Editorial

Mimicry: Ecology, evolution, and development

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1 Introduction

Mimicry occurs when one species (the "mimic") evolves to resemble a second species (the "model") because of the selective benefits associated with confusing a third species (the "receiver"). For example, natural selection can favor phenotypic convergence between completely unrelated species when an edible species receives the benefit of reduced predation by resembling an inedible species that predators avoid.

Research into mimicry has a rich history that traces back to the beginnings of modern evolutionary biology. In 1862—a scant three years after Darwin had published *The Origin of Species*—Henry Walter Bates (1862), an English explorer and naturalist, first suggested that close resemblances between unrelated species could evolve as an anti-predator adaptation. Upon reading his paper, Darwin immediately wrote to Bates that, "In my opinion it is one of the most remarkable & admirable papers I ever read in my life. ... You have most clearly stated and solved a wonderful problem" (read the full letter at: http://www.darwinproject.ac.uk/entry-3816). Even today, mimicry is widely used as a testament to natural selection's efficacy in promoting complex adaptation (Cott 1940; Edmunds 1974; Brodie and Brodie 2004; Ruxton et al. 2004; Turner 2005; Forbes 2009).

Although many types of mimicry have now been described, the most familiar type is "protective" or "defensive" mimicry. Defensive mimicry occurs when one species receives protection from predation because of its close resemblance to a second, already protected species (for a discussion of other types of mimicry, see Vane-Wright 1976; Vane-Wright 1980; Endler 1981; Pasteur 1982; Malcolm 1990; Rainey and Grether 2007). There are two common forms of defensive mimicry: Batesian and Müllerian mimicry (Wickler 1968; Pasteur 1982). With Batesian mimicry (named after H. W. Bates; see above), an edible species evolves to resemble a conspicuous, inedible species, thereby gaining protection from predation. With Müllerian mimicry (Müller

1879), multiple undesirable species (e.g., toxic species) converge on the same warning signal, thereby sharing the cost of educating predators about their undesirability.

Mimicry is among the most active research areas in all of evolutionary biology, in part because of the highly integrative nature that the study of mimicry necessarily entails. Mimicry involves asking both functional questions (it involves investigating, for example, the adaptive significance of more versus less precise resemblance between models and mimics) and mechanistic ones (it also involves investigating, for example, how mimetic phenotypes are produced). Thus, mimicry research draws on diverse fields, many of which are on the cutting edge of biological research. Indeed, as Brodie and Brodie (2004, p. 617) note, the study of mimicry could be used to illustrate virtually every major concept in a modern evolutionary biology course.

This special column of *Current Zoology* presents a range of original research and review papers, covering the ecology, evolution, and development of mimicry. Clearly, a complete discussion of mimicry is beyond the scope of a single journal issue. Nevertheless, these papers offer a flavor of ongoing work.

Below, I briefly outline some key questions in mimicry research before highlighting how the contributions of this special column address these questions.

2 Key Questions in Mimicry Research

There are many key questions that researchers of mimicry currently investigate. Here, I highlight five questions that have been particularly fruitful areas of research.

First, what proximate mechanisms underpin mimicry? Specifically, what are the genetic and developmental mechanisms that produce mimetic phenotypes? Answering this question is important, because particular proximate mechanisms might facilitate or impede the evolution of mimicry. For instance, when models and mimics share mechanisms of signal production, mimi-

cry may evolve relatively easily, as a small number of mutations may be needed for the mimic to match the phenotype of its model (Leimar et al., 2012). Despite the importance of mechanisms in influencing the ease with which mimicry evolves, little is known about how models and mimics produce their phenotypes [with the possible exception of recent research involving mimetic butterflies in the genus *Heliconius* (Reed et al., 2011)].

Second, what role does receiver "psychology" play in the evolution of mimicry? Receivers (e.g., predators, in the case of defensive mimicry) are the agents that generate the selective pressures that drive the evolution of mimicry. Thus, understanding how receivers detect and respond to signals produced by mimics is crucial for illuminating the evolution of mimicry. For instance, for effective mimicry to evolve, how important is it for predators to perceive signals emanating from mimics and models simultaneously versus consecutively?

Third, how does Müllerian mimicry generate polymorphism among mimics? Longstanding theory (reviewed in Sherratt 2008), along with field empirical tests (Kapan, 2001), demonstrate that Müllerian mimicry should favor co-mimics that share the same signal, thereby precluding the origin and maintenance of polymorphism in these mimetic signals. Yet, considerable polymorphism has been found in many Müllerian mimicry complexes (reviewed in Joron and Mallet 1998), including in millipedes (Marek and Bond, 2009), octopi (Norman et al., 2001), butterflies (Nijhout, 2003; Kunte, 2009), fish (Alexandrou et al., 2011), frogs (Darst and Cummings, 2006), and snakes (Brodie and Brodie, 2004). These observations have led researchers to propose various hypotheses for why such polymorphism may arise, such as the possibility that spatial or temporal variation may exist in the magnitude and direction of selection favoring mimicry (Joron and Iwasa, 2005; Maan and Cummings, 2008). Alternatively, polymorphism may arise as a consequence of population subdivision through the operation of shifting balance forces (Mallet and Joron, 1999).

