake and scarlet kingsnake

To determine the nature and organization of chromatophores in each color of the model and its mimic, we used transmission electron microscopy (TEM). TEM can also be used to distinguish eumelanin from phenomelanin. Pheomelanin tends to be organized into more disorganized and diffuse granules than eumelanin (Brumbaugh 1968).We obtained specimens of coral snakes from Florida that had been found recently after death (due to road kill) and immediately frozen. We also collected three scarlet kingsnakes (two from Florida and one from North Carolina) and sacrificed them by first anesthetizing them with chloroform and then severing the cervical vertebrae. Skin samples of each color were immediately collected from the sacrificed animals and fixed with 2.5%

glutaradehyde. Samples were then sent to the University of North Carolina Microscopy

Services Laboratory for further preparation.

We sampled color patches from one coral snake (the best-preserved specimen) and

the three scarlet kingsnakes using TEM. In the coral snake, there are occasionally black

speckles in the red rings. These black speckles were excluded from our samples of the red

tissue. There was also some slight fringing of black and red on the scales of the yellow

rings in some scarlet kingsnakes. When this occurred, it generally affected all the yellow

scales on the snake and therefore we could not avoid including these color elements in

our samples.

Absorbance spectra of skin extracts

To isolate pterdine and carotenoid pigments from skin samples of each color from each

snake, we finely diced them and then placed them in uniquely labeled microcentrifuge

tubes. For each snake, we used approximately equal quantities of black and yellow skin

because initial trials indicated that yellow skin contained unidentified pigments, and

black skin served as a useful control for skin with the absence of soluble pigments. We

added 1 mL 1 N NH_4OH to each tube and homogenized the tissue using a laboratory

homogenizer (Steffens and McGraw 2009). This extracted pteridine pigments, which are

well extracted by basic aqueous solutions. We then added 0.5 mL 1:1 hexanes:tert-butyl-

methyl ether (TBME) to each tube and vortexed for 30 seconds. This organic extraction

was designed to remove any organic-soluble pigments such as carotenoids (McGraw et

al. 2005). Samples were then centrifuged for 5 minutes at 8000 rpm. The organic and

aqueous fractions were separated from each sample. Their absorbencies were measured

from 200–800 nm using 1 N NH_4OH and 1:1 hexanes:TBME as blanks, respectively, on a Benkmann-Colture spectrophotometer. Most carotenoids have characteristic triplets of absorbance peaks between 400–500 nm (Britton 1985; Macedonia et al 2000).

Thin-layer chromatography of skin extracts

We next sought to identify the different pteridine pigments that might be present in our aqueous extracts. Pteridines can be identified using thin-layer chromatography (TLC). In TLC, the components of a solution that has been absorbed onto a solid medium are separated into different spots on the medium when a solvent moves across it. Chromatography of pteridines is aided by ultraviolet light because it causes fluorescence in spots that would otherwise not have any optical activity. Spots can be identified by color and by their R_f values, which indicate how far they have travelled on the solid medium.

   For each sample of skin, we spotted 10 μL of aqueous solution onto a corner of cellulose chromatography paper. We developed these chromatograms in two solvents running at right angles to each other. The first solvent was 1:1 propanol:2% ammonium acetate. After allowing each chromatogram to dry, we then developed them in 3% NH_4Cl (Wilson and Jacobson 1977; Ferre et al. 1986). Once each chromatogram had been developed, we examined it under 365 nm light, which causes each type of pteridine to fluoresce a particular color. In this way, we were able to determine the locations of each pteridine spot, including those that typically have no optical activity. We compared the R_f values and fluorescent colors of the spots isolated in each sample to those of a standard extracted from *Drosophila* eyes (strain Oregon R-P2), whose pigment identities are

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known (Wilson and Jacobson 1977; Ferre et al. 1986). We also ran conformational tests using standards of isoxanthopterin (isolated from the bodies of male *Drosophila*), sepiapterin (Sigma-Aldrich), xanthopterin, 7,8-dihydrobiopterin, and 2-amino-4-hydroxy-1H-pteridine (Fisher). In addition, when there was doubt about the identity of a spot, we repeated both the extractions and the chromatography using various solvents described in the literature (Ephrussi and Herold 1944; Grether et al. 2001).

Results

Cross-sections of skin magnified under TEM

The images obtained by exploration of prepared TEM specimens indicated that all three types of chromatophores are present in the skin of both models and mimics (Figure 4.2). In the scarlet kingsnake, red tissue contained xanthophores. Although most xanthophores were present near the epidermis, some specimens had xanthophores sparsely distributed deeper in the dermis. One specimen also had sporadic epidermal melanophores in the red tissue. Black tissue contained only melanophores, which were mostly large and found deep in the dermis, although some specimens exhibited some small epidermal melanophores. Yellow tissue consisted of an upper layer of sparsely distributed xanthophores.

We also observed a few epidermal melanophores close to the epidermis in the yellow tissue (Figure 4.3). The scales that form yellow and red tissue can be tinged with black (especially, along their rear edges of these color rings); thus, the trace epidermal melanophores may relate to such spatial variability in scale coloration. Beneath the xanthophore layer in the yellow tissue, we found a much more extensive layer of

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disorganized guanine crystals in the iridophores. The crystals were of variable size and orientation. Notably, the yellow and red tissue did not appear to contain pheomelanin-bearing melanocytes.

We found that the xanthophores in the red tissue of the coral snake appeared to be located much deeper in the skin than in the red tissue of the scarlet kingsnake, due to the thicker epidermis of the coral snake (Figure 4.2). The black skin of the coral snake contained both epidermal and dermal melanophores. The yellow coral snake skin contained iridophores deep in the dermis that appeared to be overlaid with xanthophores. Unfortunately, because our coral snake specimen was poorly preserved, its iridophore layer was a disorganized network of rounded holes, and its xanthophores did not contrast with surrounding tissue as well as they did in the scarlet kingsnake.

Absorbance of organic and aqueous skin extracts

We used absorbance spectroscopy to determine the possible presence of carotenoids in the organic fractions of our skin extracts. None of the organic fractions that we examined from either the coral snake or the scarlet kingsnakes had such peaks. Therefore, we conclude that no appreciable quantity of carotenoids was present in the skin of either the model or the mimic.

The aqueous fractions of our extractions produced nearly identical results between the coral snake and kingsnake for red, black and yellow tissue (Figure 4.4). Red tissue showed a strong, broad peak between 490–500 nm, which coincides with the absorbance maximum of drosopterin pigments. This is consistent with its red coloration. It also showed strong absorbance that increased into the ultraviolet, indicating the presence of

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other pigments, probably pteridines. Black tissue had nearly uniformly low absorbance

across the visible spectrum that increased slightly towards the ultraviolet, which is

consistent with most of its absorbance activity coming from melanin that would have

been excluded from the aqueous extraction. Yellow tissue showed a minor shoulder

beginning at 500 nm as its absorbance increased towards the ultraviolet, which may

reflect trace drosopterins from red fringing of the scales. As with the red tissue, yellow

tissue absorbed very strongly at wavelengths < 400 nm. The two skin colors appear to

share a pigment that has an absorbance peak around 340 nm in our strongly basic

extraction, and which does not appear to be a pteridine produced in quantity by

Drosophila (Figure 4.5), although there is a slight increase in absorbance at that

wavelength in the extraction of male *Drosophila* bodies, which contain mainly

isoxanthopterin.

TLC chromatography

The spots on chromatograms of red, yellow, and black-colored tissue in coral snakes and

kingsnakes showed an exact correspondence of color and R_f values. In red skin, four

drosopterins (neodrosopterin, drosopterin, isodrosopterin, and aurodrosopterin) produced

visible red, orange, and yellow fluorescent spots of great intensity. These pigments are

responsible for the red coloration of *Drosophila* eyes, and the R_f values of spots from red

skin extracts corresponded well to that of our *Drosophila* standard. Additionally, two

broad spots—one violet and the other blue—were also present. These spots did not

correspond well to those on our *Drosophila* standard in R_f values, nor did they appear to

match our other pteridine standards. In the yellow tissue, only trace drosopterins were

present, but two unidentified spots (also present in the red tissue) gave an intense fluorescence. The mean R_f values of the violet fluorescent spot was 0.4 in 1:1 isopropanol:2% ammonium acetate, and 0.34 in 3% NH_4Cl. For the blue spot, they were 0.35 and 0.55, respectively. For both spots, the R_f values in 1:1 isopropanol:2% ammonium acetate were more variable than in 3% NH_4Cl. The closest R_f values of a violet spot in *Drosophila* were for isoxanthopterin, which had values of 0.3 and 0.35 in the first and second phases, respectively.

Neither sepiapterin nor xanthopterin, which are both yellow in color, was present in any of the samples we examined. The unidentified pigments in the yellow tissue exhibited slight absorbance in the visible range (Figure 4.5). The black tissue did not show significant amounts of pigmentation.

Discussion

We studied the physiological mechanisms by which a Batesian mimic and its model produced their distinctive phenotypes. We found that coloration in the eastern coral snake and its mimic, the scarlet kingsnake, is produced via the same pigments. Specifically, red skin is colored mainly by drosopterin pigments that are sequestered in xanthophores. Black coloration is produced by eumelanin, which is contained within melanosomes in the dermis and epidermis. Yellow coloration is the product of two unidentified pteridines in a layer of xanthophores, and also a disorganized assemblage of guanine crystals beneath the xanthophores. Moreover, on the basis of data obtained from TLC and spectrophotometry, we have established that in all color patches the scarlet kingsnake and coral snake employ the same pigments, even in the yellow tissue where we were unable

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to identify the specific pigments. We found no evidence of environmentally derived pigments in either snake. Although there are minor differences between the two species in ultrastructure, the scarlet kingsnake's use of the same pigments for color production as its model may have facilitated the evolution of mimicry in this system. Such similarity in underlying mechanisms may also permit very precise color mimicry, which may be advantageous in this system, considering the diverse predator guild responsible for exerting selection on the mimic.

To understand the significance of such closely shared mechanisms of color production between a mimic and its model, we must place the mechanisms used in our system within the context of coloring mechanisms available to animals in general. There are a number of deeply conserved metabolic pathways associated with red and yellow coloration, including carotenoids, pteridines, and pheomelanins (McGraw et al. 2005). Within these biochemically complex metabolic pathways, a variety of pigments with different optical properties can be produced. Thus, even if the same metabolic pathway is involved in coloring two species, it does not necessarily mean that it will yield the same end products. Moreover, even if the same end products are produced, they may not be incorporated into tissues the same way. Very different colors can be conferred upon tissues when pigment deposition varies on the level of ultrastructure (Hoekstra, 2006; Shawkey et al. 2009). Therefore, even if two species manufacture the same pigments in the same pathways, we should not necessarily anticipate that histological examination will reveal much similarity in their tissues.

The eastern coral snake and scarlet kingsnake not only both use pteridines to color their tissues, they use the same ones among many such pigments that can be synthesized.

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At least two red pigments (erythropterin and drosopterins) and two yellow pigments (xanthopterin and sepiapterin) can be produced. The model and mimic both use drosopterins in red skin and the same two unidentified pteridines in yellow skin. We suggest that the unidentified violet spot revealed by TCL of red and yellow skin extracts may be isoxanthopterin, due to its UV absorbance peak at 340 nm (Albert 1953). To produce yellow coloration, the absorbance of isoxanthopterin may be shifted towards the visible range under physiological conditions, such as lower pH or the binding of the pigment to other elements (Wijnen et al. 2007). Finally, the model and mimic also show similarity in the histology of their chromatophores. Thus, there is similarity on multiple organizational levels.

It is also helpful to understand color production in a comparative context. Because the present study was the first to identify pigments in the skin of snakes and associate them with chromatophore structure, fine-scale inference is limited. The only other study to explore the histology of snake skin was that of Gosner (1989), who used samples of *Bothrops* vipers from museum specimens which had long lost their colors. Still, his microscopy revealed that specimens that had been green in life had a layer of xanthophores near the surface, followed by a layer of disorganized guanine crystals in the iridophores, and underneath both of those a layer of melanophores. The arrangement of chromatophores found in the green *Bothrops* by Gosner (1989) is described by a model for color production proposed by Nielsen and Dyck (1978): xanthophores remove violet and blue light from the spectrum, iridophores reflect green light through Tyndall scattering, and melanophores remove any red and yellow light that would otherwise be reflected by the white collagen lying beneath them. As a result, only green is reflected.

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Yellow can be produced by removing the melanophores, allowing the red and yellow light to be reflected with the green light (Nielsen and Dyck 1978). This model for the production of yellow coloration corresponds to our histological analysis of the coral snake and scarlet kingsnake as well as to a yellow *Bothrops* examined by Gosner (1989). Given the similarity between histology of the snakes studied here and the only other snake studied to date, it may not seem surprising that the coral snake and its mimic share such a close resemblance. However, the arrangement of chromatophores in snakes and lizards can be quite diverse. In terms of histology, lizards have more organized iridophores arranged into discrete layers of guanine crystals (Taylor and Hadley 1970; Kuriyama et al. 2006). This organization of iridophores may reflect light using thin-layer interference rather than Tyndall scattering, providing a tighter band of reflectance (Morrison 1995). Additionally, in yellow or white skin, both *Sceloporus* and *Plestiodon* lizards have melanophores present under the iridophore layer, albeit fewer than in brown skin (Morrison et al. 1995; Kuriyama et al. 2006). Green skin in *Pleistodon* contains a mixed upper layer of iridophores and xanthophores, either of which may be closest to the epidermis (Kuriyama et al. 2006), which contrasts with the mechanism of production of green in *Bothrops* and *Anolis* (Gosner 1989; Taylor and Hadley 1970). As reported by Kuriyama et al. (2006) in *Pleistodon*, we found some epidermal melanophores in yellow and black skin, but there are striking differences between the histology of snake skin observed here and those of other snakes and lizards thus far studied.

The pteridine and carotenoid pigments deposited in xanthophores can also vary widely among taxa. Within *Anolis*, those from Jamaica lack xanthopterin entirely (Macedonia et al. 2000), whereas about two-thirds of species from Puerto Rico possess

xanthopterin (Ortiz and Maldonado 1966). All possess isoxanthopterin (Macedonia et al. 2000). There is also widespread interspecific variation in the production of optically active pteridines and in the sequestration of carotenoid pigments (Ortiz et al. 1963; Ortiz and Maldonado 1966; Macedonia et al. 2000). In *Sceloporus undulatus*, skin on yellow chins contains xanthopterin and the yellow vitamin riboflavin, orange chins contain drosopterins, and both types of skin contain isoxanthopterin (Morrison et al. 1995). Taken as a whole, the panoply of pigments and variety of chromatophore arrangements found throughout the reptiles underscore the close concordance between the color production mechanisms of the eastern coral snake and the scarlet kingsnake. However, the production of yellow coloration in the distantly related viper *Bothrops* is also very similar (Gosner 1989), so our results may speak more to a conserved system of coloring mechanisms used by snakes in general rather than a particularly tight match between model and mimic.

In other words, it is unclear if the similarity between the mimic and its model in mechanisms of color production reflects convergence (by the mimic on the model), or if it reflects homology (e.g., all snakes may share the same mechanisms of color production). Future studies will be needed to clarify this matter. Specifically, it remains to be seen if a wider taxonomic sampling of color production in mechanisms in snakes reveals as much diversity as has been found in lizards.

The lack of environmentally derived pigments (e.g., carotenoids) in the skin of either the mimic or its model suggests that diet-mediated phenotypic plasticity may not have played a direct role in the evolution of mimetic coloration. This finding was somewhat surprising, because not only has the scarlet kingsnake evolved mimicry, it has also

converged on its model in *diet*. In particular, both the scarlet kingsnake and the eastern coral snake eat primarily ectothermic prey such as *Plestiodon* skinks and other small snakes (Bartlett and Bartlett 2003). An ancestral character state reconstruction of the snake clade Lampropeltini, in which the scarlet kingsnake is found, indicated that it probably arose from a larger snake that consumed a diet richer in endothermic (e.g. mammalian) prey (Pyron and Burbrink 2009). Despite this dietary convergence, the absence of environmentally derived pigments reduces the likelihood that mimicry arose as a plastic response to diet. However, it remains possible that an environmental cue, perhaps one derived from a snake's diet, could nonetheless play a role in the induction of the mimetic phenotype.

The use of exactly the same endogenous pigments in producing coloration could suggest that mimics have responded to selection for precisely matching their models in that aspect of phenotype. However, the actual colors of these two species can vary, owing to different concentrations of pigments and spatial irregularities in the distribution of color. For example, larger scarlet kingsnakes tend to have deeper yellow coloration than smaller ones, and the red rings of coral snakes are often speckled with black (Bartlett and Bartlett 2003). Ideally, one should quantify the reflectance spectra of skin samples from live snakes to compare the coloration of models and mimics objectively. It remains an open question as to how precisely the reflectance spectra of coral snakes and scarlet kingsnakes match and how strong selection favors such a resemblance.

