Mimicry

David W. Kikuchi, David W. Pfennig

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.

General Overviews

Since Henry Walter Bates first published his theories of mimicry in 1862 (see Bates 1862, cited 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.

Edmunds's 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.

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. Edited by Alessandro Finazzi-Agrò, 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, 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 attempts 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 Jersakova, 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.**

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 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 (in Bates 1862) noted the fascinating resemblance between pairs of *Heliconius* butterfly species and other butterflies in many localities throughout the Amazon basin. He 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. In Müller 1879, he 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 produced a comprehensive summary of different types of protective coloration in animals (Poulton 1890). The work also contains many of Poulton's thoughts on how mimicry should be defined and how it evolved. Fisher 1958 summarizes much of Fisher's contemporaries' thought on both Batesian and Müllerian mimicry. Brower 1958 reports on a series of experiments verifying the efficacy of Batesian mimicry. Duncan and Sheppard 1963 applies 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 experiments 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 the theory's 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.**

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 o London*** **1879: xx–xxiv.**

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

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 (see Reproductive Batesian Mimicry.

CLASSICAL BATESIAN MIMICRY

Research on Batesian mimicry has had a long history of theoretical predictions supported by empirical experiments. Brower 1960 verifies the prediction that Batesian mimicry could be selected for even when mimics outnumbered models. Oaten, et al. 1975 makes one of the more detailed signal detection models of Batesian mimicry. McGuire, et al. 2006 uses 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 finds 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 disincentive 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 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 benefited more from more toxic and more numerous models. Novel world experiments have played an important role in mimicry research.

McGuire, Liam, Hans Van Gossum, 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.

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 use 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 employs 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.

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, Sara 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 (Slagsvold 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.

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 Van Dongen, Janice J. Ting, Hans Van Gossum, 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.

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, under Historical Background), 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 contend that a major mutation was necessary for the evolution of Batesian mimicry. Others support 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 and Charlesworth 1975 concludes that a two-step process is theoretically likely. More recently, Kikuchi and Pfennig 2010 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.

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. *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.

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 indispensable 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, Marianne, Zachariah Gompert, Chris Jiggins, and Keith Willmott. 2008. Mutualistic interactions drive ecological niche convergence in a diverse butterfly community. *PLoS Biology* 6.12: e300.

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, Graeme 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 play an important role in sexual selection (see Jiggins, et al. 2001, cited under Genetics of Mimicry).

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 deter both predators and rodents that might wish to occupy their burrows (see also Rainey and Grether 2007, cited under Defining Mimicry).

Imperfect Mimicry

Intuitively, one might think that 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 of 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 support 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.

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, under Historical Background; and Nijhout 2003, under Polymorphic and Sex-Limited Mimicry). 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.

Baxter, Simon W., Nicola J. Nadeau, Luana S. Maroja, et al. 2010. Genomic hotspots for adaptation: The population genetics of Müllerian mimicry in the Heliconius melpomene clade. *PLoS Genetics* 6.2: e1000794.

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

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.

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. *PLoS Biology* 4.10: e303.

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.

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 and citations under Genetics of Mimicry) and 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 (*Trends in Ecology & Evolution*) 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, et al. 2007). Mavárez, 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, cited under Genetics of Mimicry). 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 (Stökl, 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. *BMC Evolutionary Biology* 7.1: 28.

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.

Mavárez, 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. *PLoS Genetics* 6.4: e1000930.

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 in Chittka and Osorio 2007, Balogh, et al. 2010 simulates 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 data set 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 2010 and Spottiswoode 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 argues 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 data set 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 toward 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. *PLoS Biology* 5.12: e339.

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. 2010. 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 show 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.

LAST MODIFIED: 05/23/2012

DOI: 10.1093/OBO/9780199830060-0027

BACK TO TOP