Fourth, why is mimicry frequently imprecise? Although mimicry is widely used to exemplify natural selection's power in promoting adaptation, it has nevertheless become increasingly clear that mimicry is frequently imprecise (Edmunds, 2000; Sherratt, 2002; Pfennig and Kikuchi, 2012b). Thus, why are imperfect mimics not further improved by natural selection? Although a number of hypotheses have been proposed to explain the evolution of imprecise mimicry (reviewed in Pfennig and Kikuchi 2012a), one leading hypothesis is

that imperfect mimics represents a trade-off between predator-mediated selection favoring mimetic convergence on the one hand and other agents of selection (such as mate choice) favoring divergence on the other hand (Pfennig and Kikuchi, 2012a). Moreover, there may be little selective benefit to refine mimetic resemblance beyond a certain point, if (for example) the model/co-mimic is common or especially noxious (Schmidt, 1958; Duncan and Sheppard, 1963; Sherratt, 2002; Harper and Pfennig, 2007), or if the mimic is likely to be especially unprofitable to predators (Sherratt, 2002). For instance, because larger prey are generally more profitable for predators, there should be greater selection pressure on larger individuals in a population to become better mimics than on their smaller counterparts, a prediction recently confirmed in hoverflies (Penney et al., 2012).

Fifth, what is mimicry's role in speciation and diversification? As with other forms of strong ecologically based selection, mimicry has long been regarded as a factor that can contribute to speciation and adaptive radiation. For instance, because mimicry is often expected to generate strong frequency dependent selection, it should tend to act as a strong agent that selects against hybrid individuals; that is, it should select against those individuals that possess phenotypes that are intermediate between cryptic and mimetic phenotypes. In this way, mimicry may contribute to the formation and maintenance of species barriers (Mallet and Barton, 1989; Mallet and Joron, 1999; Jiggins et al., 2001; Naisbit et al., 2001; Jiggins, 2008; Chamberlain et al., 2009; Pfennig and Mullen, 2010).

In sum, as the above questions make clear, studies of mimicry address topics as diverse as how novel, complex traits arise; how animals make complex decisions; and how new species originate and diversify. The papers in this issue of *Current Zoology* touch on these questions.

3 Contributions to the Special Column

This special column consists of six papers, three of which are review papers and three of which are original research papers. In the first of the review papers, Pfennig and Kikuchi (2012a) discuss the evidence for a novel hypothesis on the evolution of imperfect mimicry. Specifically, they suggest that imperfect mimicry potentially represents an evolutionary compromise between predator-mediated selection favoring mimetic convergence on the one hand and competitively mediated selection favoring divergence on the other hand (whether

this competition arises over access to resources or ~~mates~~). They suggest that, because competition is ubiquitous in natural populations, competitively mediated selection may play an underappreciated role in fostering inexact mimicry.

Next, Nelson and Jackson (2012) discuss how spiders practice aggressive and Batesian mimicry. Aggressive mimicry (in which the mimic has ~~an active~~ negative impact on the fitness of the receiver) has received relatively little attention. Yet, as Nelson and Jackson (2012) describe, aggressive mimicry has been documented in a growing number of systems. Focusing on spiders, ~~they~~ authors describe how aggressive mimicry and Batesian mimicry—which have traditionally been viewed as distinct—are actually related phenomena.

Stoddard (2012) then examines defensive mimicry and ~~masquerade~~—which occurs when an organism mimics an inedible or uninteresting object, such as a leaf, stick, or pebble—from the avian visual perspective (birds are common predators, in many mimicry complexes). Using examples of defensive visual mimicry by both insects and birds, Stoddard (2012) shows how quantitative models of avian color, luminance, and pattern vision can be used to enhance ~~an~~ understanding of mimicry in many systems and generate new hypotheses concerning the evolution and diversity of signals.

In the first of the three research papers, Beatty and Franks (2012) investigate a key issue regarding receiver psychology: whether signal receivers may be less able to discriminate between signals that are presented sequentially compared to ones presented simultaneously (see above). Beatty and Franks (2012) set up a computer survey of artificially manipulated butterfly images to explore the relationship between discriminability and presentation style. Using human test subjects, they find a lessened ability to discriminate between sequentially presented images versus simultaneously presented ones, supporting their hypothesis. This study has implications for understanding how receiver psychology may affect the evolution of mimicry.

Next, Kikuchi and Pfennig (2012) examine the proximate mechanisms of mimicry in a well-studied Batesian mimicry complex—a coral snake and its mimic—in which the mimic has converged on the same coloration as its model. They specifically report an analysis of the pigments used to produce warning signals in this complex, as well as explore the cellular structures associated with coloration in the skin of models and mimics. Their results suggest that the mimic produces its coloration using the same physiological mechanisms as does its model, suggesting that precise color mimicry may have been relatively easy to evolve in this system.

Finally, Yeager et al. (2012) test for selection on color and pattern in a mimetic radiation. They demonstrate dramatic divergence between four distinct morphs of a mimic poison frog. Their results point to an important role for selection in driving divergence between these populations, which emphasizes the potential for mimicry to drive diversification and possibly even speciation.

Together, these papers offer a sense of the breadth of questions and approaches that make mimicry an exciting field, 150 years after Bates (1862) initial discovery.

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