Much is known about how natural selection acts on color *pattern* in this system. Specifically, the relative width of black and red rings on the bodies of the snakes is a target of selection, and this finding is emphasized by stronger selection where coral

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snakes are rare relative to where they are common (Harper and Pfennig 2007). We would expect to find a similar trend in coloration. Nevertheless, the order in which rings are arranged (eastern coral snakes and scarlet kingsnakes always differ in the order of their rings) is not under selection by predators (Kikuchi and Pfennig 2010a). We might therefore anticipate that genes controlling the arrangement of colored rings will differ between the model and the mimic. Although there should be strong selection on genes controlling the width of the rings, these genes may not necessarily be the same in the two snakes. At present, genes controlling patterns involving pteridine pigments are poorly known (Hubbard et al. 2010).

In sum, our results reveal that a Batesian mimic, the scarlet kingsnake *Lampropeltis elapsoides*, produces its distinctive coloration using the same physiological mechanisms as its model, the eastern coral snake *Micrurus fulvius*. Precise color mimicry may therefore have evolved relatively easily in this mimicry complex. However, we know relatively little about the genetic mechanisms underlying mimicry in this system. Future studies are needed to resolve whether the same genes regulate color production in the mimic as in the model, whether these genes involve substitutions in *cis*-regulatory regions or in coding sequence, and (perhaps most importantly) whether the observed similarity in color production mechanisms reflects homology or convergence (see above). These are some of the issues that pigment research can address (Protas and Patel 2008), and doing so in a Batesian mimicry complex may be particularly informative.

Figure Legends

Figure 4.1. The venomous eastern coral snake, *Micrurus fulvius* (*a*), is mimicked by the nonvenomous scarlet kingsnake *Lampropeltis elapsoides* (*b*). Both snakes have brightly colored rings of red, yellow, and black, which deter predators. Photos by W. Van Devender and D. Kikuchi.

Figure 4.2. These TEM micrographs of cross-sectioned snake skin show that in red skin of both (*a*) the eastern coral snake and (*b*) the scarlet kingsnake, xanthophores (marked with x) lie close to the epidermis (marked with e). Black skin of the (*c*) coral snake and (*d*) kingsnake contains a layer of large, dark melanophores (marked with m) that reside deeper in the dermis than the xanthophores found in red skin. It also contains smaller epidermal melanophores (marked with em). Yellow skin of the (*e*) coral snake and (*f*) kingsnake shows a layer of xanthophores above a layer of iridophores (marked with i), which contain guanine crystals of irregular size, shape, and orientation. Panels (*a*) and (*b*) are 2500x; Panels (*c*), (*d*), (*e*), and (*f*) are 5000x.

Figure 4.3. This cross-section of yellow skin from the scarlet kingsnake reveals a epidermal melanophore (marked with em) that lies above the xanthophores (x) and iridophores (i), which allows it to absorb light of all wavelengths before it reaches the reflective iridophores. It may represent some of the dark fringing visible on the edges of yellow scales. Its grains are far finer than those in dermal melanophores. Scale bar in upper left = 2 μm.

Figure 4.4. Absorbance of water-soluble pigments in skin samples of the (*a*) eastern coral snake and (*b*) scarlet kingsnake. Absorbance of red, yellow, and black skin samples is plotted in the corresponding color. The strong peaks of absorbance between 490–500 nm are indicative of drosopterin pigments in the red skin, which is absent in other colors of skin. The yellow and red skin contains unidentified pigments (probably pteridines) that absorb light < 400 nm. Solid line = black skin, dashed line = red skin, dotted line = yellow skin.

Figure 4.5. Absorbance of yellow and red skin from the scarlet kingsnake in the ultraviolet, showing identical peaks near 340 nm, followed by very strong absorbance in the mid ultraviolet. Solid line = extract of male *Drosophila* bodies, which contain isoxanthopterin; dashed line = red skin; dotted line = yellow skin; dotted-dashed line represents *Drosophila* head extract.

Figure 4.1

Figure 4.2
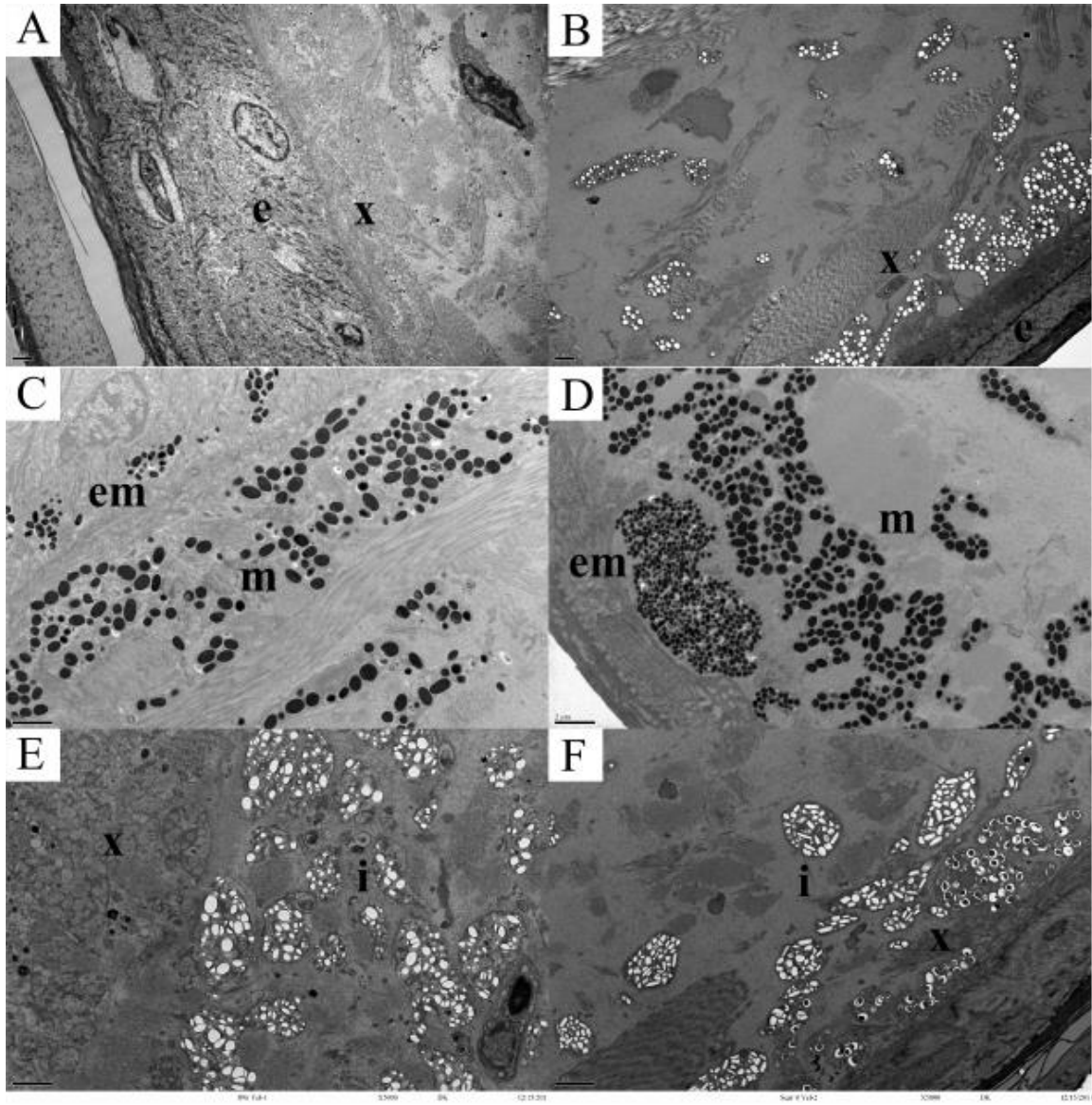
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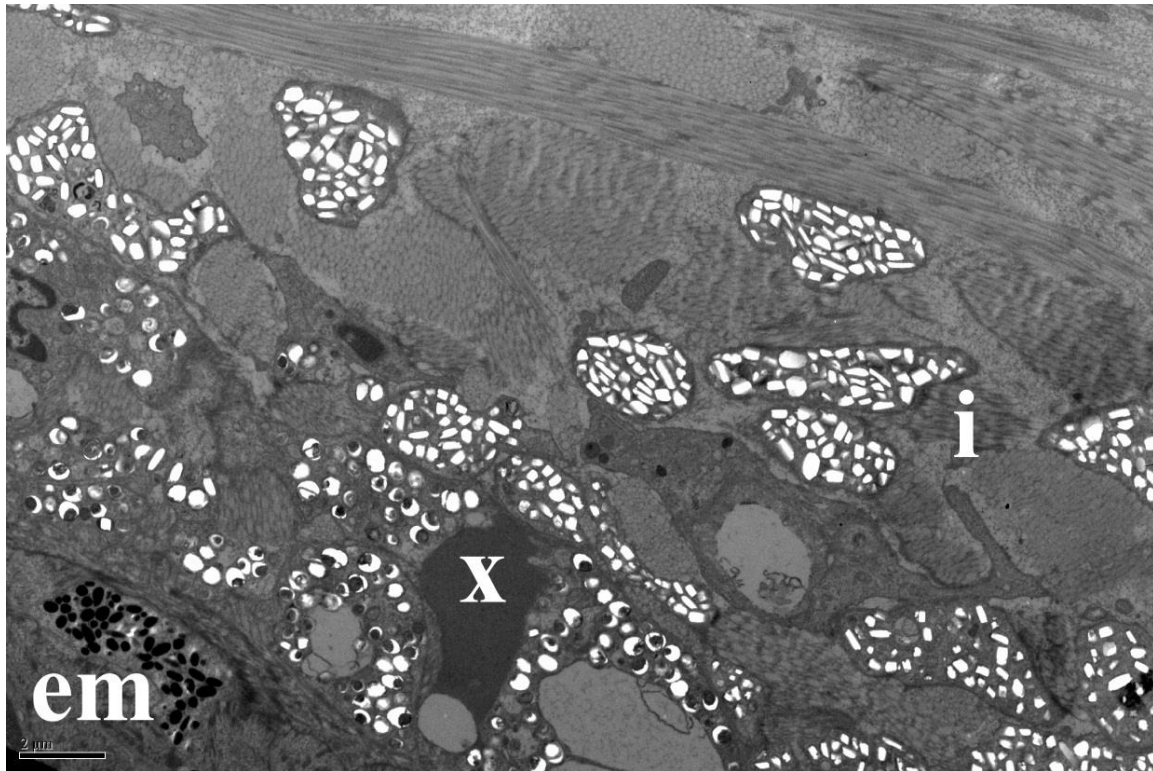
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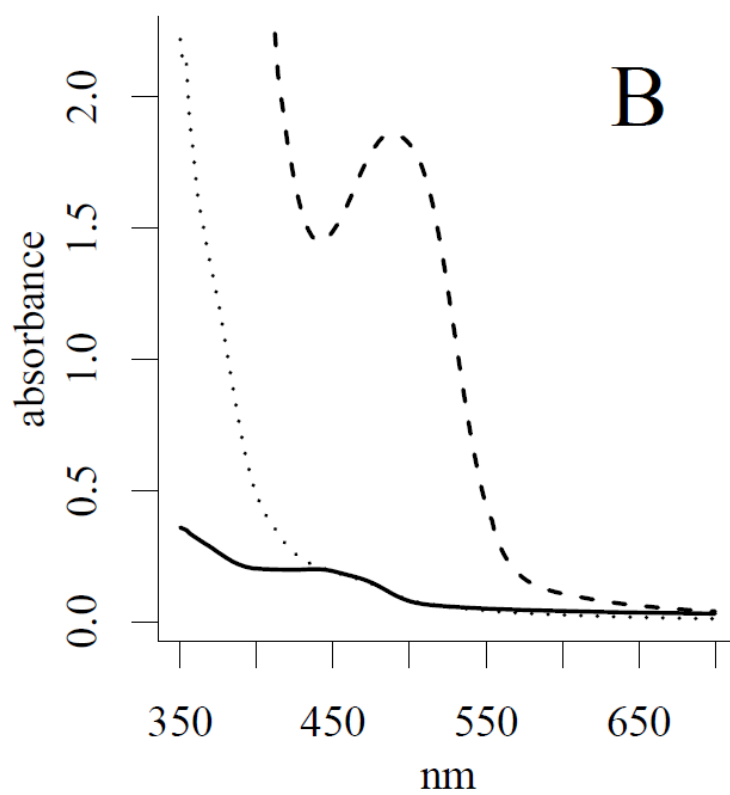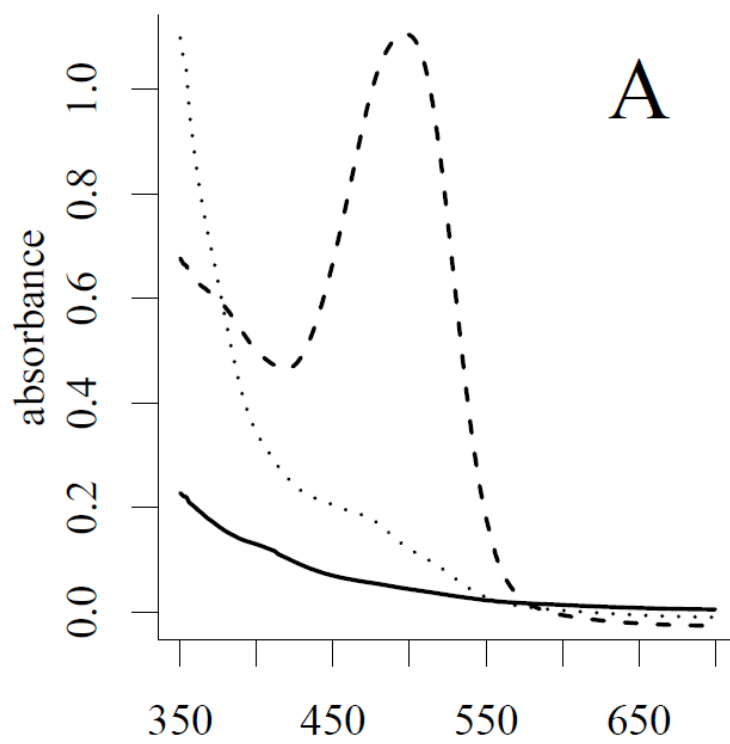
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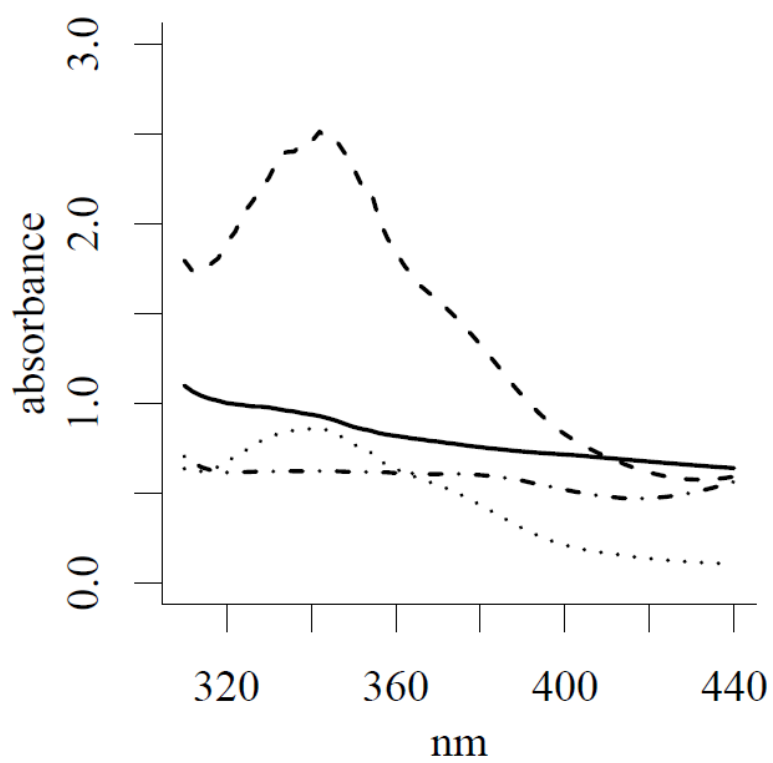
CHAPTER V

MIMICRY'S PALETTE: WIDESPREAD USE OF CONSERVED PIGMENTS

IN THE APOSEMATIC SIGNALS OF SNAKES

Summary

Mimicry, where one species resembles another species because of the selective benefits of sharing a common signal, is especially common in snakes. Snakes might be particularly prone to evolve mimicry if different species share the same proximate mechanisms used to produce aposematic signals. We evaluated this possibility by examining color pigments in 11 species of snakes from four different families, three of which participate in a coral snake mimicry complex involving convergence in coloration. We found that all 11 species used two pteridine pigments to produce coloration, regardless of whether or not they were mimics. Furthermore, the presence or absence of red pteridines was strongly correlated with the relative excitation of medium- and long-wavelength photoreceptors in birds, thereby linking shared pigmentation to perception of those pigments by likely agents of color mimicry. Thus, precise color mimicry might be relatively easy to evolve among snakes owing to symplesiomorphies in pigmentation.

Introduction

Convergent evolution—where two or more species evolve similar phenotypes in response to similar selective pressures—may be the product of different developmental pathways or, alternatively, of developmental systems that are shared on some proximate level (Arendt and Reznick 2007; Manceau et al. 2010). Either route may underpin defensive mimicry, where a species converges on the aposematic signals of another species (the model) because resemblance is favored when predators cannot distinguish between the two (Ruxton et al. 2004). Because mimicry can be highly selectively advantageous (e.g. Pfennig et al. 2001), convergence between taxa in the aposematic/mimetic signals might occur even when species possess novel ways of producing these signals. However, because aposematism is often distinctive (Ruxton 2004), shared developmental systems might expedite phenotypic convergence and therefore mimicry.

Despite the potential importance of proximate mechanisms in facilitating the evolution of mimicry, relatively little is known about how mimetic phenotypes are produced. Most of what we do know comes from studies of *Heliconius* butterflies (Belade and Brakefield 2002; Papa et al. 2008). Mimicry among closely related, distasteful species of *Heliconius* is controlled by three major loci that appear to have allelic effects on color pattern across species (Joron et al. 2011; Reed et al. 2011; Martin et al. 2012). Furthermore, species appear to have exchanged alleles regularly throughout their evolutionary history via hybridization (Dasmahapatra et al. 2012). Thus, in *Heliconius*, shared proximate mechanisms have promoted convergence on a complex phenotypic adaptation. However, most species involved in mimicry are more distantly

related to each other than are different species of *Heliconius*. Moreover, introgression of genes via hybridization is not a likely general explanation for the evolution of mimicry.

Snakes are an excellent taxon for studying how mimetic phenotypes arise but have not been well studied. Mimicry appears to be particularly common among snakes—especially mimicry of brightly colored, highly venomous coral snakes (family Elapidae; Brodie and Brodie 2004). Indeed, one of the first reported cases of mimicry involved coral snake mimicry (Wallace 1867), and up to eighteen percent (115 species) of New World snakes are thought to mimic coral snakes (Savage and Slowinski 1992). Why so many species converge on the coral snakes' distinctive patterns of red, yellow (or white), and black (i.e., tricolor) rings remains one of herpetology's most enduring problems (reviewed in Brodie and Brodie 2004).

Here, we consider one reason why coral snake mimicry is common: that snakes might share common developmental mechanisms for producing tricolor patterns. Recent research supports this hypothesis. Coral snakes, *Micrurus fulvius*, and their harmless mimics, scarlet kingsnakes, *Lampropeltis elapsoides*, share proximate mechanisms on some levels (Kikuchi and Pfennig 2012b). Specifically, the pigments used to produce coloration, and the organization of their color-producing cells (chromatophores), are the same for both species (Kikuchi and Pfennig 2012b). This earlier study therefore suggests that sharing metabolic pathways for pigment production, and developmental pathways for tissue organization, might have facilitated the evolution of coral snake mimicry. Nonetheless, it is unclear whether the proximate similarity between these two species reflects a shared, inherited character (i.e., a symplesiomorphy) in color production systems in snakes generally or whether it represents a unique instance of convergence.

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We specifically evaluated coloration across a diverse array of snakes to determine if similar pigments occur in diverse taxa of snakes, thereby helping to explain why coral snake mimicry is so widespread. Because coral snake mimicry involves distantly related taxa (i.e., species from different families), studying mimicry within this group could provide more general insight into the mechanisms behind mimetic convergence.

Methods

We focused on a coral snake mimicry complex from the southwestern United States. The venomous Arizona coral snake, *Micruroides euryxanthus* (family Elapidae; Figure 5.1*a*) is the most basal taxon of the New World coral snakes (Pyron et al. 2011). Its potential mimics include Arizona mountain kingsnakes, *Lampropeltis pyromelana* (family Colubridae; Figure 5.1*b*) and long-nosed snakes, *Rhinochelius lecontei* (family Colubridae; Figure 5.1C). We also collected eight species found in sympatry with coral snakes that do not participate in this mimicry complex. Sampling the latter eight species allowed us to compare pigments and coloration across a wide taxonomic set. These species (and families) included: rosy boa, *Lichanura trivirgata* (Boidae); Yaqui black-headed snake, *Tantilla yaqui* (Colubridae; Figure 5.1*d*); plains black-headed snake, *Tantilla nigriceps* (Colubridae); gopher snake, *Pituophis catenifer* (Colubridae; Figure 5.1*e*); Western hognose snake, *Heterodon nasicus* (Colubridae); whip snake, *Masticophus flagellum* (Colubridae); green rat snake, *Senticolis triaspis* (Colubridae; Figure 5.1*f*); and black-tailed rattlesnake, *Crotalus molossus* (Viperadae).

Lower vertebrates (including snakes) produce colors by selectively reflecting or absorbing certain wavelengths of light with specialized cells called chromatophores

(reviewed in Cooper and Greenberg 1992). There are three principle kinds of chromatophores: erythrophores, iridophores, and melanophores. Erythrophores (sometimes called xanthophores) can contain a variety of blue, green, and ultraviolet-absorbing pigments. Pteridines and carotenoids comprise the two groups of pigments that have been found in erythrophores. Animals produce pteridines endogenously, whereas they must acquire carotenoids from their environment (McGraw et al. 2005). Iridophores contain guanine crystals that reflect certain wavelengths of light (Nielsen and Dyck 1978; Gosner 1989; Morrison 1995; Morrison et al. 1995; Kuriyama et al. 2006). Melanophores in lower vertebrates have thus far been found to contain only the black pigment eumelanin, which absorbs light evenly across the spectrum. Typically, chromatophores are arranged from the surface of the skin in the order erythrophores, iridophores, melanophores, and beneath them lies a basement membrane that is highly and evenly reflective (Cooper and Greenberg 1992). However, not all types of chromatophores have been found in all colors of tissue (e.g., Gosner 1989; Kikuchi and Pfennig 2012b).

In this study, we focused on the pigments sequestered in erythrophores. We did so because red coloration (sequestered in erythrophores) plays a key role in protecting snakes from potential predators (Smith 1975, 1977; Harper and Pfennig 2007; Kikuchi and Pfennig 2010b). Moreover, the pigment responsible for one of the other tricolors—black— is eumelanin (Kikuchi and Pfennig 2012b), which is highly conserved across animals (Ito and Wakamatsu 2003).

All snakes used in the procedures described below were collected in Cochise County, AZ. Live snakes were captured and held at the Southwestern Research Station (SWRS) in Portal, AZ until the reflectance of their colors could be measured with a

spectrophotometer. They were then released where they were captured. Snakes found dead on roads were collected and frozen immediately. Their reflectance was measured a few days later (after the snakes were thawed). Then they were moved to -80°C where they remained for several months until pigment analysis. We sacrificed a live coral snake immediately before measuring its reflectance by anesthetizing it with chloroform and severing the cervical vertebrae. It was then frozen until pigment analysis could be performed.

To identify the pigments in each snake's color patches, we took small skin samples. We washed each sample and blotted it dry on Kimwipes to remove any pigments that might be present in the blood. We then finely diced the tissue sample before placing it in a microcentrifuge tube and homogenizing it in 1 mL 1 N NH_4OH. Next, we added 0.5 mL 1:1 hexanes:tert-butyl methyl ether, vortexed the sample, and centrifuged it at 8000 RPM for five minutes. The rationale behind this extraction was to isolate polar and organic pigments in two separate phases (pteridines and carotenoids are polar and organic, respectively; Steffen and McGraw 2009). Kikuchi and Pfennig (2012b) previously identified drosopterins as the principle pigment of red skin in *M. fulvius* and *L. elapsoides*, and proposed that a pigment that absorbed strongly in the ultraviolet was isoxanthopterin. We therefore used thin-layer chromatography (TLC) of our aqueous pigment extract of the coral snake's white tissue and an isoxanthopterin standard to confirm this. For TLC, we used cellulose on glass plate as the solid phase and a 1:1 isopropanol:2% ethyl acetate mixture as the mobile phase.

We then measured the absorbance of each phase of each sample between 200 – 800 nm. Carotenoid pigments can be identified by a characteristic triplet of absorbance peaks

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(Britton 1985). The red pteridine pigments known as drosopterins have a single broad absorbance maximum between 490-500 nm, while isoxanthopterin has an absorbance maximum around 340 nm (Albert and Wood 1953). We looked for these characteristic spectral peaks to identify pigments in our sample of snakes. We scored snake color patches as having the presence or absence of carotenoids, drosopterins, and isoxanthopterin.

In studying the mechanisms behind visual mimicry (e.g., the pigments involved), it is important to relate them to the way models and mimics are perceived by relevant agents of selection (e.g., predators). Color discrimination depends on the overlap between the spectral sensitivities of cone photoreceptors in animals' eyes (Kelber et al. 2003), so human evaluation of how a pigment impinges on a snake's color is not necessarily relevant. Stronger inference can be made by modeling color perception through the eyes of relevant predators (Stoddard 2012). It is also important to verify the effects of pigments on coloration: pigment concentration can be decoupled from color (Steffen and McGraw 2009), or pigments can produce different colors in vivo than they do in vitro (Wijnen et al. 2007). For these reasons, we sought to determine the effect that snake skin pigments have on the way that they are perceived by avian predators.

We characterized the reflectance spectra of a subset of the snakes we collected (because of transportation considerations, we were unable to measure reflectance of all snakes). We used a UV-vis spectrophotometer (USB2000 with PX-2 pulsed xenon light source, Ocean Optics, Dunedin, FL, USA) to measure reflectance. Reflectance spectra were measured in a dark room with the reflectance probe positioned perpendicular to the desired patch and were measured relative to a Spectralon diffuse reflectance white

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standard (Labsphere, Inc., North Sutton, NH, USA) as used by Taylor et al. (2011). To capture the measured reflectance spectra, we used the program Spectrasuite (Ocean Optics, Dunedin, FL, USA) to collect reflectance from 300nm to 700nm. The spectra were then compiled into one nanometer bins using CLR files (Montgomerie 2008). We measured each color patch on the snakes twice and took the midpoint of these two measurements. When snakes had multiple patches of the same color, we measured up to three of them and averaged them to get a mean value of that color for the snake. Finally, for analysis, we averaged the spectra of each color for each species.

To relate a snake's pigmentation to the way that natural predators see it, we correlated the presence of drosopterins with avian cone excitation. We used the program Tetracolorspace to describe how the reflectance spectra of each color patch excite avian cones (Stoddard and Prum 2008). Tetracolorspace output includes the measures θ, ϕ, and r for all colors, which describe the position of a color in a three-dimensional space defined by the relative excitation of the four avian cone types. Of these variables, we were chiefly interested in θ, which indicates the relative stimulation of medium- and long-wavelength sensitive cones. Those cones are responsible for distinguishing between the reddish and greenish aspects of hues (those ranging from 500-700 nm), and should be most responsive to variation in drosopterins. We used the blue tit to represent avian vision, as its visual system is a well-established model, and medium- and long-wavelength photoreceptors vary little across the avian phylogeny in their peak sensitivity (Hart et al. 2000; Hart 2001; Hart and Vorobyev 2005). We built a simple regression model to test the prediction that the presence of drosopterins causes the ratio of medium:long cone stimulation to decrease (meaning that heuristically, colors look

"redder") by coding θ as a dependent variable and the presence or absence of drosopterins as an independent predictor.

Results and Discussion

We found no evidence of carotenoid pigments in any of the color patches that we sampled. In contrast, pteridine pigments were widespread – snake tissue that appeared reddish contained drosopterins, and almost all contained isoxanthopterin, which strongly absorbs ultraviolet and whose identity was confirmed in our TLC test (Table 5.1). Only the ventrum of both *Tantilla* and the gray neck of *M. bilineatus* lacked isoxanthopterin.

Among the sample of snakes that we had both reflectance spectra and pigment data for, we found that the presence of red pigment was strongly correlated with the relative excitation of avian medium- and long-wavelength cones (df = 12, r^2 = 0.65, P = 0.0004; Figure 5.2). This demonstrates the dependence of coloration on the shared pigments of snakes, rather than other physiological processes that produce convergent coloration.

Our results, together with those of an earlier study (Kikuchi and Pfennig 2012b), reveal that coral snakes and their putative mimics share a pigment production system that is widely distributed among snakes. Furthermore, we have shown that the shared red drosopterin pigments in snakes predict how their skin color appears to birds, which are key predators of snakes and therefore likely agents of selection on their coloration. Although this study represents a first step in deciphering the proximate mechanisms by which snakes produce coloration, it supports the hypothesis that mimetic convergence can be facilitated by conserved developmental systems.

Explanations for why certain taxa are mimetic often refer to body plan or ecology (Ruxton et al. 2004). However, our results also underscore the importance of other factors in deciding which taxa evolve mimicry. In particular, shared developmental systems may predispose certain taxa to mimicry. Yet although many snakes might be capable of producing tricolor pigments, not all do. Coral snake mimics tend to be slender, fossorial, nocturnal, and (most importantly) syntopic with coral snakes. Thus, shared developmental systems may predispose many species of snakes to evolve coral snake mimicry, but the above additional factors may be critical for predicting its precise occurrence. Indeed, phylogenetic analyses suggest that body size and diet type are important for explaining mimicry in the colubrid tribe Lampropeltini (Pyron and Burbrink 2009). A broader and more extensive taxonomic study could shed more light on the factors that select for snake mimicry in general, and coral snake mimicry in particular.

Drosopterins produce an effect that is not only visible to humans, but also to relevant predators (i.e., birds). Therefore, their expression is likely under predator-mediated selection. Very strong selective forces are often detected in field studies of coral snake mimicry (e.g. Brodie 1993; Pfennig et al. 2001; Wüster et al. 2004; Kikuchi and Pfennig 2010a; Valkonen et al. 2011), and (as noted earlier) red coloration has been shown to play an important role in predators' response to aposematic signals on snakes (Smith 1975, 1977; Harper and Pfennig 2007; Kikuchi and Pfennig 2010b). It appears that potential coral snake mimics have the ability to produce a vital component of the mimetic phenotype in common with their models, which might help explain why so many serpents participate in mimicry.

Mimicry complexes that do not rely on *visual* mimicry have been valuable for understanding signal convergence at the proximate level. For example, Vereeken and Schiestl (2008) have shown that deceptive orchids (i.e., species that do not provide nectar rewards to pollinators) mimic pheromone compounds that their bee pollinators prefer. The metabolic pathways that underlie the production of alkenes are not homologous between orchids and bees (Schlüter et al. 2011). Thus, although some taxa may be predisposed to evolving mimicry, convergence without homology between models and mimics can occur. Convergent coloration that does not result in mimicry has been extensively studied in phenotypes that rely on the relatively well-understood melanin pigments (e.g., Rosenblum 2005; Hoekstra 2006). However, complex mimetic patterns often depend on the regulation of pteridine and carotenoid pigmentation, which is less well understood. Application of approaches used in the study of melanin adaptations might be helpful in elucidating mechanisms of convergent coloration in general, but will require a more comprehensive understanding of how other pigments are incorporated into color patterns. Butterflies use both carotenoid and pteridine pigments (Ford 1953), and so genes involved in the formation of their color patterns may also be applicable to other systems. Even if they are not, ongoing work in vertebrate systems may illuminate the developmental processes responsible for pteridine coloration in vertebrates (Ziegler 2003; Protas and Patel 2008). Either of these eventualities may greatly augment our ability to study these unique adaptations.

Our results show that the presence of pteridine pigments influences skin coloration in snakes. This is important to verify because the complexity of chromatophores makes it difficult to predict the influence of pigments on the spectrum of light reflected from a

patch of skin. Studies attempting to relate pigment concentrations to coloration have produced mixed results. For example, in *Anolis*, the concentration of xanthophyll is only weakly correlated with measures of dewlap color (Steffen and McGraw 2009). Variation in the concentrations of carotenoid pigments also failed to explain color variation in the lizard *Lacerta vivipara*, where changes in iridophore configuration likely govern changes in coloration (San-Jose et al. 2013). Pteridine concentrations are more correlated with measures of color in *Anolis* (Steffen and McGraw 2009).

Nonetheless, straightforward relationships between pigment concentration and reflectance are enigmatic. The Beer-Lambert law implies that the shape of reflectance spectra will change nonlinearly with pigment concentration and the path length of light through the tissue (Wijnen et al. 2007). Therefore, the reflectance spectrum of a tissue will depend on a pigment's concentration in erythrophores, the density and dispersion of erythrophores in the tissue, and the arrangements of other types of chromatophores that direct light through the erythrophores. Furthermore, in vivo pigment absorption spectra may differ from those measured in vitro. Thus, directly relating pigment concentrations to reflectance spectra is challenging. In contrast to concentration, the presence or absence of pigments is often strongly related to tissue color in lower vertebrates (e.g., Morrison et al. 1995, Macedonia et al. 2000, Kuriyama et al. 2006, this study). Such an approach may be more expedient for analyzing the role of pigmentation in affecting coloration when precise histological and cytological data are not available.

Table 5.1. Snakes pigments by tissue type: pigment presence and absence among a taxonomically diverse assemblage of snakes from the western United States. The absence of a pigment is denoted by ∅ and its presence by + for each type of skin tissue that we sampled. Tissues marked in **bold** are included in our reflectance spectra sampling. Abbreviations: car = carotenoids, dros = drosopterins, isox = isoxanthopterin.

Species	Tissue	Pigment presence and absence		
		car	dros	isox
Micruroides euryxanthus	**red dorsum**	∅	+	+
	white dorsum	∅	∅	+
Tantilla nigriceps	**dorsum**	∅	∅	+
	ventrum	∅	+	∅
Tantilla yaqui	dorsum	∅	∅	+
	ventrum	∅	∅	∅
Rhinocheilus lecontei	**red dorsum**	∅	+	+
	white dorsum	∅	∅	+
Lichanura trivirgata	red dorsum	∅	+	+
	white dorsum	∅	∅	+
Heterodon nasicus	brown dorsum	∅	∅	+
Masticophus bilineatus	**gray dorsum**	∅	∅	∅
	reddish dorsum	∅	∅	+
	light stripe	∅	∅	+
Gonyosoma oxycephalum	**light dorsum**	∅	∅	+
	dark dorsum	∅	∅	+

Crotalus molossus	light dorsum	∅	∅	+
	dark dorsum	∅	∅	+
Lampropeltis pyromelana	**red dorsum**	∅	+	+
	white dorsum	∅	∅	+
Pituophis catenifer	**light dorsum**	∅	+	+
	dark dorsum	∅	+	+

Figure Legends

Figure 5.1. Representative taxa sampled for pigment analysis. (*a*) Arizona coral snake, *Micruroides euryxanthus*. (*b*) Arizona mountain kingsnake, *Lampropeltis.* (*c*) Long-nosed snake, *Rhinochelius lecontei*. (*d*) Yaqui black-headed snake, *Tantilla yaqui*. (*e*) Gopher snake, *Pituophis catenifer*. (*f*) Green rat snake, *Senticolis triaspis*.

Figure 5.2. The effect of the presence or absence of red drosopterin pigments on how birds perceive snake color. Theta describes the relative excitation of medium- and long-wavelength sensitive cones in the avian eye. More negative theta values indicate a higher relative excitement of long-wavelength cones. From the human perspective, this is analogous to red:green color vision, although humans are most sensitive at different wavelengths than are birds.

Figure 5.1
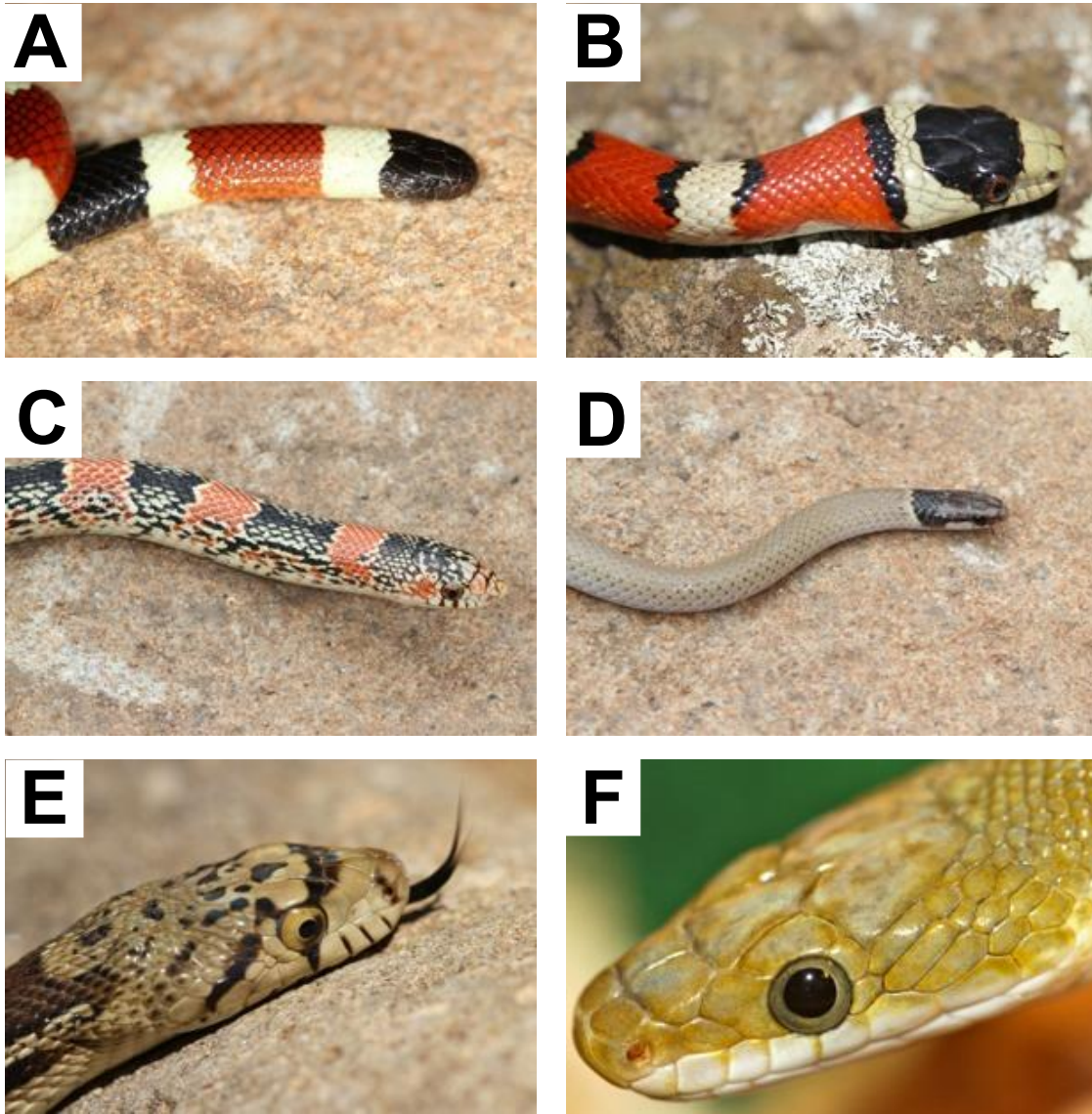
Figure 5.2
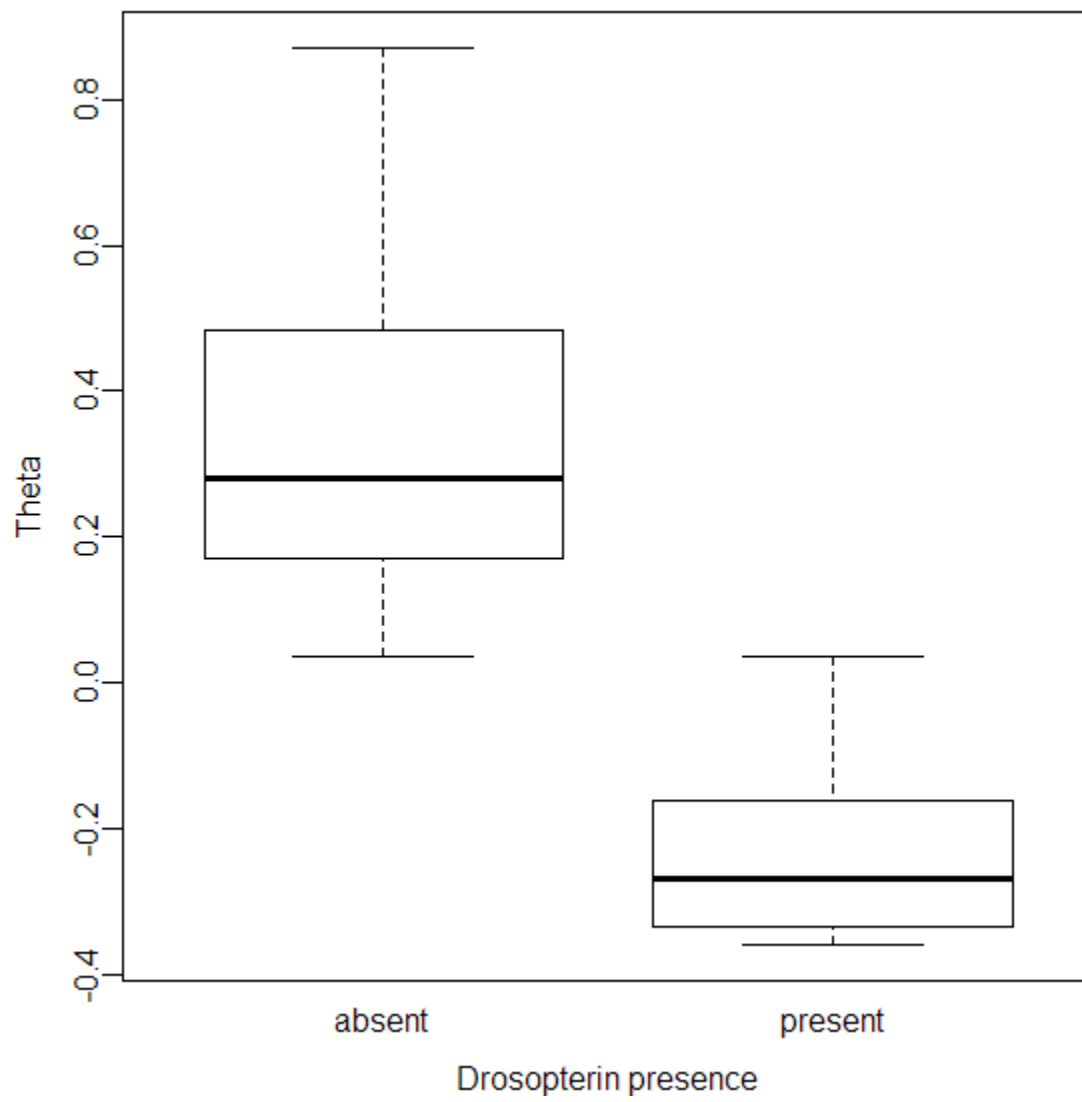
CHAPTER VI

HIGH MODEL ABUNDANCE MAY PERMIT THE GRADUAL EVOLUTION OF BATESIAN MIMICRY: AN EXPERIMENTAL TEST[4]

Summary

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 abundance. 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

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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.

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., see Nicholson 1927; Charlesworth and 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 and Charlesworth 1975; Mappes and Alatalo 1997; but see Fisher 1958; Schmidt 1958; Schmidt 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 presumedly low fitness, some have suggested a two-step evolutionary model in lieu of the gradual process of incremental evolution (Nicholson 1927; Charlesworth and 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: (1) high model toxicity (Duncan and Sheppard 1965; Pilecki and O'Donald 1971; Goodale and Sneddon 1977; Lindström et al. 1997), and (2) high model abundance (Brower 1960; Lindström et al. 1997; Harper and 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 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 and McDiarmid 1981; Pfennig et al. 2001; Brodie and Brodie 2004; Harper and Pfennig 2007; Harper and Pfennig 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.

Methods

Study System

In the southeastern United States, the highly venomous eastern coral snake (Elapidae:

Micrurus fulvius) is the model for a nonvenomous 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; Smith 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 and Pfennig 2007). *Lampropeltis elapsoides* is avoided by predators

in sympatry with coral snakes, but not in allopatry (Pfennig et al. 2001), confirming that

they are indeed Batesian mimics of *M. fulvius*. Also, *M. fulvius* is relatively more

abundant than *L. elapsoides* in Florida than it is in southern North Carolina (Harper and

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 and Pfennig 2007). In Florida *L. elapsoides* are 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 and 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.

Ancestral character state reconstruction of colour pattern

To test whether the mimic, *L. elapsoides*, likely evolved from a cryptic ancestor (as assumed; see Introduction), 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 and 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 and 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); 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 likely 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 (Madison and Madison 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.

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 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 (e.g., 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., see Madsen 1987; Brodie 1993; Brodie and Janzen 1995; Hinman et al. 1997; Pfennig et al. 2001; Wüster et al. 2004; Niskanen and Mappes 2005; Buasso et al. 2006; Harper and Pfennig 2007; Pfennig et al. 2007), indicating that it is robust to different predator guilds and environments. We constructed our replicas with pre-coloured, nontoxic 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, unpubl. data) of museum specimens of eastern milksnakes (*Lampropeltis triangulum triangulum*; $n = 16$) and published data on *L. elapsoides* (Harper and Pfennig 2007). We included twelve dimensions to describe colour pattern. Phylogenetic analyses show that *L. t. triangulum* is an appropriate representative of a cryptic ancestral phenotype (see Results). To create a 50% intermediate phenotype, we used the average value of the cryptic and mimetic phenotype for each dimension of colour pattern measured. Our intermediate phenotype resembled *L. t. syspila* and *L. t. temporalis*, indicating that it was within the natural range of variation in this genus (compare figure 6.1*c* to figure 6.1*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

microhabitats. Members of each triad were placed in realistic microhabitats such as the edges of logs and grass clumps (Figure 6.1). 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 analyzing 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 and 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), since 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 6.1). 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 analyzed 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) 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.

Results

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 6.2). 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 6.1*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 *Pseudelaphe flavirufa* and *Pantherophis guttatus*, both of which were difficult to classify due 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 crypsis. 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.

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%) due to loss, fire, or human interference. Out 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 6.3*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 6.3*b*; $n = 359$, $Z = 1.95$, $P = 0.05$).

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

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single clade of Lampropeltini from cryptic ancestors. Moreover, our field experiment confirmed our prediction (see Introduction to Ch. VI) 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 likely 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 the Introduction to Chapter VI, 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 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. 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 and 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 United States conforms to the theoretical expectations of a Batesian mimicry system. Previous research established the 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 and 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 and 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 theoretic 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 (see also 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 plays 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

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inaccurate representation of conditions present when mimicry first originated. We do not believe 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 larva (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 and Hesse 1985; Nelson and 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.

Figure Legends

Figure 6.1. 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, *Lampropeltis triangulum triangulum* (photo by Roger W. Barbour); (*c*) intermediate phenotype, which resembled (*d*) the coastal plains milksnake, *Lampropeltis t. temporalis* (photo by Richard D. Bartlett); (*e*) mimetic phenotype, which resembled (*f*) the scarlet kingsnake, *L. elapsoides* (inset: the eastern coral snake, *Micrurus fulvius*, which *L. elapsoides* mimics; photos by Wayne Van Devender).

Figure 6.2. Ancestral character state reconstruction of color 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 outgoups. Black = mimetic (color pattern score > 1.33); gray = intermediate (1.33 ≥ color pattern score ≥ 0.66); white = cryptic (color pattern score < 0.66).

Figure 6.3. 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.) vs. 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.

Figure 6.1

Figure 6.2

Coronella austriaca
Pituophis deppei
Pituophis lineaticollis
Pituophis melanoleucus
Pituophis ruthveni
Pituophis catenifer
Pituophis vertebralis
Pantherophis vulpinus
Pantherophis guttatus
Pantherophis slowinskii
Pantherophis emoryi
Pantherophis spiloides
Pantherophis alleghaniensis
Pantherophis bairdi
Pantherophis obsoletus
Arizona elegans
Rhinocheilus lecontei
Cemophora coccinea
Lampropeltis calligaster
Lampropeltis elapsoides
Lampropeltis mexicana
Lampropeltis ruthveni
Lampropeltis pyromelana
Lampropeltis zonata
Lampropeltis triangulum
Stilosoma extenuatum
Lampropeltis getula
Lampropeltis alterna
Pseudelaphe flavirufa
Bogertophis subocularis
Bogertophis rosaliae
Senticolis triaspis
Rhinechis scalaris
Elaphe carinata
Gonyosoma oxycephalum

Figure 6.3

CHAPTER VII

IMPERFECT MIMICRY AND THE LIMITS OF NATURAL SELECTION[5]

Summary

Mimicry—when one organism (the mimic) evolves a phenotypic resemblance to another (the model) due to selective benefits—is widely used to illustrate natural selection's power to generate adaptations. However, many putative mimics resemble their models imprecisely, and such imperfect mimicry represents a specific challenge to mimicry theory and a general one to evolutionary theory. Here, we discuss 11 nonmutually exclusive hypotheses for imperfect mimicry. We group these hypotheses according to whether imperfect mimicry reflects: an artifact of human perception, which is not shared by any naturally occurring predators and therefore is not truly an instance of imperfect mimicry; genetic, developmental, or time-lag constraints, which (temporarily) prevent a response to selection for perfect mimicry; relaxed selection, where imperfect mimicry is as adaptive as perfect mimicry; or tradeoffs, where imperfect mimicry is (locally) more adaptive than perfect mimicry. We find that the relaxed selection hypothesis has garnered the most support. However, because only a few study systems have thus far been comprehensively evaluated, the relative contributions of the various hypotheses toward

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[5] This chapter is based on Kikuchi, D. W., and D. W. Pfennig. in press. Imperfect mimicry and the limits of natural selection. Quarterly Review of Biology.

explaining the evolution of imperfect mimicry remain unclear. Ultimately, clarifying why imperfect mimicry exists should provide critical insights into the limits of natural selection in producing complex adaptations.

Introduction

Natural selection's power to produce remarkable adaptations is beautifully exemplified by mimicry, which occurs when one organism (the mimic) converges on phenotypic features of another (the model) because of the selective benefits of sharing such a resemblance (see reviews in Wickler 1968; Edmunds 1974; Endler 1981; Waldbauer 1988; Malcolm 1990; Mallet and Joron 1999; Ruxton et al. 2004; Forbes 2009; Kikuchi and Pfennig 2012a; Grim 2013). It has long been assumed that mimics should always experience selection to resemble their models closely (Ruxton et al. 2004), yet it has become increasingly clear that many resemble their models less precisely than biologists have expected them to (Sherratt 2002; Gilbert 2005). For instance, many species of harmless Neotropical snakes resemble highly venomous coral snakes (Brodie and Brodie 2004). Although some species are amazingly similar to coral snakes (Greene and McDiarmid 2005), most species have only a coarse resemblance (Savage and Slowinski 1992). The existence of such imperfect mimicry poses a central challenge to traditional theory (Edmunds 2000; Sherratt 2002; Ruxton et al. 2004:159–161).

Although numerous hypotheses have been put forth to explain imperfect mimicry (Penney et al. 2012; Pfennig and Kikuchi 2012), the relationships among these hypotheses, and their mutually exclusive predictions, have not been explored comprehensively. Moreover, most of these hypotheses have been tested unevenly, with

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some having been tested rigorously and others having received little, if any, empirical attention (Penney et al. 2012; Pfennig and Kikuchi 2012). In this review, we seek to classify and clarify the various hypotheses that have been advanced for imprecise mimicry's persistence. We also describe the empirical evidence in support of the various hypotheses to point out the ones that appear to have broad relevance and those that require more investigation. Finally, we provide a roadmap for future research into the evolution of imperfect mimicry.

We have defined "mimicry" as occurring when one organism converges on phenotypic features of another because of the selective benefits of sharing a resemblance, although in many cases commonly assumed to be mimicry, selective benefits have not been directly tested. This definition implies that the evolved resemblance must involve signals. Signals can be thought of as an "act or structure that alters the behaviour of another organism, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (Maynard-Smith and Harper 2003:15; see also Bradbury and Vehrencamp 2011). Signals are the basis of both mimicry and "aposematism" (when a dangerous species evolves a phenotype that accurately warns others of the danger). Mimicry occurs when a signal borne by one organism (the model) to communicate some quality to others (the receivers), is copied by another organism (the mimic) to convey the same message to the same receivers, whether it is honest or not. This relationship may involve three or more species (e.g., multiple prey species and their predators), two species (as is sometimes the case in aggressive mimicry), or even take place within a single species (as occurs in reproductive mimicry). Signals may travel via

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any media, including visual, auditory, and chemical; they may also be multimodal and include more than one of those senses.

The two best-known forms of mimicry are: "Batesian mimicry" (Bates 1862), which occurs when an edible species (the mimic) evolves to resemble a conspicuous, inedible species (the model), thereby gaining protection from predation; and "Müllerian mimicry" (Müller 1879), which occurs when multiple defended species (co-mimics) converge on the same warning signal, thereby sharing the cost of educating predators about their unpalatability. Although there are other types of mimicry, such as aggressive mimicry and reproductive mimicry (where mimicry evolves in response to sexual selection; Vane-Wright 1976; Endler 1981; Kikuchi and Pfennig 2012a), we will not dwell on specific types of mimicry except when a particular hypothesis requires that we do so.

With this background in mind, we now turn to hypotheses that have been advanced to explain the evolution of imperfect mimicry.

Hypotheses for Imperfect Mimicry's Existence and Persistence

Many explanations have been proposed to explain imperfect mimicry, some more plausible than others (Ruxton et al. 2004). In this section, we discuss 11 nonmutually exclusive hypotheses. As summarized in Table 7.1, each hypothesis can be grouped into one of four categories, depending upon whether the hypothesis posits that putative cases of imperfect mimicry reflect: an artifact of human perception that does not pertain to mimicry; genetic or developmental constraints, which prevent a response to selection for better mimicry; relaxed selection, where imperfect mimicry is as adaptive as perfect mimicry; or tradeoffs, where imperfect mimicry is locally more adaptive than perfect

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mimicry (for general models of how tradeoff costs can lead to imperfect mimicry, see

Servedio and Lande 2003; Holen and Johnstone 2004). Below, we describe each

hypothesis in detail. In Table 7.2, we provide a brief summary of the hypotheses.

Eye-of-the-Beholder Hypothesis

This hypothesis suggests that some cases of imperfect mimicry are not mimicry at all

(Cuthill and Bennett 1993; Dittrich et al. 1993). Instead, human perception detects

imperfections that natural signal receivers cannot. Therefore, "imperfect" mimicry does

not represent a challenge to natural selection because the "imperfections" are not relevant

for the intended signal receivers. Real organisms have an almost limitless number of

phenotypic dimensions into which they can be decomposed, so it is unsurprising that

some cases of imperfect mimicry might be attributable to differences between the

dimensions of organisms that humans notice versus the ones their ecologically relevant

signal receivers pay attention to.

Developmental and Genetic Constraints Hypothesis

Rather than being an artifact of human perception, as in the eye-of-the-beholder

hypothesis above, imperfect mimicry may reflect a constraint on signal production, which

(at least temporarily) prevents a response to selection for better mimicry. For example, a

population of imprecise mimics may lack the genetic variation needed to evolve a closer

match to the model (in the case of Batesian mimicry) or co-mimics (in the case of

Müllerian mimicry). It is important to point out that most constraints can likely be

overcome, given enough time and sufficiently strong selection (Maynard Smith et al.

1985). For this reason, constraints probably do not offer a universal explanation for imprecise mimicry.

Chase-Away Hypothesis

This hypothesis, like the constraints hypothesis above, assumes that imperfect Batesian mimicry reflects an inability to (at least temporarily) respond to selection for perfect mimicry. According to this hypothesis, imperfect Batesian mimics could evolve to become better mimics, but their models are also under selection to evolve away from them to avoid the fitness cost of having a "parasitic" mimic. As a result of such "chase-away" selection, mimics lag behind models in phenotypic evolution because models evolve away from mimics as soon as they are approached too closely in signal space. Essentially, when we observe instances of imperfect mimicry, we see the outcome of an evolutionary arms race between mimic and model, which the model has won (as least temporarily). In these cases, time lags (between when the model moves away from the mimic in phenotypic space and when the mimic can evolve the new phenotype of the model) lead to imperfect mimicry.

Chase-away is predicted to occur by many theoretical models (e.g., Oaten et al. 1975; Holland and Rice 1998; Holmgren and Enqvist 1999; Franks and Noble 2004; Franks et al. 2009). However, mimics should generally experience stronger selection to match their models than models do to evolve away from their mimics. This is because changes in a mimic's phenotype that make it more like its model will often provide a selective advantage (Ruxton et al. 2004). Models, on the other hand, will generally receive less benefit from changing their phenotype because rare mutants from the model population

would be poorly protected and therefore risk increased predation (Nur 1970).

Consequently, even in the presence of chase-away selection, models may generally not

evolve to escape their mimics.

Relaxed Selection Hypothesis

The relaxed selection hypothesis assumes that imperfect mimicry reflects a lack of

selection, where some imperfect mimics have fitness equal to that of the model because

predators do not discriminate between the two. This hypothesis is predicated on the

notion that, when models and mimics share signal dimensions, it is impossible for signal

receivers to discriminate them perfectly. This occurs because the strength of selection for

better resemblance is relaxed as the mimic evolves toward the model's phenotype

(Duncan and Sheppard 1965; Sherratt 2001, 2002). Signal receivers must balance

correctly accepting mimics against mistakenly accepting models, a situation analogous to

managing Type I and II error in statistics. There may be actual phenotypic overlap

between models and mimics, or noise in the signal receiver's senses.

To explain this phenomenon, many mathematical models of selection in mimicry

have used signal detection theory (e.g., Oaten et al. 1975; Getty 1985; Sherratt 2001,

2002), which is designed to optimize correct responses to signals and minimize errors.

Results show that receivers should select a phenotypic threshold that guarantees them a

positive average payoff if they accept all signalers that fall on one side of that threshold

(Figure 7.1). The position of the threshold depends on the costs of accepting a model, the

benefits of accepting a mimic, and the relative abundance of the two (as well as alternate,

nonmimetic signalers; Dill 1975; Sherratt and Beatty 2003; Lindström et al. 2004). When

models are very aversive/abundant, mimics are relatively unrewarding/rare, or—

sometimes—when models and mimics appear to overlap more in phenotype, a smaller

percentage of the mimic population is attacked, and therefore selection for mimicry is

weaker. The result is that there is often a wide range of phenotypes near the phenotype of

the model that have nearly equal fitness (Figure 7.2).

The relaxed selection hypothesis yields clear predictions based on the strength of

selection as mimics approach models in phenotypic space and as the cost:benefit ratio of

attacking models and mimics changes. The strength of selection for better mimicry

decreases as the mimic approaches the model in phenotype; mimetic precision decreases

with model abundance and costliness (such as toxicity, aggression, or handling time), and

nonaversive alternative signalers; and it increases with the mimic's relative abundance

and benefits (for example, caloric reward).

Mimetic Breakdown Hypothesis

In the remaining seven hypotheses, imperfect mimicry is assumed to arise from some sort

of tradeoff, where imperfect mimicry is (locally) more adaptive than perfect mimicry.

Under the first of these hypotheses—the mimetic breakdown hypothesis—imprecise

mimicry reflects an evolutionary compromise between gene flow on the one hand and

selection on the other.

Indeed, a classic explanation for a mismatch between mimics and their models is that

mimicry no longer serves any benefit and, consequently, precise mimicry has been

degraded by natural selection (Brower 1960). Such mimetic breakdown should happen

when mimics occur in areas where their model is rare or absent. Batesian mimicry theory

generally predicts that mimics should occur only in areas where their model occurs (i.e., sympatry; Ruxton et al. 2004). This is because protection from predation should break down where the model is absent. Many mimics violate this prediction and also occur in areas where their model is absent (i.e., allopatry; Pfennig and Mullen 2010).

Mimics that occur in both sympatry and allopatry with their model should experience strong divergent selection. On the one hand, selection should always favor the maintenance, and even enhancement, of the mimetic phenotype in sympatry. On the other hand, selection should favor the breakdown of this phenotype in allopatry, because mimics (like their models) are often conspicuous (Ruxton et al. 2004). Allopatric mimics should generally experience increased predation pressure relative to less noticeable types. If such selection is strong, then allopatric mimics should evolve less conspicuous (nonmimetic) phenotypes. Thus, imprecise mimics may be in the process of evolving nonmimetic phenotypes, have imperfect mimetic phenotypes that are to some degree maintained by gene flow (Harper and Pfennig 2008), or retain their mimetic coloration for an alternative reason such as flicker-fusion coloration (Pough 1976) or sexual selection. Under this hypothesis, an imperfect mimic would have higher fitness than a perfect mimic in the allopatric environment. We should note, however, that some populations of allopatric mimics may be under selection by predators migrating from sympatry, and that under those circumstances this hypothesis would not be expected to apply.

Perceptual Exploitation Hypothesis

Under this hypothesis, mimics exploit an innate perceptual bias in signal receivers that is shifted away from the model's signal. Such "sensory drive" hypotheses are often invoked to explain the evolution of sexual signals (e.g., Basolo 1990; Ryan et al. 1990), but seldom to explain imperfect mimicry. This is because ecological conditions that select for receivers that respond most strongly to something other than the model's signal may be rare (given some cost of producing and bearing signals, models are expected to evolve signals that elicit the strongest possible response from the receiver).

Satyric Mimicry Hypothesis

The satyric mimicry hypothesis proposes that, while some mimics may be good enough that they cannot be distinguished from the model, others benefit from expressing components of aposematic signals in inappropriate contexts (e.g., a wasp's stripes on a fly's body). In doing so, these individuals confuse predators long enough to allow the individual to escape (Howse and Allen 1994). Howse and Allen (1994:113) further elaborated their theory to predict, "opposing features will tend to be favoured by natural selection so that a high degree of ambiguity is achieved." Thus, imperfect mimics with a mixture of traits from the model and alternative prey should have higher fitness than imperfect mimics that resemble the model more, but are still distinguishable.

Multiple Models Hypothesis

Edmunds (2000) hypothesized that, in mimics that occur over a wide geographical area that contain multiple models, selection will favor those individuals that imprecisely

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resemble many different species of models over those individuals that precisely resemble only one species of model. In such circumstances, Edmunds (2000) showed that generalist mimics have higher population sizes than specialist mimics of single models. Sherratt (2002) reexamined this hypothesis in a mathematical framework where he assumed that model and mimic phenotypes vary continuously and that predators use signal detection theory to set optimal thresholds for attacking prey. He found that when multiple sympatric models exist, mimics evolve to mimic one of them or adopt an intermediate phenotype. Which result occurs depends on whether or not models are similar enough to confuse predators. When models are allopatric from one another, mimics evolve intermediate phenotypes, although their intermediate phenotype should be weighted toward the less defended or numerous model.

Multiple Predators Hypothesis

Pekár et al. (2011) proposed that Batesian mimics may be exposed to some predators that respond to mimicry according to Bates' original theory (1862), but that they may, as a consequence, suffer increased predation by specialist predators of their models (Pekár et al. 2011). Therefore, the optimal mimetic phenotype represents a compromise between duping generalist predators and being able to escape from specialist ones.

Kin Selection Hypothesis

According to this hypothesis, Batesian mimics pay an inclusive fitness cost of improving mimicry, because doing so increases overall attacks on a population that includes close kin (Johnstone 2002). When models are sufficiently rare and/or weakly aversive,

predators should always attack prey that perfectly resemble them, because the odds of

encountering a beneficial mimic make such behavior worthwhile (Oaten et al. 1975).

With such a weak and outnumbered model, the population of mimics will actually benefit

from lower attack rates when it is, on average, imperfect. This is because predators will

focus their attacks on the most imprecise mimics in the population rather than the whole

population, so at least the better mimics in the population will benefit from mimicry. The

better mimics will experience individual (direct) selection for improved mimicry, but if

the population is related enough, the negative indirect effects of increased predation on

the whole population may cancel out direct fitness benefits, leading to a stable

equilibrium of imperfect mimicry (Johnstone 2002).

Character Displacement Hypothesis

According to this hypothesis, imprecise mimicry represents an evolutionary compromise

between *predator-mediated selection* favoring phenotypic convergence (i.e., precise

mimicry) on the one hand and *competitively mediated selection* favoring phenotypic

divergence (i.e., imprecise mimicry) on the other (Pfennig and Kikuchi 2012). In other

words, imprecise mimicry is a manifestation of "character displacement"—trait evolution

that arises as an adaptive response to resource competition or deleterious reproductive

interactions between species (*sensu* Brown and Wilson 1956; see also Grant 1972;

Schluter 2000; Dayan and Simberloff 2005; Grether et al. 2009; Pfennig and Pfennig

2009, 2012).

To understand how this hypothesis works, consider that for mimicry to be an effective

deterrent to predation, mimics and their models (in the case of Batesian mimicry) or co-

mimics (in the case of Müllerian mimicry) should not only be phenotypically similar to each other, but they should also occur together in the same location and at the same time (Beatty and Franks 2012). Yet co-occurring, phenotypically similar species often compete with each other for resources, successful reproduction, or both (here, "competition" refers to any direct or indirect interaction between species or populations that reduces access to vital resources or successful reproductive opportunities and that is therefore deleterious—on average—to both parties; see Pfennig and Pfennig 2012). As an adaptive response to minimize such costly interactions, competitively mediated selection favors individuals that differ from their heterospecific competitors (reviewed in Schluter 2000; Dayan and Simberloff 2005; Pfennig and Pfennig 2009, 2012). Consequently, interacting species diverge phenotypically through the process known as character displacement. Such divergence between mimics and their models/co-mimics thereby results in imperfect mimicry (Pfennig and Kikuchi 2012).

Imprecise mimicry may arise through either reproductive or ecological character displacement. Reproductive character displacement may generate imperfect mimicry if signals aimed at potential predators also target prospective mates (Estrada and Jiggins 2008). Such shared signals may increase the risk that mimics and their models/co-mimics will engage in costly hybridization with each other or interfere with each other's ability to identify high-quality mates. In such situations, selection may favor reproductive character displacement as a means of reducing costly reproductive interactions between mimics and their models/co-mimics.

Ecological character displacement may generate imprecise mimicry if aposematic/mimetic signals aimed at potential predators are in some way

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environmentally dependent, such that their production requires some limited resource (e.g., a food item or a particular habitat). In such cases, if mimics compete with their models/co-mimics for this resource, then ecological character displacement leads to a change in diet. Consequently, the production of mimetic phenotypes may be affected also, possibly even leading to the evolution of imprecise mimicry.

Finally, competition for space may also promote imprecise mimicry through relaxed selection for precise mimicry. For instance, if mimics and their models/co-mimics compete for a particular microhabitat, ecological character displacement may promote a habitat shift. If the mimetic species is forced into a microhabitat not occupied by its model, then selection for precise mimicry may be relaxed, leading instead to imprecise mimicry (recall from above that for mimicry to be an effective deterrent to predation, mimics and their models/co-mimics should occur together).

Regardless of whether reproductive or ecological character displacement is responsible, this hypothesis generally predicts that imprecise mimicry should evolve whenever predator-mediated selection is weak relative to competitively mediated selection (Pfennig and Kikuchi 2012).

Empirical Hypothesis Support

Eye-of-the-Beholder Hypothesis

One of the first studies to explicitly address the "eye-of-the-beholder" hypothesis was that of Dittrich et al. (1993), who trained pigeons to avoid images of wasps but to attack their hoverfly mimics. They used a morphometric approach to describe objective similarity between hoverflies and their models, and found that pigeon attack rates

declined sigmoidally with resemblance to the wasps so that even a 50% objective match to the model conferred the full benefit of mimicry. The authors concluded that apparently poor mimics to human eyes might be quite good from the perspective of other animals. Cuthill and Bennett (1993) suggested that the mechanistic explanation for the sigmoid curve might be that the images used were optimized for human rather than avian vision, so birds could not use all of the information that would normally be available to them.

This hypothesis may not, in fact, be sufficient to explain imperfect mimicry in the wasp-hoverfly system in which it was first suggested. Penney et al. (2012) found that humans rank the similarity between wasps and hoverflies more like pigeons than an objective morphometric analysis. Indeed, pigeons used only some of the potentially informative traits on the hoverflies to discriminate them from wasps (Bain et al. 2007). Thus, in this instance, imperfect mimicry is probably not entirely the result of a discrepancy between what humans intuit a good mimic should look like and what is required to fool a predator.

Another example of how human perspective can explain an apparent case of imperfect mimicry can be found among coral snakes and their mimics, scarlet kingsnakes. In the southeastern United States, venomous coral snakes have red, yellow, and black rings arranged in the order Y-R-Y-B. Nonvenomous scarlet kingsnakes have the same three colors arranged into rings with a different order: Y-B-R-B. The relative proportions of red:black are under strong selection (Harper and Pfennig 2007), as is the general ringed appearance (Pfennig et al. 2001), but the order of the colored rings is probably not (Kikuchi and Pfennig 2010a). It seems likely that while colored rings with a certain proportion of red:black constitute a warning signal, the order in which the rings

develop is an arbitrary byproduct of their evolution. This case of imperfect mimicry can indeed be attributed to humans projecting their own perception onto a system, which emphasizes the importance of correctly identifying a model's actual signal.

Developmental and Genetic Constraints Hypothesis

Presently, few studies have thus far examined the proximate bases of mimetic phenotypes, so it is unclear to what degree imperfect mimicry reflects an underlying constraint on signal production. Of those studies that have looked into proximate mechanisms, models and mimics appear to use at least some of the same genes and/or physiological pathways to produce shared signals (Ford 1953; Joron et al. 2011; Heliconius Genome Consortium 2012; Kikuchi and Pfennig 2012b; Martin et al. 2012). An exception to this trend are certain unrewarding orchids, which attract male bees to pollinate them by mimicking the exact chemical compounds exuded by female bees (Vereeken and Schiestl 2008). In this case, the orchids produce their pheromones by using enzymes that are unrelated to those found in their pollinators (Schlüter et al. 2011). Generally, species that share the same proximate mechanisms used to produce aposematic signals may be more prone to evolve precise mimicry. Yet, as the orchid example above illustrates, sharing similar proximate mechanisms is not a necessity for precise mimicry.

Chase-Away Hypothesis

An empirical study with human subjects selecting between two species of computer-generated prey was able to produce chase-away, but the difference between models and

mimics was quite small relative to the range of potential phenotypic difference (McGuire et al. 2006). We are unaware of any study that adequately demonstrates a model evolving away from its mimic in nature, or resultant imperfect mimicry.

Relaxed Selection Hypothesis

All of the predictions of this hypothesis have been confirmed in empirical systems. Many studies have documented selective surfaces that correspond to those outlined in Figure 7.2: animals or humans trained to respond to artificial prey (or flowers, in the case of plants) reduce attack rates nonlinearly as mimics approach models in phenotype (Schmidt 1958; Duncan and Sheppard 1965; Ford 1971; Caley and Schluter 2003; Lynn et al. 2005; McGuire et al. 2006). Furthermore, changing the relative abundance of models and mimics alters the amount of phenotypic space in which imperfect mimics receive protection: the precision of coral snake mimicry by scarlet kingsnakes (and selection for better mimicry) increases across the kingsnake's range as the abundance of coral snakes decreases (Harper and Pfennig 2007; Kikuchi and Pfennig 2010b), and the mimetic precision of andromorphs (male-mimicking females) increases with the proportion of andromorphs:males in damselfly populations (females resemble males to escape sexual harassment; Iserbyt et al. 2011). Changing the cost:benefit ratio of attacking models and mimics also changes the phenotypic space in which imperfect mimics are protected: artificial Batesian mimicry systems show that mimics are better defended when models are more toxic, so increasing costs relaxes selection on mimics (Goodale and Sneddon 1977; Lindström et al. 1997), while mimetic precision in hoverflies appears to increase with their size, suggesting that increased benefits of attacking mimics also can select for

better mimicry (Penney et al. 2012). Finally, increasing the availability of alternative prey (and hence the relative dietary importance of mimics) relaxes selection for better mimicry (Lindström et al. 2004).

The widespread support for the relaxed selection hypothesis illustrates its generality across different taxa and types of mimetic relationships. Signal detection problems are pervasive in animal communication (Rowe 1999; Wiley 2006), having also played an important role in discussions of kin recognition (e.g., Reeve 1989) and sexual selection (e.g., Getty 1999). Indeed, as there will always be some error in receivers' sensory systems, there is likely an area of relaxed selection on some phenotypic scale in every system. However, given the large potential risks associated with mistakenly accepting models in some systems, the phenotypic space of nearly neutral selection around model phenotypes can be quite wide.

Many studies that find support for the relaxed selection hypothesis use a single dimension or synthesize multiple dimensions with equal weightings; i.e., they assume that multiple dimensions of phenotype are synthesized into a single continuous metric of mimetic resemblance at some higher level of cognition in the receiver's brain. Considering the importance of this assumption, additional research should be conducted to evaluate its validity. However, there is support for this assumption from damselflies (Iserbyt et al. 2011) and hoverflies (Penney et al. 2012).

Mimetic Breakdown Hypothesis

There is empirical evidence for mimetic breakdown. In a coral snake mimicry complex in the southeastern U.S., scarlet kingsnakes occur in both sympatry and allopatry with their

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coral snake model. In sympatry, mimics are favored by natural selection. In allopatry, however, they suffer increased attacks from predators (Pfennig et al. 2001, 2007). Genetic analyses indicate that gene flow from sympatry to allopatry explains the occurrence of scarlet kingsnakes in allopatry with their model (Harper and Pfennig 2008). However, morphometric analyses reveal that populations in allopatry have much more red on their dorsum than populations in sympatry, which closely resemble their coral snake model in amount of red (Harper and Pfennig 2008). Thus, despite gene flow from sympatric and allopatric populations, selection has led to a breakdown of the mimetic phenotype.

Another example comes from mimetic butterflies in Africa, where Sheppard (1959) showed that imperfect mimics were more common in areas with few models. However, breakdown may not explain imperfect mimicry in species that have mimetic and nonmimetic morphs, as sharp clines between mimics and nonmimics may form along the sympatry-allopatry boundary with the model, as occurs in admiral butterflies (Ries and Mullen 2008).

Perceptual Exploitation Hypothesis
Empirical support for the perceptual exploitation hypothesis comes from studies of unrewarding orchids that dupe male bees into pollinating them by mimicking the pheromones of female bees. In this system, an exotic ratio of volatile odor compounds leads to a stronger pollination response (Vereecken and Schieslt 2008). This is because male bees prefer females from allopatric populations that have different chemical "dialects," which presumably promotes outbreeding (Vereecken et al. 2007). Sensory

exploitation is not limited to olfactory stimuli, however. Benitez-Vieyra et al. (2009) found disruptive selection on the shape of a sexually deceptive orchid that resembles female bees, suggesting perceptual exploitation of male bees' visual preferences as well.

Satyric Mimicry Hypothesis

The predictions of this hypothesis are not supported by the original dataset of Dittrich et al. (1993) that motivated Howse and Allen (1994) to come up with this hypothesis; the fitness of hoverflies increases monotonically with their resemblance to wasps. Schmidt (1958) and Caley and Schluter (2003) also found monotonic increases in fitness with mimetic precision for butterflies and pufferfish mimics, respectively, which is also inconsistent with the expectation for a local fitness peak for some imperfect mimics.

Although not all of the predictions of Howse and Allen's model (1994) may be supported, the general idea of jamming a predator's sensory system with conflicting information remains intriguing. The satyric mimicry hypothesis connects predator psychology to imperfect mimicry in a mechanistic way. Without a doubt, generalization acts to benefit imperfect mimics (e.g., Schmidt 1958; Ford 1971; Pilecki and O'Donald 1971; Lindström et al. 1997; Caley and Schluter 2003; Lynn et al. 2005; McGuire et al. 2006; Rowland et al. 2007; Kikuchi and Pfennig 2010a,b; Iserbyt et al. 2011; Ihalainen et al. 2012; Penney et al. 2012). However, no experiment has been explicitly designed to test the effect of signal elements presented in conjunction with novel phenotypic elements. More research is needed on how receivers perceive and process signals, as well as how these processes affect receiver behavior and subsequent signal evolution.

Multiple Models Hypothesis

Empirical tests of, and support for, the multiple-models hypothesis are scanty. On the one hand, Edmunds (1978) observed that ant-mimicking spiders with narrow distributions and a single model were better mimics than a wide-ranging species that overlapped with several models. On the other hand, Penney et al. (2012) did not find any evidence of intermediate phenotypes between different models among poor hoverfly mimics of wasps and bees, suggesting that multiple models have little relevance in that system. This hypothesis remains plausible and awaits further testing.

Multiple Predators Hypothesis

Pekár et al. (2011) found empirical support for their hypothesis in a study of myrmecomorphic (ant-mimicking) spiders. Many predators display a generalized avoidance of ants, which selects for mimicry, but some predators preferentially attack ants. There appears to be a tradeoff between being a good ant mimic and being able to escape the specialized ant predators quickly, which selects for imperfect mimicry. Because Pekár et al. (2011) examined only a few taxa of imperfect mimics, future studies are needed to determine if a tradeoff between mimetic accuracy and movement speed is consistent across phylogeny. However, this hypothesis is highly persuasive and consistent with empirical measurements. Endler and Mappes (2004) showed that multiple predators may select for weakly conspicuous aposematic signals among defended prey, so the potential implications of multiple predators on the evolution of mimicry may be more extensive that the current incarnation of this hypothesis implies.

Kin Selection Hypothesis

This hypothesis predicts that inaccurate mimicry will be most likely when models are weakly defended and uncommon, and that it will be more prevalent in species with limited dispersal and high degrees of family grouping (Johnstone 2002). The first prediction is at odds with the predictions of the relaxed selection hypothesis. Therefore, studies of mimetic precision over a range of model abundance that have found that better mimics are favored when models are rare do not support kin selection as a mechanism for maintaining imperfect mimicry (e.g., Harper and Pfennig 2007; Iserbyt et al. 2011; Penney et al. 2012). However, to our knowledge, no study has explicitly measured relatedness within any natural population of mimics.

Character Displacement Hypothesis

Although empirical tests of the character displacement hypothesis for the evolution of imprecise mimicry are lacking, a growing number of studies have documented reproductive and resource competition among the members of the same mimicry complex (reviewed in Rainey and Grether 2007; Pfennig and Kikuchi 2012). For instance, Müllerian co-mimics may often risk engaging in deleterious reproductive interactions with each other if the same signals used to warn potential predators are also used to attract mates. A recent test of this hypothesis comes from butterfly species of the genus *Heliconius*, where numerous species have converged on the same wing color patterns, owing to Müllerian mimicry. In this group, not only is wing coloration used to signal unpalatability to potential predators, it is also used to signal to prospective mates, which may increase the risk of costly reproductive interactions between species. Estrada and

Jiggins (2008) studied interspecific attraction between two species, *Heliconius erato* and *H. melpomene*, and found that both species do indeed spend considerable time approaching and courting females of the co-mimic species. Such mistakes in mate choice may favor reproductive character displacement as a means of reducing these costly reproductive interactions, which could result in imperfect mimicry in some cases.

Resource competition—and possibly ecological character displacement—has also been documented among the members of the same mimicry complex. For example, syntopic Müllerian co-mimics of neotropical catfish differ in resource use (Alexandrou et al. 2011), suggesting scope for resource competition to cause character displacement (and therefore possibly imperfect mimicry) in mimicry complexes.

However, as noted above, for ecological character displacement to promote the evolution of imperfect mimicry, aposematic/mimetic signals aimed at potential predators must be in some way environmentally dependent, such that their production requires some limited resource (e.g., a food item or a particular habitat). Only a handful of studies have examined empirically whether resource competition affects the production of aposematic signals, but the results of these studies suggest that ecological character displacement could promote imperfect mimicry. For example, Blount et al. (2012) found that in seven-spot ladybird beetles (*Coccinella septempunctata*), which possess both toxins and warning coloration, resource (i.e., food) availability affects both toxin levels and warning coloration. Moreover, many toxic fish species use warning coloration to alert potential predators of their noxiousness (reviewed in Cott 1940; Edmunds 1974), and other species sometimes mimic these colors (e.g., Moland et al. 2005; Alexandrou et al. 2011). Coloration in many species of fish is diet dependent, such that dietary

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components (e.g., carotenoids) are required for these displays (e.g., Seehausen and van Alphen 1998; Boughman 2001). If ecological character displacement were to cause such species to shift their diet, so that the dietary components used to generate a mimetic signal were no longer available (or where to costly to obtain), then imprecise mimicry may result.

Tests of Multiple Hypotheses in Single Systems

To determine if one hypothesis (or category of hypotheses) is more crucial than the others in explaining the evolution of mimicry, we need to determine the relative contributions of each hypothesis toward the evolution of imperfect mimicry. The best way to do so is to identify mimicry complexes in which multiple hypotheses can be evaluated simultaneously.

To date, only two mimicry complexes have been subjected to tests aimed at evaluating multiple hypotheses. In one such study, Penney et al. (2012) sought to explain imprecise mimicry of wasps by hoverflies (see above) by testing the eye-of-the-beholder, relaxed selection, kin selection, and multiple model hypotheses. They predicted that there would be a discrepancy between human and avian rankings of model-mimic similarity if the eye-of-the-beholder hypothesis held, and that mimics would fall between models in phenotype if they used more than one model. They also predicted that mimics would decrease in precision with their relative abundance if kin selection affected their populations, but that precision would increase with mimic abundance if the relaxed selection hypothesis were correct. Their tests of these predictions were facilitated by four major factors: multiple populations of models and mimics with different model:mimic

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abundance ratios; a phylogenetic tree of the mimics to account for phylogenetic signal in mimicry; a large museum dataset from which to obtain morphometric measures of models and mimics; and empirical discrimination data from both likely signal receivers and humans. Their dataset for bird discrimination of hoverflies and wasps is from Dittrich et al. (1993), and they focused their morphometric analyses on traits that a simulation showed to be important for birds' decision-making (Bain et al. 2007). Once they had accounted for phylogenetic signal, their results supported the relaxed selection hypothesis. Results were also consistent with some of the other hypotheses that we have classified as tradeoffs or constraints, but were not designed to discriminate between them.

The second mimicry complex that has been subjected to tests aimed at evaluating multiple hypotheses is a coral snake mimicry complex in the southeastern United States. Early work demonstrated that scarlet kingsnakes were in fact Batesian mimics of coral snakes (Pfennig et al. 2001). Later work showed that imperfect mimicry in the ratio of red:black in the scarlet kingsnake's dorsal rings could be explained by the relaxed selection hypothesis (Harper and Pfennig 2007). Studies also showed that some allopatric scarlet kingsnakes were not mimics, but were in the process of evolving new, less mimetic phenotypes (Harper and Pfennig 2008), thereby supporting the mimetic breakdown hypothesis. Additionally, other studies found that imperfect mimicry in snake dorsal color ring order was not used by predators in discriminating between the deadly model and its mimic (Kikuchi and Pfennig 2010a), supporting the eye-of-the-beholder hypothesis. Therefore, at least three hypotheses— the relaxed selection hypothesis, the mimetic breakdown hypothesis, and the eye-of-the-beholder hypothesis—can explain the apparent occurrence of imperfect mimicry in this system.

More generally, these studies of imperfect mimicry in a coral snake mimicry complex serve to illustrate an important point. Namely, that the 11 hypotheses that we have discussed here are not mutually exclusive, and that multiple explanations may therefore account for the existence of imprecise mimicry in any one system/mimicry complex. The challenge for future empirical work is to determine which, if any, of the hypotheses is more important than the others in promoting the evolution of imperfect mimicry.

Unexplained Phenomena

Although we have here explored the evidence for 11 existing hypotheses for imperfect mimicry, there are still some phenomena that probably cannot be explained by any of them. Below, we present two such empirical problems that will likely require the development of new theory.

First, consider European vipers and their colubrid mimics. The vipers have at least two components to their aposematic signal: a dark dorsal zigzag and a triangular head (Wüster et al. 2004; Niskanen and Mappes 2005; Valkonen et al. 2011). However, colubrid mimics need bear only one of those two signal elements to receive as much protection from predators as vipers do (Valkonen et al. 2011). Predators avoid replica snakes to the same degree whether they have triangular heads, dorsal zigzags, or both. At first glance, this nonadditive interaction between signal components seems reminiscent of the relaxed selection hypothesis (because imperfect mimics are protected as well as perfect mimics). Yet, this example cannot be explained by the relaxed selection hypothesis, because the viper's signal occupies two dimensions of signal space, and imperfect mimics can be completely nonoverlapping with their models in either one of

them. The relaxed selection hypothesis depends on partial overlap between models and mimics *within* a single dimension, so unless multiple components of aposematic signals are combined into one at some level of neural processing, it cannot explain this instance of imperfect mimicry. Therefore, to explain such imprecise mimicry, we need to understand: why multicomponent aposematic signals evolve; and why not all components of aposematic signals are needed to elicit full predator avoidance.

Second, recent data suggest that the complexity of prey communities alters selection for signal mimicry, but no theory consistently anticipates this result. Beatty et al. (2004) conducted a series of experiments that measured human predators as they learned to discriminate between computer-generated profitable and unprofitable prey. They altered the phenotypic variety of both profitable and unprofitable prey, and measured the fitness of imperfect Müllerian mimics depending on whether they shared a single trait (also known as a feature) in common with their models. They found that in simple communities, there was little selection for mimicry at all because humans learned to identify each prey phenotype uniquely. In complex communities, selection favored imperfect mimics that shared a feature with other unprofitable prey. Beatty et al. (2004) interpreted their results as illustrating the difficulty of memorizing multiple prey phenotypes, and suggested that, in general, more complex communities may select for Müllerian mimicry by favoring imperfect mimics.

Ihalainen et al. (2012) revisited this topic and trained birds to forage in communities of artificial prey with varying levels of complexity in the phenotypes of defended and undefended prey. They then tested the responses of the trained birds to a quantitative gradient of signals based on a single aposematic signal that was present in all of the

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training communities. They found that birds trained in simple communities selected for very precise mimicry, but birds trained in complex ones did not discriminate at all among the gradient of phenotypes presented. They interpreted the difference between their results and those of Beatty et al. (2004) as being at least partially attributable to the behavior of naive and trained predators and suggested that a mixture of naive (coarsely discriminating) and refined (finely discriminating) predators might select for both the initial evolution of mimicry and its improvement.

The use of independent features on the imperfect mimics in Beatty et al. (2004) as opposed to the continuous gradient of phenotypes tested by Ihalainen et al. (2012) complicates direct comparison between the two studies because they might involve different psychological processes. Chittka and Osorio (2007) proposed that predators in complex prey communities might use discrete features of prey to classify them, while Ihalainen et al. (2012) speculated that predators trained on diets of limited variety were less willing to attack unfamiliar prey because they generalized very narrowly (i.e., discriminated within a single continuous dimension of phenotype). In response to the issues raised by these studies, we need to know not only how the number of prey species in a community affects the precision of mimicry, but also take into consideration the experience and variety of predators, and the nature of the phenotypes being evaluated (multicomponent or single dimension, and continuous or discrete variation).

Conclusions

We have presented and evaluated the evidence for the major hypotheses for imperfect mimicry. Although only two systems have been subjected to multiple tests, empirical

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support for individual hypotheses for imperfect mimicry comes from many systems. Particularly, many studies have found results consistent with the predictions of the relaxed selection hypothesis. The eye-of-the-beholder hypothesis is also widely applicable, because it is often difficult to know exactly what aspects of the model's phenotype constitute its signal to receivers. By contrast, mimetic breakdown has only been found in systems with allopatric mimics. Chase-away, perceptual exploitation, and multiple predators have been each supported by one or two studies. That imperfect mimicry is caused by developmental or genetic constraints is difficult to demonstrate, but the shared supergenes of *Heliconius* indicate a role for phylogeny and hybridization in facilitating the evolution of mimicry. The multiple models and kin selection have not been supported in the study systems where some of their predictions have been tested, and the satyric mimicry and character displacement hypotheses await direct tests.

It is important to stress that some of the hypotheses have been developed from studies that have focused on the natural history of particular systems (e.g., Vereeken and Schiestl 2008; Benitez-Vieyra et al. 2009; Pekár et al. 2011). For this reason, these studies have not tested any alternative hypotheses for imperfect mimicry. Other hypotheses were developed largely from plausible theoretical arguments, but are much more difficult to test than others. Thus, it is premature to rank them in terms of their likely importance in promoting the evolution of imperfect mimicry. Additionally, multiple hypotheses may operate simultaneously in many systems and, together, they may contribute to the evolution of imperfect mimicry.

Ideally, studies of imperfect mimicry should establish that mimicry in fact occurs and identify the aspects of phenotype that constitute the signal (i.e., test the mimetic

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breakdown and eye-of-the-beholder hypotheses). The remaining hypotheses that can be tested may be contingent on the details of the study system. Systems that span geographical areas where the model:mimic ratio varies and is easily measured are ideal for testing the relaxed selection hypothesis, as are those where models and mimics vary in the costs and benefits they offer. The presence of multiple models, specialist predators, strong spatial grouping of kin, and likely competition between mimics and their models/co-mimics are prerequisites for testing the multiple model, multiple predators, kin selection, and character displacement hypotheses, respectively. The satyric mimicry hypothesis would have to be evaluated in conditions where the cognitive mechanisms of signal receivers can be directly studied or at least inferred.

In the future, we must gather more information on the fitness consequences of imperfect mimicry in natural populations. Such studies are needed to determine if imprecise mimicry is disfavored, as highly favored as precise mimicry, or even more highly favored than precise mimicry. This information is key to differentiating among the various hypotheses for imprecise mimicry (see Table 7.1). Given the attention Batesian mimicry complexes have received, greater effort should go into evaluating the various hypotheses for imperfect mimicry in Müllerian mimicry complexes. Fortunately, new cases of mimicry are constantly being discovered (e.g., Brown 2006; Marek and Bond 2009; Wilson et al. 2012). With such a profusion of mimicry complexes, it should become easier to find appropriate study systems in which to address any given hypothesis for imprecise mimicry.

We also need to uncover the proximate mechanisms that generate mimetic phenotypes. Although a number of recent studies have shown promise in this area (e.g.,

see Reed et al. 2011; Kikuchi and Pfennig 2012b), we still know virtually nothing about the proximate mechanisms by which mimetic phenotypes are produced and, hence, whether or not genetic or developmental constraints play a role in explaining the persistence of imperfect mimics. To resolve the unexplained phenomena in imperfect mimicry that we introduced above, theories of optimal decision-making and cognitive psychology may be helpful (e.g., Rowe 1999; Darst 2006; Sherratt 2011). We urgently require empirical work to challenge and improve theory (e.g., Hansen et al. 2010; Rowland et al. 2010). Directly measuring animal decision-making (e.g., Alatalo and Mappes 1996) and incorporating physiology and neurobiology into perceptual models can produce dramatic advances in our ability to explain how animals see and evaluate the world. Finally, recognizing that mimicry occurs within complex communities of prey must also be a major thrust of future research.

Such studies are important, because the existence of imperfect mimicry represents a key challenge to mimicry theory (Ruxton et al. 2004). More generally, clarifying why imperfect mimicry exists promises to provide critical insights into the limits of natural selection in producing complex adaptations.

Table 7.1. A classification scheme for eleven, non-mutually exclusive hypotheses on the evolution of imperfect mimicry

Hypothesis	Imperfect mimicry reflects...			
	an artifact of human perception not shared by natural signal receivers	genetic or developmental constraints, which (temporarily) limit a response to selection	relaxed selection, where imperfect mimics are as fit as perfect mimics	an (at least locally) adaptive peak
1. Eye-of-the-beholder	X			
2. Developmental constraints		X		
3. Chase-away		X		
4. Relaxed selection			X	
5. Mimetic Breakdown				X
6. Perceptual exploitation				X
7. Satyric mimicry				X
8. Multiple models				X
9. Multiple predators				X
10. Kin selection				X
11. Character displacement				X

Table 7.2. Summary of eleven hypotheses for imperfect mimicry and their critical predictions

Hypothesis	Mechanism	Critical Predictions	Key References
1. Eye-of-the-beholder	Imperfect mimicry is an anthropocentric projection; real predators do not distinguish between models and "imperfect" mimics	Humans score model-mimic similarity differently from predators (under similar conditions)	Dittrich et al. (1993); Cuthill and Bennett (1993)
2. Developmental and genetic constraints	Production of better mimetic signals is constrained by an intrinsic inability to produce them	Imperfect mimics are less fit than perfect mimics; proximate mechanisms reveal constraints.	Maynard-Smith et al. (1985)
3. Chase-away	Models evolve away from their Batesian mimics; time-lag prevents immediate mimic response	Similar to (2); plus evolutionary change in model phenotype due to negative fitness consequences of Batesian mimics	Nur (1970); McGuire et al. 2006); Franks et al. (2009)
4. Relaxed selection	Mimics are under little selection to evolve better mimicry because of the risks of accidentally attacking a model	Mimetic precision correlates positively with relative mimic abundance/benefits and negatively with alternative prey	Schmidt (1958); Duncan and Sheppard (1965); Sherratt (2002); Penney et al. (2012)
5. Mimetic breakdown	Mimicry is no longer advantageous due to a paucity of models	Imperfect mimicry is favored relative to perfect mimicry in the absence of models	Sheppard (1959); Brower (1960); Pfennig and Mullen (2010)
6. Perceptual exploitation	Signal receivers have a bias towards signals that are displaced from the model's signal	Imperfect mimics elicit a stronger response from signal receivers than their models do	Vereecken and Schiestl (2008)

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7. Satyric mimicry	Imperfect mimics that blend some components of the model's signal with irrelevant stimuli confuse signal receivers, resulting in better protection than imperfect mimics that do not.	Components of the aposematic signal elicit greater receiver avoidance/latency to respond when presented with irrelevant stimuli than without	Howse and Allen (1994)
8. Multiple models	When multiple models exist, mimics adopt an intermediate phenotype between them to receive protection from more than one of them.	Imperfect mimics are phenotypic intermediates between models and have higher fitness than mimics more closely resembling any one.	Edmunds (2000); Sherratt (2002)
9. Multiple predators	Imperfect mimics are a compromise between duping generalist predators and avoiding specialist predators	Opposing selective pressures on mimetic phenotype by generalist and specialist predators	Pekar et al. (2011)
10. Kin selection	Imperfect mimicry persists because it lowers overall attack rates on a population of related mimics	Mimetic precision is inversely correlated with relatedness of mimetic populations and mimic abundance.	Johnstone (2002); Penney et al. (2012)
11. Character displacement (CD)	Competition between models and mimics displaces phenotypic optimum away from perfect mimicry	For reproductive CD, poor mimics have higher mating success than better mimics. For ecological CD, model/mimic fitness costs for competing over resources essential to signals; less selection for mimicry when mimetic individuals are forced into allotopy from their models.	Pfennig and Kikuchi (2012)

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Figure Legends

Figure 7.1. Threshold for selecting imperfect mimics when their phenotypic distribution differs from that of their models. The signal receiver should choose all organisms encountered to the right of the threshold (shaded area), as they offer an average positive return.

Figure 7.2. Variation in the strength of selection for mimicry (not relative fitness) with respect to mimetic phenotype. The phenotype of the model is marked with an arrow at 0.0, so phenotypes closer to either end of the x-axis resemble the model less. Mimics more distant from their model in phenotype are under stronger selection to improve mimicry than ones which already resemble their models closely (i.e., selection is nonlinear). Furthermore, the shape of the curve changes with different cost:benefit ratios for attacking models and mimics (dotted line). Relatively less costly/abundant models create a smaller area of phenotypic space around them in which mimics are under little selection to improve. Adapted from Sherratt (2002).
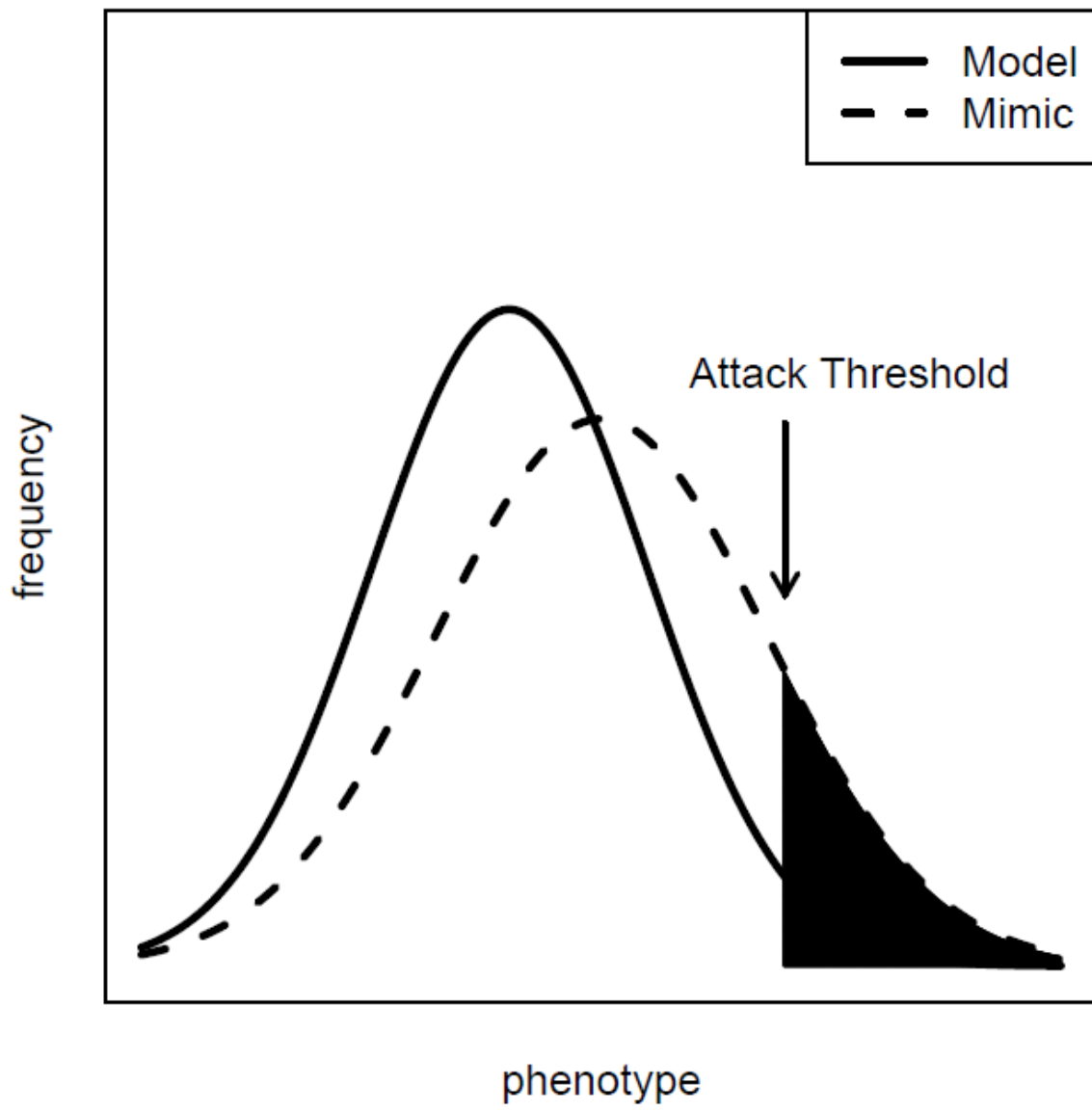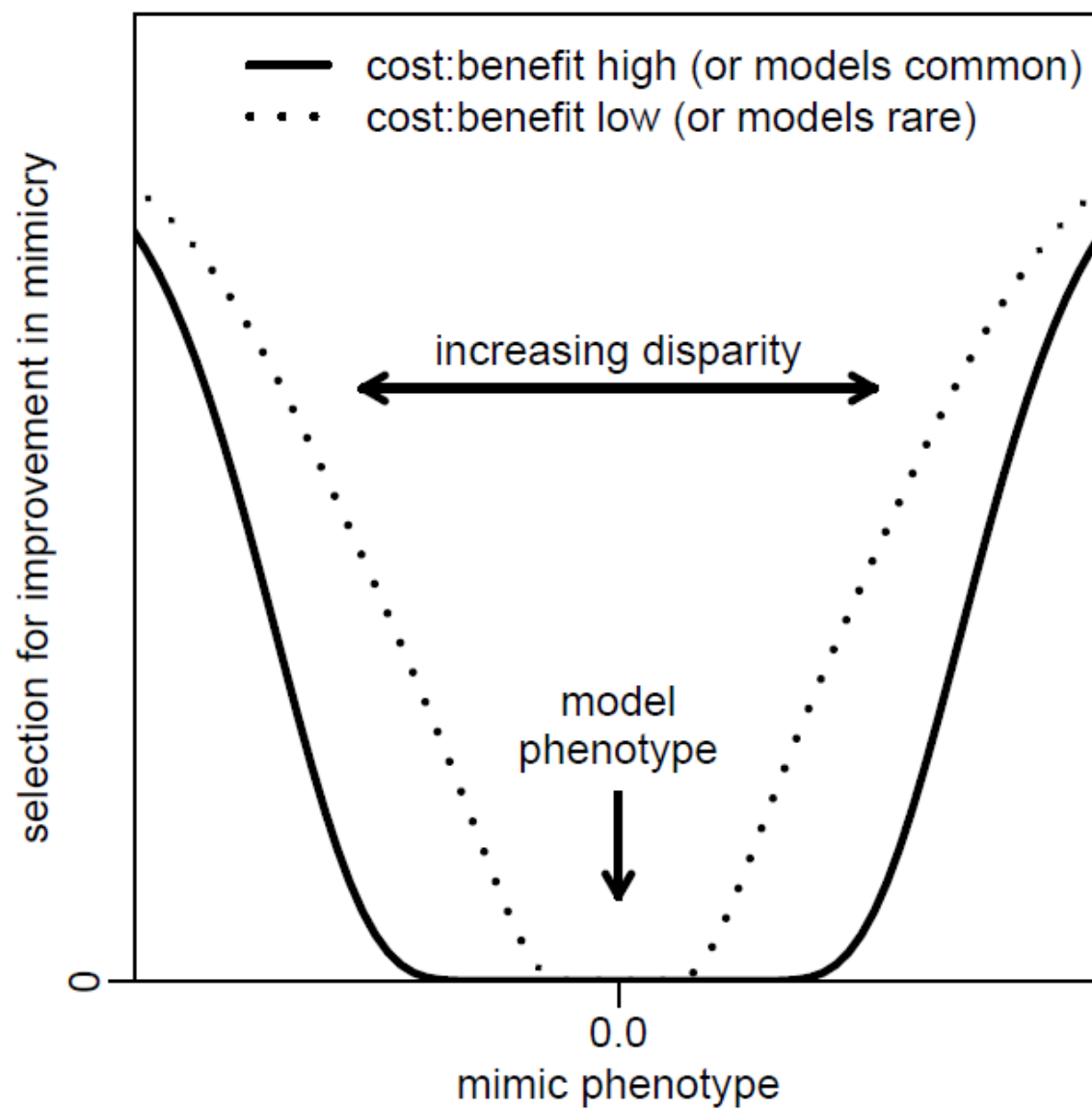
Figure 7.1

Figure 7.2

CHAPTER VIII

CONCLUSIONS

In this thesis, I have examined the mechanisms of adaptation from behavioral, developmental, and ecological perspectives. I have argued that Batesian mimicry in the coral snake mimicry complex is imperfect because predators cannot perceive imperfections in mimetic signals that are apparent to humans; that the evolution of coral snake mimicry may be facilitated by proximate mechanisms of phenotype production across snakes; and that coral snake mimicry may not have required populations of incipient mimics to cross an adaptive valley due to high model abundance. I have also reviewed mimicry as a whole and examined the evidence for various hypotheses for imperfect mimicry, finding that relaxed selection explains the most cases of imperfect mimicry to date. To conclude, I will summarize the current understanding of the coral snake mimicry complex studied in this thesis, and discuss some unresolved issues that provide opportunities for future work.

Coral snake mimicry was first conclusively demonstrated by examining the fitness of *Lampropeltis elapsoides* in allopatry and sympatry with the coral snake *Micrurus fulvius* (Pfennig et a. 2001). Fitness of *L. elapsoides* decreased with distance from the center of the coral snake's distribution, which matches the critical prediction of Batesian mimicry:

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the fitness of the mimic depends on the presence of the model. This study by Pfennig et al. (2001) was pivotal because for decades, many researchers had doubted that coral snake mimicry occurred (e.g. Brattstrom 1954; Wickler 1968; Pough 1974), thinking that coral snakes were too deadly to serve as models for Batesian mimics because predators would never have a chance to learn their signals.

Having established that coral snake mimicry actually takes place, the system became a proving ground for other hypotheses related to mimicry theory. Pfennig et al. (2007) addressed the question of how fit Batesian mimics are in allopatry: they found data consistent with apostatic predation on allopatric mimics, meaning that they are best protected in areas where they are rare. Harper and Pfennig (2007) performed an instantly classic study that tested the hypothesis that the precision of mimicry selected for should vary with the abundance of the model (Sherratt 2002). They found that in Florida where models were abundant, mimics were imprecise, but in North Carolina, where mimics are rare, they were almost exact matches to their coral snake models. Measurements of fitness with respect to predation revealed that predation rates on imprecise mimics were higher in North Carolina than in Florida. Subsequently, Harper and Pfennig (2008) showed that allopatric Batesian mimics differed in phenotype from sympatric Batesian mimics, but that they appeared to be derived from sympatric populations. Gene flow at nuclear markers indicated that male-biased dispersal might maintain maladaptive mimetic phenotypes in allopatry.

During my thesis, I built upon the work of Pfennig and colleagues by investigating the implications for variation in predator abundance on the presence or absence of a selective valley in the adaptive landscape over which mimicry evolves. I also found that

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the evolution of mimicry was probably facilitated by conserved pigment production systems across snakes. Finally, I explored whether or not selection operated on dimensions of mimic phenotype other than those that Harper and Pfennig (2007) explored, finding that it did not. The details of the methods and results of these projects have been discussed in the preceding chapters, but not all of the "loose ends" that inevitably remain in the wake of empirical research have been dealt with.

The most intuitive piece of unfinished business that this thesis has produced is an ambiguity in the traits that elicit avoidance of coral snake patterns. In Kikuchi and Pfennig (2010a), we evaluated the fitness of three different snake phenotypes: inaccurate mimics in red:black ratio & ring order, inaccurate mimics in ring order, and perfect mimics. Based on our data, we concluded that predators ignored the information in ring order, as they attacked both types of imperfect mimics with equal frequency. However, subsequent to the publication of that article, Valkonen et al. (2011) showed that mimics of European adders were protected as long as they had *either* a triangular head or a zigzag dorsal stripe, which are traits that adders possess (but always together). In Valkonen et al (2011), only unmarked control snakes were attacked at higher rates. Thus, predators appeared to evaluate aposematic markings in a non-additive fashion. In Kikuchi and Pfennig (2010a), we did not include a phenotype with the coral snake's ring order but an inaccurate proportion of red:black because such snakes do not exist in nature. However, it is eminently possible that predators might also avoid such replicas if they evaluate the components of aposematic signals non-additively in the coral snake mimicry complex as they do in the European viper complex. Finding such a result would alter how imperfect

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mimicry is understood in this system; currently, it is regarded as an "eye-of-the-beholder" phenomenon (see Chapters III and VII), but might not truly be so.

The way that avian predators perceive the coloration of snakes is an interesting question that has implications for the evolution of mimicry and other antipredator strategies. Aposematic and mimetic taxa are expected to be perceived as similar by their common predators, and indeed the red coloration of coral snakes and their putative mimics appears similar to birds because of the presence of drosopterin pigments (Chapter V). However, that does not tell us about other salient questions, like how distinctive the different colors of various species of snakes are from one another in general, nor does it tell us how conspicuous they are.

The use of color space models for predator visual systems has the potential to answer questions like these. Animals perceive the colors of their world in terms of the relative excitation of their photoreceptors; this excitation can be described in a coordinate system referred to as a color space (Stoddard and Prum 2011). A set of colors (for example, those produced by the taxon Serpentes) is referred to as a gamut and occupies a certain volume of that color space (Stoddard and Prum 2011). Currently, a color space model is available for avian vision (Stoddard and Prum 2008).

Characterizing the snake color gamut would allow several fascinating questions about signal design to be answered. For example, are coral snakes and their mimics consistently closer to one another in color space than they are to other snakes, or than other snakes are to each other? Do aposematic species and their mimics differ in coloration from their backgrounds more than non-aposematic species? How does the color space occupied by the snake color gamut compare with that of other taxa, such as birds (Stoddard and Prum

2011), which produce their colors using different proximate mechanisms? Can trends in coloration within and between taxa be explained by phylogeny, habitat, body size, prey type, or other ecological factors? The ease of collecting spectral data from snakes once they have been collected makes this approach to studying animal coloration feasible. Other approaches such as directly measuring fitness in the wild provide irreplaceable opportunity to demonstrate causality, but cannot be applied to more than a few taxa at once and also make their own assumptions. Conducting a study of the snake color gamut would dramatically increase our descriptive knowledge of animal coloration and at the same time address many interesting questions about its form and function.

   Another potential avenue for further investigation is the proximate mechanisms behind the formation of aposematic signals in the coral snake mimicry complex. Although this thesis has explored the topic, there is infinitely more to learn than what has been revealed to date, and furthermore the sequencing of the python genome will make studying snake development feasible (Castoe et al. 2011). Major questions of interest could be answered with this line of inquiry, including: how similar are the genes involved in pattern formation between coral snakes and kingsnakes? how much of their similarity is the product of convergent mutations within genes that were already shared? how many genes related to coloration differ between coral snake mimics and their most recent cryptic ancestor, and what were the likely intermediate phenotypes? why are some coral snake mimics nearly perfect, while other so poor? How does the genetics of adaptation in coral snake mimicry compare with that of other color pattern adaptations, such as Müllerian mimicry in *Heliconius* and cryptic coloration in mice (*Peromyscus*)? The discrete color patterning involved in this mimicry complex coupled with its ecological

importance make it one of the most compelling candidate systems for examining pattern formation.

Kingsnakes are easily raised in captivity, which adds to their appeal as a system for studying development. Many of the subspecies of *Lampropeltis triangulum* are popular in the pet trade and do well in the lab. They also cost relatively little to keep and maintain compared with conventional model organisms such as mice. Assuming that they could be successfully bred at least once a year, techniques such as RT-PCR of candidate genes and transcriptome analyses from developing color patches could be useful springboards for answering many of the questions we have about adaptation. Candidate genes might be identified through the pteridine or melanin synthesis pathways, as these pathways produce the pigments found in snakes (Kikuchi and Pfennig 2012b; Chapter V). The ease of field studies to evaluate the fitness effect sizes of various genes contributing to pattern development makes this system even more attractive for such ventures.

For over 150 years, mimicry has been a rich field for testing evolutionary theory. Clearly, however, there still remains a tremendous lode of unanswered questions along many potential veins of inquiry. Current trends in the field of biology have made questions about the genetics and development of mimicry more salient, but many questions about the behavioral and evolutionary ecology of mimicry also remain unexplored. Because of it is a nexus of so many processes, mimicry forms a space where new methods can be immediately applied, yet old methods still furnish novel insights. This is fortunate for everyone who works in the field: rather than being pushed in any one direction by a technological advance, researchers are free to exercise their creativity using whatever method might be sufficient to do the job. Furthermore, steady advances in

such a wide array of study areas constantly creates new questions at different levels of

analysis. Mimicry may be studied for the next 15 years or the next 150 years, but

whatever the case, the proximate and ultimate lines of inquiry will continue to be

intertwined in explaining this remarkable instance of adaptation.

APPENDIX

APPENDIX 6.1

SITES USED FOR SELECTION EXPERIMENTS ON POLYMER CLAY SNAKE REPLICAS

Abbreviations: r.a = relative model abundance (H = high, L = low), lat = latitude (degrees N), long = longitude (degrees W), days = days exposed to predators, NWR = National Wildlife Refuge, NF = National Forest, OHV = off-highway vehicle, WMA = Wildlife Management Area, CA = Conservation Area.

site name	r.a	state	lat	long	days
Archbold Biological Station	H	FL	27.18288	81.35197	32
Lake Kissimmee State Park	H	FL	27.97198	81.38023	31
Annutteliga Hammock	H	FL	28.61465	82.54396	31
Withlacoochee State Forest	H	FL	28.73222	82.41938	31
Goethe State Forest	H	FL	29.12833	82.56149	31
Lower Suwannee NWR	H	FL	29.3464	83.05194	31
Grove Park	H	FL	29.52541	82.2035	30
Ocala NF (OHV path 42)	H	FL	29.3681	81.83283	31
Ocala NF (Alexander Springs)	H	FL	29.06442	81.59944	31
Lake George WMA	H	FL	29.34531	81.54111	30
Mike Roess State Park	H	FL	29.84764	81.96128	30
Osceola National Forest	H	FL	30.19032	82.42611	30
Jennings State Forest	H	FL	30.12868	81.96421	30
Sandhills Game Land (19 Frog Pond)	L	NC	34.99071	79.51179	32
Sandhills Game Land (Fish Hatchery)	L	NC	35.00908	79.62762	32
Holly Shelter Game Land (A)	L	NC	34.54876	77.6889	31
Holly Shelter Game Land (B)	L	NC	34.5689	77.77297	31
Carolina Sandhills NWR (A)	L	SC	34.53275	80.22995	32
Carolina Sandhills NWR (B)	L	SC	34.57235	80.22363	32
Suggs Mill Pond	L	NC	34.81089	78.66737	36
Jones Lake State Park	L	NC	34.68182	78.59732	36
Boiling Spring Lakes CA	L	NC	34.02115	78.06343	31
Green Swamp Preserve (A)	L	NC	34.09318	78.29855	32
Green Swamp Preserve (B)	L	NC	34.06407	78.29138	32
Lake Waccaman State Park	L	NC	34.25949	78.47694	30
Lumber River State Park	L	NC	34.38799	79.00132	30

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